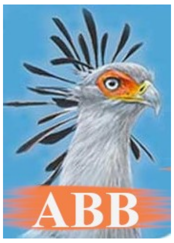

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The breeding biology of the Cape Parrot *Poicephalus robustus* in the Eastern Cape Province, South Africa

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Abstract

Cape Parrots *Poicephalus robustus* are endemic to South Africa where they typically occur in high-altitude Mistbelt forests. They are listed as Vulnerable internationally with habitat loss being the primary threat to the species. They nest in natural tree hollows in large forest hardwoods which were the target of historical, exploitative harvesting, and which continue to be harvested legally but on a smaller scale. The breeding biology of the species has been described for the central population, but not yet for the southern population. In the Eastern Cape Province, the stronghold of the population, few nest sites have been located. This study aims to characterise natural nesting sites in the Eastern Cape, describe breeding behaviour and investigate breeding success during 2017–2021. A total of 43 nesting sites were located. During the study period we recorded 26 breeding attempts of which and at least 58% of attempts fledged one or more chicks. No pairs attempted breeding in 2019. As found in other parts of the range, Cape Parrots in the study area nest in existing hollows predominantly in large, mature, yellowwood *Afrocarpus falcatus* trees but sometimes also in exotic species. They showed no consistent nest orientation and nested as close as 69 m away from their nearest neighbour. Most nest cavities were inaccessible to field researchers and could only be monitored from the ground, but some nests were successfully examined using a drone. Information gathered in this study will guide the design and installation of more nest boxes in future, to assist in the conservation of this threatened species.

Keywords: breeding, Cape Parrot, conservation, nests, South Africa
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Introduction

Cape Parrots (*Poicephalus robustus*) are secondary cavity nesters, dependent on the development of natural cavities in trees, or cavities produced by other species such as woodpeckers (Picidae) which are categorised as primary cavity nesters. Primary cavity nesters tend to be less limited by nesting sites because of their ability to construct their own nest hollows, provided there is suitable substrate in which to do so (Newton 1994). Secondary cavity nesters however can be constrained by a lack of suitable nesting sites (Newton 1994). This can either be due to a lack of suitable nests, or through inter- and intra-specific competition for tree hollows (Wiebe 2011). A lack of nesting sites can be addressed by supplementation with artificial nests, or through the protection of existing nesting sites (Williams et al. 2013). Indeed, ensuring the availability of cavities is considered a global conservation priority as tree cavities provide nesting sites for many species of birds (van der Hoek et al. 2017).

At least 70% of parrot species are secondary cavity nesters and almost a third are threatened with extinction (Forshaw 2010; IUCN 2021). Many parrot species are dependent on forests, and habitat loss is considered the main threat for the group (Vergara-Tabares et al. 2016). The Cape Parrot, a South African endemic, is listed internationally as "Vulnerable" (Birdlife International 2017) and "Endangered" nationally with fewer than 1600 mature individuals in the wild (Downs 2015). Found in indigenous Afromontane forests that are naturally fragmented in the landscape (Downs 2015, Coetzer et al. 2020), Cape Parrots occupy existing tree hollows in mature forest hardwood species, particularly yellowwoods (Wirminghaus et al. 2001, Symes et al. 2004), which are also targeted by logging (Leaver et al. in review). Historical exploitative logging resulted in the loss of large numbers of mature forest hardwoods in the indigenous forests of South Africa (Lawes et al. 2004, Wirminghaus et al. 1999). For these reasons, nesting sites are considered to be in short supply for Cape Parrots and other secondary cavity nesters that occupy the Afromontane Forest habitat (Wirminghaus 2001, Downs 2015).

The Cape Parrot distribution stretches across the Eastern Cape, KwaZulu-Natal (KZN) and Limpopo provinces in South Africa (Downs 2015, Coetzer et al. 2020). The Eastern Cape Province is the stronghold of the population, with an estimated 800 individuals occurring there (Downs et al. 2014). Cape Parrot breeding behaviour in the wild has only been described from six pairs in KZN (Wirminghaus et al. 2001, Symes et al. 2004). Furthermore, only 17 natural nest sites have been formally identified in the last two decades (Wirminghaus et al. 2001, Symes et al. 2004), mostly in KZN, with only four from the Eastern Cape province (Wirminghaus et al. 2001). The aim of this study was to collect information on the breeding biology of Cape Parrots in the Eastern Cape Province to fill a key knowledge gap for the conservation of the species. We located natural nesting sites, described nest characteristics and estimated breeding success in the wild. This was done to inform conservation actions such as the supplementation of natural nesting sites with artificial nests. To determine whether certain behaviours are signatures of specific nest stages, observational data were collected on adult behaviour at the nest during prospecting, incubation and nestling periods.

Methods

Nests were classified as either natural tree hollows that were occupied at least once during the study period (hereafter "natural nest") or as natural tree hollows where pairs were observed entering the cavity but no breeding attempts were made (hereafter "potential nest").

Study area

This study took place during August 2016–February 2021 in three forest patches centred around the town of Hogsback (32°35′ S, 26°56′ E) in the Eastern Cape province of South Africa. These high-altitude Southern Mistbelt forest patches occur between 700–1300 m.a.s.l and are naturally fragmented in the landscape (Mucina and Geldenhuys 2006). The tall canopies are typically dominated by *Afrocarpus falcatus*, *Podocarpus latifolius*, *Celtis africana*, *Calodendrum capense* and *Zanthozylum davyi* trees (Mucina and Geldenhuys 2006). The forests occur on steep, east-facing slopes and fire-resistant valleys that receive an average of 1000 mm of rainfall annually, typically in summer (December–February). Mean monthly temperatures range from 30°C in summer, down to 5°C in winter with occasional snowfall.

Nest searches

In 2016, one potential nest site was located opportunistically while doing other field work in the forest. From 2017 onwards, nest searches were routinely conducted, starting in late winter when Cape Parrots began prospecting or displaying at potential nest sites. Nest searching began with an observer stationed at a site in the forest before daybreak (before parrots left their roosting areas to locate prospecting pairs by following their display calls, until display calling ceased (typically around 10h00 each day). Nest searches would commence again the following day until each forest patch was fully covered. Nest searches concluded in late summer at the end of the fledging period. Each forest patch was re-visited at least twice per week to locate as many displaying pairs as possible during the breeding season. In addition, one natural nest and one potential nest were found in residential gardens by the landowners, who reported frequent Cape Parrot activity.

Nest characteristics

The following characteristics of nests were recorded: tree species, diameter at breast height, tree height and height of the cavity entrance above ground (both calculated using a Bushnell Bowhunter rangefinder), as well as location, altitude and orientation of the entrance all calculated using a Garmin GPS 60CSX. Nest orientations were grouped into five categories: north-facing, 316°–45°; east-facing, 46°–135°; south-facing, 136°–225°; west-facing 226°–315°; top-facing (a chimney-like hollow open to the sky). Tree successional stage on a scale of increasing levels of decay from 1 to 8 was recorded according to Downs and Symes (2004), where stage 1 described living trees with some signs of branches dying and stage 8 described dead trees where only a portion of stump remains. Trees were visited annually to track changes in tree successional stages over time. Nearest neighbour distances between nests were calculated by using the nearest neighbour tool in QGIS (v. 3.20). Cavity measurements (depth, entrance size and floor area) were taken at two accessible nests. All metric measurements of characteristics are provided as means with standard deviations, and with range in parenthesis. The characteristics of occupied and potential nests were compared using Kruskal-Wallis rank sum tests (altitude, DBH, tree height and nest height above ground) and Pearson's Chi-squared tests (orientation, tree species, tree stage) in R (v. 4.1.2, R Core Team, 2014). Characteristics of only natural nests are described in this study to allow for meaningful comparisons with natural nests in other areas. Characteristics of natural and potential nests combined are described elsewhere (Leaver et al, in press).

Nest inspections

Three methods were used to inspect nests to determine whether they were occupied. A wireless camera connected to a hand-held monitor, and mounted on a 12 m telescopic pole (4Kam PK Pro NightVision pole inspection camera) was used to inspect nests with entrances <12 m off the ground. An unmanned aerial vehicle (DJI Mavic Pro 2, hereafter 'drone') was used to inspect nests that were open from above. The drone was launched from the forest floor near the nest tree if there was a suitable gap in the forest canopy. Alternatively, the drone was launched from the nearest road, which required the pilot to remain at the roadside and communicate via hand-held radios (Kenwood TK-3000) to a spotter standing beneath the nest tree who assisted with navigating the drone safely above the nest. The drone was flown more than 5 m above the nest opening to minimise disturbance, and the camera's zoom function was then used to photograph and film the nest floor where possible. Nests in trees considered safe enough to climb were accessed directly using climbing ropes and ascenders and the nest contents inspected using a GoPro (Hero 5 Session) mounted on a monopod (WOH Lang-arm) while using a small hand-held flashlight to illuminate the cavity floor.

Nests were directly inspected throughout the season to confirm the presence of eggs and/or nestlings. Direct inspections occurred during fair weather and during 11h00-14h00 (when activity around the nest was quietest). The first inspection was within the first two weeks of noticing regular pair activity to see if eggs were present. If eggs were found, the nest was inspected again after four weeks to see if nestlings were present. If nestlings were found, the nest was inspected ~10 days thereafter until the nest was empty. If a nest was found empty during the first inspection, the nest was inspected again a month later if there was still pair activity.

Nest monitoring

Nests were observed over four breeding seasons during October 2017–February 2021, with 25–50x85 spotting scope (Swarovski) and either 10x42 binoculars (Vortex) or

8x32 binoculars (Swarovski) from the forest floor. Observers wore dark camouflaged clothing, sat against a tree trunk 10 –50 m from the base of the cavity tree and remained as still and quiet as possible throughout the duration of the observation. Nests were prioritised based on the visibility of the nest entrance from the ground. Where possible, observations began soon after the day the pair was first seen prospecting, and terminated when there was no longer any activity at the nest. Initially, full-day observations at one nest from dawn to dusk revealed two peaks in activity around the cavity: the first peak typically lasting from dawn (half an hour before sunrise) to 10h00, and the second peak from 16h00 to dusk. Observations at nests were therefore prioritised to include the morning peak only, starting at dawn and lasting for approximately four hours. Some nests were found late in the season but were still monitored.

Nests were visited about once per month during the breeding season to check for signs of breeding activity. A nest was confirmed as active once the presence of eggs or nestlings was confirmed either by direct inspection of contents, hearing the begging calls of nestlings during ground observations, or by seeing nestlings at the nest entrance during ground observations. If chicks were heard begging, then those nests were visited every 7–10 days thereafter to try to estimate fledging dates as accurately as possible. Fledging dates were estimated where possible by adding seven days from when a chick was first observed at the nest entrance as per Wirminghaus et al. (2001). Estimated egg-laying and hatching dates were inferred by backdating from the estimated fledging date. The duration of incubation and nestling periods were taken as 30 days and 63 days, respectively (Wirminghaus et al. 2001). These dates were used to retroactively infer the nesting stages during monitoring for occupied nests visited each season when describing and comparing behaviours at the nest by pairs during the three nest stages as described below.

To determine whether certain behaviours are signatures of specific nest stages i.e. prospecting, incubation and nestling stage, various behaviours were recorded at nests during each observation session. These behaviours included: (a) the rate of individual and pair displays (no. of *archangel* calls and/or displays per hour), (b) nest visitation rate (number of times per hour that an individual entered the nest), (c) time at the nest entrance (minutes that an individual perched at the entrance to the nest), (d) time perched in the nest tree as well as (e) time spent inside the nest (time in minutes spent at either location). If the female entered the nest but did not emerge again before the observation period ended, the event end-time was recorded as the observation end-time. Adult females at the nest were distinguished from adult males by the orange/red crown present in females, a feature not present in adult males. Adult birds were distinguishable from juvenile or immature birds by the orange-red shoulder patch and leg feathers which are absent in young birds.

The display used for point ‘a’ above, called the *archangel* display, involves the backward extension of the shoulders and wings and is used in sexual and aggressive contexts (Wirminghaus et al. 2000). The call typically given with the display is a 3–4 syllable call produced either individually (Cape Parrot Project unpub. data.) or as part of a duet (Wirminghaus et al. 2000). The proximity of the nest was defined, as per Koenig et al. (2008), to be an area approximately 50 m in radius, based on (a) the distance from the nest tree that pairs perched to engage in territorial vocalisations with other parrots, and (b) the location where pairs made their initial perch following their arrival from foraging, or exit from the nest. The duration of all behaviours was rounded to the nearest minute. Wilcoxon rank sum tests were conducted in R to investigate differences in behaviours around the cavity by females and males at the different nesting stages.

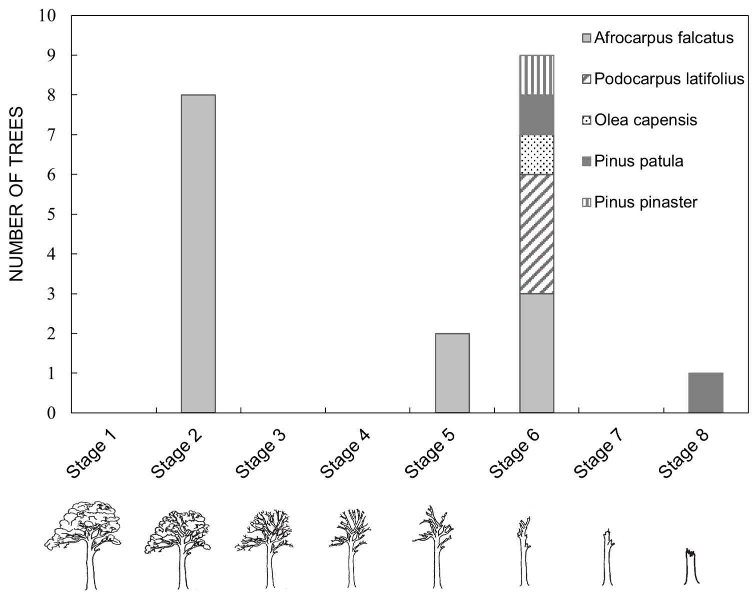

Figure 1. Successional stage classification of 20 trees containing Cape Parrot *Poicephalus robustus* natural nests. Tree successional stages from Downs and Symes (2004).

Results

A total of 20 natural and 23 potential nest sites were located over five breeding seasons during 2016–2020.

Characteristics of natural nests

Cape Parrots occupied nests predominantly in Outeniqua Yellowwood *Afrocarpus falcatus* trees (65% of all nests, Figure 1). Parrots nested both in relatively intact trees (stage 2) as well as those in a more advanced stage of decay (> stage 5, Figure 1). Tree successional stages remained static throughout the study for most natural nest trees, with two exceptions: (a) one nest tree changed from a stage 2 to a stage 3 after two years of monitoring when a large side branch containing a natural nest collapsed due to strong winds; and (b) a stage 8 tree containing a natural nest collapsed also due to strong winds. *Podocarpus latifolius*, *Olea capensis* and two exotic *Pinus* species were also used for nesting (Figure 1). Nest trees had a mean DBH of 130±32 cm (73–180 cm) and were on average 24±6 m high (12–33 m). Nests were located at an average of 1125±113 m.a.s.l (891–1305 m.a.s.l). Cape Parrots occupied nests mostly in natural forest (95%), including one nest in an exotic *Pinus pinaster* inside the forest; while one nest, in a *Pinus patula*, occurred in a residential garden 100 m from the nearest forest edge.

Cape Parrots occupied existing tree hollows typically formed by rotting of the tree core where a side branch or main stem collapsed, with only a single nest apparently formed by enlarging a cavity made by a primary excavator. Cape Parrots appeared to show no preference for orientation ($\chi^2 = 7$, df = 4, $p>0.05$), namely north-facing (n = 1), east-facing (n = 3), south-facing (n = 3), west-facing (n = 5) and top-facing nests (n = 8). Nests were located at the canopy level, with entrances 18±5 m above ground (10–28 m). Two nests were accessible to climbing and could thus have the interior measured. The entrances of these two nests were 310x220 mm and 120x160 mm (lxb), respectively. Both nests were 700 mm deep and had elliptical floors that were 200x150 mm and 350x250 mm, respectively. The average distance between displaying pairs with nests was 293±403 m (69–1909 m), and nests were often loosely clustered within the forest landscape. Pairs were observed making modifications to the nest entrance, sometimes enlarging the hole before the breeding season began. No significant differences were found in the tree characteristics of natural nests and potential nests (data available on request).

Nest inspections

Of the 43 natural and potential nesting sites, 23 could be monitored from the ground only, nine by rope-climbing, eight using a drone and three using a pole camera. In general, Cape Parrots were tolerant of human observers if the observer was already present before the parrots arrived. However, an approach to an active nest tree after sunrise resulted in flushing of any parrot that was perched near or at the nest entrance. If disturbed, the parrot would fly off giving a loud series of alarm calls, sometimes circling around the nest tree before flying away, only to return after a few minutes. The female was never observed to flush from inside the cavity if a human approached the tree, and only did so if the nest was directly inspected. Females occasionally sat tight in the nest and emitted a loud, low frequency growl if inside the cavity during direct inspection.

Nest monitoring

Over the four-year study, 119 nest observations totalling 629 hours were made at 39 out of 43 nests. Observations at four potential nests were not possible because the tree or branch containing the cavity collapsed (n = 3), or the tree was felled for forestry management purposes (n = 1), soon after the nest was discovered. An increase in the number of pairs lingering in the forest at dawn rather than flying off to other patches to feed, signalled that pairs had begun prospecting cavities. The breeding season typically began in winter and an average of 64% of known natural nests were occupied each season (Table 1). No breeding was observed in 2019 despite monitoring territorial pairs and previously known nesting sites. Three of 39 monitored nests (8%), each occupied by a different pair, were occupied more than once during the study period, and in all cases there was a hiatus of at least one breeding season between nesting attempts by the same pair.

Breeding success

Breeding success was estimated to be 58%, where at least 15 of 26 breeding attempts fledged at least one nestling (Table 1). At least three breeding attempts failed (11%). In one instance, the tree canopy with an active nest collapsed during strong winds. For two nests confirmed to have eggs, the breeding attempt likely failed due to suspected nest predators: Samango Monkey *Cercopithecus albogularis* and African Harrier-Hawk *Polyboroides typus*, which were observed at the nests; subsequent nest checks revealed no

Table 1. Breeding activity of Cape Parrots (*Poicephalus robustus*) in the Amathole region, Eastern Cape during the 2016–2020 breeding seasons.

Breeding season	2016	2017	2018	2019	2020
Duration	Aug 2016– Nov 2016	Oct 2017– Feb 2018	Jul 2018– Feb 2019	Did not breed	Jun 2020– Feb 2021
No. breeding attempts (% known)	1 (100)	3 (75)	10 (83)	0	12 (60)
No. nests that fledged at least one chick	1	0	8	0	6
No. displaying pairs	7	13	40	51 59	

further activity by the pairs. Pairs did not attempt nesting more than once per season if the first attempt failed. The outcome of eight nesting attempts (31%) could not be confirmed, but during the last monitoring all of these nests had reached the nestling stage and begging calls of nestlings could be heard.

Breeding behaviour - prospecting

During the prospecting stage, males performed an archangel call and/or display up to five times per hour typically from the nest tree. Males displayed alone and with the female, but females rarely displayed alone. Duets and male displays were noted throughout the breeding cycle, and there was no significant difference in the rates of the duets and male archangel displays during the prospecting period and the other nest stages (Table 2). Females and males visited the nest up to four times an hour, typically up to 15 mins each time, to perform nest maintenance activities such as chewing the nest entrance, excavating the nest cavity and preparing the nest floor with wood-chip lining created by excavating the nest interior. While one individual was inside the nest, the other remained outside in the nest tree, typically on a branch near the nest entrance from which they would swap roles. Each individual spent 2–3 mins on average sitting at the nest entrance peering out during nest preparation activities. After a bout of excavation, the individual would emerge from the cavity covered in sawdust, which was shed outside the cavity when feathers were ruffled. Neighbouring pairs occasionally participated in counter-calling and interactions between pairs were not seen to escalate beyond this. Prospecting pairs were visited occasionally by single individuals. Immature birds watched prospecting adult pairs excavating and chewing at cavity entrances, and mimicked this behaviour in nearby shallow cavities and tree knots in the same tree. Copulation is described in detail by Carstens (2016).

Breeding behaviour - incubation

During the incubation phase, the male was relatively quiet around the nest compared to the prospecting phase, and displayed once every two hours on average (up to three times per hour) where duets occurred no more than once per hour (Table 2). The timing of breeding could be estimated from 17 of 26 breeding attempts by either (a) nestlings being seen at the nest entrance (n = 15) who were assumed to have fledged seven days later, (b) nest inspection coinciding with egg-laying (n = 1), or (c) by estimating the age of the chicks based on photographs in a nest. The timing of clutch initiation was asynchronous in 2018 with eight months separating the initiation of the first and last clutch of the season (Figure 2). In 2020, by contrast, seven pairs initiated breeding in the space of three weeks from the end of August until mid-September 2020 (Figure 2).

Females alone incubated and spent considerable time in the nest. After overnighting in the nest, a female typically joined the male for a brief excursion during the early morning and returned to the nest shortly thereafter where she remained during the observation period. Since observations ended before she emerged, time in cavity was likely an underestimate, but lasted 45 mins on average and was significantly longer than the male (Table 2). Females spent minimal time perched at the entrance or in the canopy of the nest tree compared to the male who lingered significantly longer in both instances (Table 2). The male only ever entered the nest if the female was already inside, and would presumably provision her with food while inside the nest since no allofeeding was observed outside of the cavity during this nesting stage.

Breeding behaviour - nestling

During the nestling phase, the male displayed once every two hours on average (up to three times per hour) and duets occurred no more than once per hour. Pair visits were synchronised and both individuals provisioned food to the nestlings, taking turns to enter the nest, typically for 10 mins each time and up to twice per hour. After each feed, they

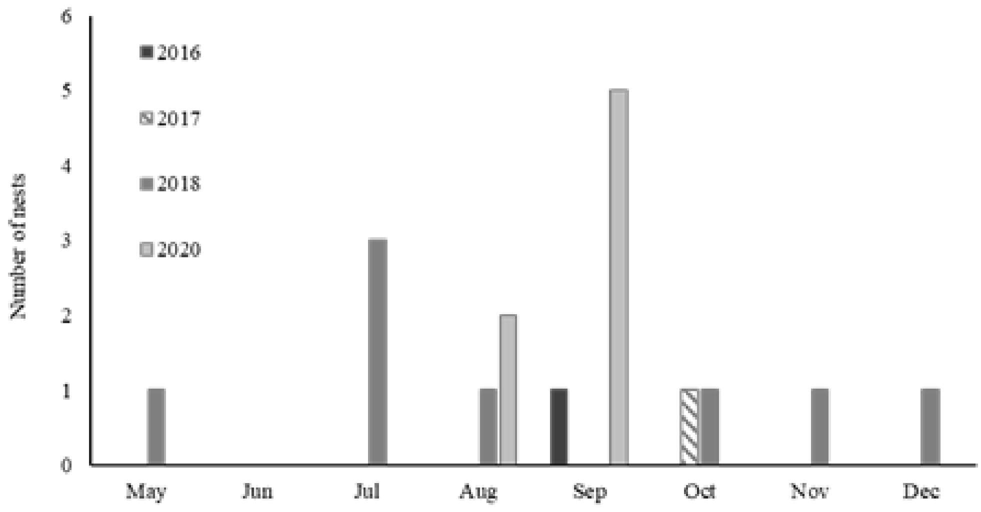

Figure 2. Clutch initiation of 17 Cape Parrot nests in the Eastern Cape province. No breeding attempts took place in 2019.

spent 2–3 mins at the entrance looking out or cleaning their bills before flying off either to perch in the nest tree or to resume foraging. As the nestlings developed, vocal solicitation of food from deep in the cavity was audible from the forest floor below. A week before fledging, nestlings would appear at the nest entrance, looking out from within and occasionally standing at the entrance. Recently fledged offspring were not observed to return to the nest tree with the parents when they were provisioning the remaining chicks in the nest.

Discussion

Despite the Cape Parrot being South Africa's only endemic parrot, ecological information about the species is lacking for large parts of the distribution range and has been based predominantly on studies conducted in the province of KZN. This study is the first to collect breeding information on the species in an area that is the stronghold of the population, doubling the number of previously known wild Cape Parrot nests.

Nest characteristics

Most psittacines show a preference for nesting in particular tree species (de la Parra-Martínez et al. 2015, De Labra-Hernández and Renton 2016, Renton and Brightsmith 2009, Symes and Perrin 2004, Boyes and Perrin 2010). Cape Parrots nested predominantly in the two yellowwoods, as found in KZN (Wirminghaus et al 2001). However, the low density of yellowwoods in the study area due to historical exploitative logging (Leaver et al. in review, Wilson et al. 2017), might explain why Cape Parrots also occupied nests in large, mature exotic *Pinus* trees. One Cape Parrot nest out of 13 identified in KZN was classified as 'away from the forest', with the rest all occurring in indigenous forest (Wirminghaus et al. 2001). Further research on nest sites should be conducted to determine factors influencing nest site selection. Cape Parrots in KZN nested predominantly in cavities 6–12 m high (Wirminghaus et al. 2001), lower than found in this study (10–28 m). This difference may be due to the slightly smaller size of nest trees available in the KZN site (9–25 m, Wirminghaus et al. 2001) compared to 12–33 m in this study.

Nest inspections

Cape Parrot nest sites were difficult to access by field researchers and most (~75%) could only be observed from the forest floor. This study was the first to explore the use of a drone and a pole-camera for nest inspections in this species. The pole camera was used successfully to inspect several potential nests but the short length of the pole was restrictive in accessing active nests. Accessing nests using a drone was preferred as inspection took <10 mins from launch to landing, compared to rope-climbing which typically took 30 mins or longer. A drone was flown over a nest that was occupied at the time, and appeared to not disturb the birds, as this particular nest succeeded in fledging young. Drones have been used in many other studies of birds to monitor and inspect nests (see review by Nowak et al. 2018). The factors limiting the use of drones in this study were: (a) nests had to be open from above to allow for inspection of the cavity, (b) deep cavities had dark nest floors which were often difficult to view during image processing after inspection, and (c) the entrances to some nests may have been smaller than the nest floor, or with small side chambers, so that the nest contents were hidden, giving a false impression of inactivity. Despite these limitations, both the drone and pole-camera increase the number of nests that can be monitored for breeding success, helping to improve estimates of the timing and success of breeding attempts.

Breeding frequency and success

Generally, food availability is a critical factor affecting both the onset of breeding in birds and the success of nesting attempts (Perrins 1991, Siikamäki 1998, Morrison and Bolger 2002), but not all species are affected by food shortages (Perrins 1970). No Cape Parrot breeding attempts occurred in 2019, possibly due to the lack of food

Table 2. Behaviours observed during Cape Parrot (*Poicephalus robustus*) nest observations. Behaviours identified as significantly different between the sexes are presented in bold text.

Activity		*Prospecting*	*Incubation*	*Nestling*
Archangel	F	0.5[1]	0.2, 0.3[1]	0.1, 0.2[1]
display rate	M	1.3 ± 1.5 (0–5.3)[2, 3]	0.5 ± 0.5 (0–1.4)[2]	0.6 ± 1.0 (0–3.2)[3]
(# displays / hour)	Duet	0.8 ± 1.3 (0–5.3)[4, 5]	0.2 ± 0.5 (0–1.2)[4]	0.2 ± 0.3 (0–1.0)[5]
Cavity visitation rate	F	0.6 ± 0.7 (0–3.7)	0.4 ± 0.4 (0–1.1)	0.7 ± 0.5 (0–1.9)
(# visits / hour)	M	0.7 ± 0.5 (0–2.9)	0.5 ± 0.3 (0–1.1)	0.7 ± 0.5 (0–2.2)
Time at cavity	F	2 ± 5 (0–46)	**1 ± 1 (0–4)[6]**	2 ± 2 (0–10)
entrance (mins)	M	3 ± 5 (0–24)	**4 ± 5 (0–22)[6]**	3 ± 4 (0–39)
Time in cavity	F	8 ± 10 (0–45)	**1 ± 1 (<1–5)[7]**	4 ± 6 (0–40)
tree (mins)	M	9 ± 11 (<1–92)	**11± 23 (<1–97)[7]**	3 ± 4 (0–26)
Time in	F	14 ± 24 (<1–138)[8]	**45 ± 33 (<1–95)[9]**	8 ± 21 (<1–204)[10]
cavity (mins)	M	8 ± 9 (<1–45)[8]	**8 ± 6 (<1–25)[9]**	4 ±6 (<1–55)[10]

[1]Females rarely displayed alone; [2]W = 125, ns; [3]W = 222, ns; [4]W = 120, ns; [5]W = 27, ns; **[6]W = 161, p < 0.01**; **[7]W = 135, p < 0.01**; [8]W = 8039, ns; **[9]W = 378, p < 0.01**; [10]W = 8817, ns

during a prolonged drought (Cape Parrot Project unpubl. data). In KZN, the Cape Parrot breeding season occurred when their main food sources, *Afrocarpus* and *Podocarpus* trees were fruiting (Wirminghaus et al, 2001). Similarly, fruit availability was an important factor determining the onset of breeding in the closely-related Grey-headed Parrot *Poicephalus fuscicollis* (Symes and Perrin 2004). Cape Parrots in this study had a breeding success rate of 58% which was similar to Meyer's Parrot *Poicephalus meyeri* in southern Africa (54%, Boyes 2008). and comparatively higher than many parrot species in other parts of the world (see review in Murphy et al. 2003). No breeding success data was available for the Grey-headed Parrot (Symes and Perrin 2004, Symes 2005). Ongoing monitoring of Cape Parrot nests should continue to investigate the influence of direct and indirect factors such as climate and food availability on breeding attempts and breeding success,

Breeding behaviour

The breeding behaviour of Cape Parrot pairs in the Eastern Cape was similar to that described in KZN by Wirminghaus et al. (2001) in most aspects. The male and female both participated in nest preparation activities and provisioned food to their young. Nest visits were highly synchronised by the pair, which in birds helps to decrease the activity around the nest, and increase brood survival through decreased predator detection rates (Leniowski and Węgrzyn 2018, Raihani et al. 2010). Females only incubated, with males visiting during the incubation stage only while the female was inside. In this study we found both the female and male visited and fed the brood with equal frequency, whereas Wirminghaus et al. (2001) noted that females fed more frequently than males, but with no supportive data presented.

We provided the first description of the rates of a specific type of call and display combination typically produced by the pair while in or near the nest tree. Although pairs were mostly quiet around the nest, our study found both individual displays and duetting at all nest stages, with no significant differences in the rates of displays given between the nest stages. Furthermore, the number of displaying birds in the study area exceeded the number of breeding pairs each season. This may indicate that not all displaying pairs have access to a suitable nest site, but could be excavating potential nest sites which may become more suitable in future seasons. Since most nest sites could not be directly accessed to measure the nest interior, it was not possible to compare the interior characteristics of potential nests to used nest sites. Alternatively, perhaps not all displaying pairs breed each season, which is likely given that Cape Parrots were found in this study to skip a year between breeding attempts.

We observed behaviours of the adult pairs that could be used as indicators of the general stages in a breeding cycle. The prospecting stage was characterised by pairs searching trees and snags for hollows and chewing around the nest entrance, expelling wood chips from the cavity, and entering the nest usually only for brief bouts, with males and females both taking turns. During incubation and early brooding, females returned quickly to the nest, sat for long periods of time, and spent little time in the nest tree or at the cavity entrance. The males were mostly seen alone out of the nest. During the nestling stage, males and females frequently visited the nest and would often wipe their bills after emerging from the nest, and, later in the season, chicks could be heard soliciting food from the floor below. These behavioural observations allow for an assessment of breeding success without climbing nest trees.

Implications for conservation

The exploitative harvesting of indigenous forest hardwoods that occurred before the 1940's in South Africa is considered the leading cause of the shortage of nest sites for Cape Parrots (Wirminghaus et al. 1999, 2001, Downs 2005, Coetzer et al. 2020). The characteristics and placement of artificial nest boxes can influence breeding success if designed and installed correctly (Carstens et al. 2019, Williams et al. 2013). If suitable nest boxes are provided, these can boost the breeding success and ultimately population size of this threatened species in the wild. In 2001, 200 nest boxes were installed in the study area, but to date they remain unoccupied. Possibly these nest boxes are too shallow, making the nest easily accessible to potential nest predators (Wimberger et al. 2017). Furthermore, most boxes were occupied by African Honey Bees *Apis mellifera* despite the installation of bee boxes near nest boxes. Nest boxes installed in other parts of the range of the species have been similarly unsuccessful and are quickly occupied by bees (Wagh 2016, Downs 2005).

Nest characteristics and breeding behaviour information gathered in this study provide a practical foundation for the optimisation of the design and installation of more nest boxes in future. Large areas in the forest between loose nesting colonies that are currently devoid of nest sites may provide suitable space to create new loose clusters, and nest boxes should be installed no closer than 60 m apart. Cape Parrots did not appear to show preference for nest orientation which indicates that any future installation of nest boxes should instead focus on tree species and height. Nest boxes should be installed in large mature trees in the forest so that nest entrances are >10 m above the ground but ideally around 18 m above ground. Nests should be designed with natural wood to allow parrots to create their own nest lining made by chewing wood chips off the interior walls of the nest cavity. Deep nest floors, >70 cm from the entrance to the nest floor, will ensure the incubating female and her brood are out of reach of Samango Monkeys and African Harrier-Hawks. Other practical solutions to avoid occupancy by bees should also be tested (Efstathion et al. 2015). However, in this study area, bees may continue to compete with Cape Parrots until competition for cavities is reduced.

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Data availability
All data are available upon reasonable request.

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