



Breeding biology of the African Pygmy Falcon: long-term variation and seasonal decline in breeding performance of an arid zone raptor

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Abstract

Birds of prey are apex predators and understanding their life history can serve as a valuable baseline for investigating their ecological role. Pygmy Falcons (*Polihierax semitorquatus*), Africa's smallest diurnal raptor, have evolved to be obligate associates of Sociable Weaver (*Philetairus socius*) colonies throughout their southern African range. As a predator, Pygmy Falcons likely impact prey communities in this system including their host and other colony associates. However, no study has explored their breeding biology in detail using long-term data. We provide results from 10 years of data collected between 2011 and 2020. We followed 66 unique Pygmy Falcon territories and 323 breeding attempts in the Kalahari, South Africa. We explored annual variation in the population density of Pygmy Falcons and investigated between- and within-season variation in reproductive investment and output. The highest average density was recorded in 2015 and the lowest in 2019 and 2020. Our results show that the breeding occurs between early austral spring (August) and late summer (February), with a peak from September to December. The maximum and most frequent clutch size was three eggs and falcons usually initiated only one breeding attempt (but up to three) in a season. The incubation and nestling periods lasted on average 33 (\pm SD 4) and 37 (\pm 5) days, respectively. A three-egg clutch size and number of fledglings produced varied between seasons, and breeding success showed a seasonal decline across the breeding season. Falcons were 7 times less likely to lay a 3-egg clutch in 2019 than in 2011 and 2012, and breeding attempts initiated in September were 3.4 times more likely to be successful than those initiated in November. Predation accounted for 49.5% of breeding failures. Our results show significant variation in the breeding parameters of these falcons, but further studies are needed to understand what drives these variations.

Keywords Raptor breeding · Arid zone birds · Nesting association · Long-term study · African raptors

Zusammenfassung

Brutbiologie afrikanischer Halsband-Zwergfalken: langfristige Variation und saisonales Absinken des Bruterfolges bei einer Falkenart der Trockengebiete

Falken und Greifvögel gehören zu den Spitzenprädatoren, daher kann die Kenntnis ihrer Biologie als nützlicher Ausgangspunkt für die Erforschung ihrer Rolle im Ökosystem dienen. Der Halsband-Zwergfalke *Polihierax semitorquatus*, Afrikas kleinster tagaktiver Beutegreifer, hat sich im Laufe seiner Evolution in seinem gesamten südafrikanischen Verbreitungsgebiet zum obligaten Begleiter von Siedelweber (*Philetairus socius*)-Kolonien entwickelt. Halsband-Zwergfalken beeinflussen

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als Prädatoren höchstwahrscheinlich die Beutetiergemeinschaften in diesem System, einschließlich ihrer Wirtsart sowie anderer Koloniewohner. Bisher gibt es allerdings noch keine detaillierte Untersuchung ihrer Brutbiologie auf der Basis von Langzeitdaten. Wir präsentieren hier die Ergebnisse einer zehnjährigen Datenerfassung zwischen 2011 und 2020. Wir dokumentierten 66 individuelle Halsband-Zwergfalken-Reviere und 323 Brutversuche in der Kalahari, Südafrika. Wir untersuchten die jährliche Variation in der Populationsdichte der Zwergfalken und erforschten Unterschiede in der elterlichen Investition und dem Fortpflanzungsergebnis zwischen und innerhalb von Brutsaisons. Die höchste Durchschnittsdichte wurde 2015 festgestellt, die niedrigste 2019 und 2020. Unsere Ergebnisse zeigen, dass Bruten zwischen dem zeitigen Südhalkugel-Frühjahr (August) und dem Spätsommer (Februar) stattfinden, mit einem Verteilungsgipfel zwischen September und Dezember. Die höchste und häufigste Anzahl von Eiern je Gelege war drei; die Falken starteten in der Regel pro Saison nur einen (aber bis zu drei) Brutversuche. Brutdauer und Nestlingsphase dauerten jeweils 33 ± 4 beziehungsweise 37 ± 5 Tage. Die Anzahl von Dreiergelegen und die Anzahl flügger Jungvögel variierte zwischen den Brutsaisons, der Bruterfolg nahm jeweils im Verlauf der Brutsaison ab. Im Jahr 2019 legten die Falken mit siebenmal geringerer Wahrscheinlichkeit ein Gelege mit drei Eiern als in den Jahren 2011 und 2012; im September begonnene Brutversuche waren mit 3,4-mal höherer Wahrscheinlichkeit erfolgreich als solche aus dem November. 49,5% der Brutaufälle wurden durch Prädation verursacht. Unsere Ergebnisse belegen eine deutliche Variation der brutbiologischen Parameter dieser Falkenart; allerdings sind weitere Untersuchungen notwendig, um zu verstehen, was diese Variation antreibt.

Introduction

Predators spatially structure communities and impact the behaviour, and demography of their prey (Caro 2005; Johnson and Belk 2020). Predators have direct effects mediated by lethal predation, and indirect effects causing predation risk in prey species (Preisser et al. 2005; Thomson et al. 2006; Quinn and Ueta 2008; Lima 2009). These effects may drive risk-induced prey traits (Lima and Dill 1990), numeric responses in prey population (Zanette and Clinchy 2020), predator–prey dynamics (Cresswell 2008; Anson et al. 2013), changes in space use (Morosinotto et al. 2010) and trophic cascades affecting community structure and entire ecosystems (Greeney et al. 2015; Mueller et al. 2016). In birds, raptors are often the top predators (Sergio et al. 2008; Donazar et al. 2016); therefore, knowledge of their life history traits such as timing of breeding, breeding densities, clutch and brood size, the size and sex ratio of offspring and reproductive age are valuable indices of raptor population growth and dynamics that can provide useful insight into their impacts more broadly (Sæther et al. 1996; Marti 1997).

Life history and other demographic traits of a species can be determined by the local environmental conditions (Sauve et al. 2021; Nægeli et al. 2022). Short-term unpredictable weather conditions and scarce resources characterise desert environments (Morton et al. 2011; Botai et al. 2018) and desert species are adapted to survive their environment (Tieleman et al. 2003; Williams and Tieleman 2005; McKechie et al. 2012; Wu et al. 2014; Cunningham et al. 2015). Desert birds show dramatic variations in annual reproductive output (Yosef and Zduniak 2008; Mares et al. 2017; Bourne et al. 2020; van de Ven et al. 2020), and some avian traits and mating systems are thought to be selected by these arid environments (du Plessis et al. 1995; Ward et al. 2002; Cockburn 2006; Rubenstein and Lovette 2007; Hatchwell

2009; Cockburn and Russell 2011; Jetz and Rubenstein 2011; van de Ven et al. 2016). High unpredictability and variation emphasise the need for long-term studies of these demographic and life history traits to get a holistic understanding of the variation that occurs between different years and seasons (Hughes et al. 2017).

The Pygmy Falcon (*Polihierax semitorquatus*) is a raptor species that inhabits dry savannas and deserts in Africa. The species includes a southern Africa (*P. s. semitorquatus*) and eastern Africa subspecies (*P. s. castanotus*), with very little natural history information known for both, although aspects of *P. s. semitorquatus* have received recent attention (Lowney et al. 2017; Krochuk et al. 2018; Bolopo et al. 2019; Lund et al. 2020; Oschadleus 2022). Pygmy Falcon breeding biology was described by Maclean (1970), but this study relied on a small sample size collected over only 2 years. This subspecies with average mass of 53 g and wing length of 93 mm (unpublished data) has evolved to be an obligate breeding associate of Sociable Weaver (*Philetairus socius*) colonies (Oschadleus 2022), but also utilises these structures year-round for roosting (Maclean 1970; Mendelsohn and Anderson 1997). Sociable weavers which weigh between 26 and 32 g build their large communal nests on trees (averaging 4–5 m in height; Aikins et al. 2023) and manmade structures. These nest colonies have multiple nest chambers, each chamber with a unique entrance tunnel that is accessed from the underside of the nest mass by the weavers and other associates including Pygmy Falcons (Maclean 1973a; Krochuk et al. 2018). Colonies can have hundreds of chambers which offer insulation from temperature extremes and buffer their occupants from the harsh weather conditions (van Dijk et al. 2013; Lowney et al. 2020a). The colonies appear to be centres of animal interactions and activity (Rymer et al. 2014; Lowney and Thomson 2021),

and through amelioration of conditions, and facilitation of resources, function as an ecosystem engineering structure (Lowney and Thomson 2022), with islands of enriched soils forming directly below these structures (Prayag et al. 2020; Aikins et al. 2023).

The nature of the interaction between Pygmy Falcons, Sociable Weavers and other colony associates is still largely unknown. Pygmy Falcons impact their weaver hosts in numerous ways including lethal predation on weaver nestlings and possibly adults (Maclean 1973b; Covas et al. 2004; Lowney 2020), while their presence creates fear, causing weavers to alarm and disperse (Lowney et al. 2020b). However, falcons may positively impact the weavers by defending the nests from snakes (Maclean 1970; Lowney 2020) because Cape cobras (*Naja nivea*) and Boomslang (*Dispholidus typus*) are frequent predators of weaver colonies (Covas 2002; Lowney et al. 2022). Only recently has research attention been given to the cooperative breeding propensity and group composition of Pygmy Falcons (Spottiswoode et al. 2004; Bolopo et al. 2019). Both studies highlighted that a family group may occupy several chambers in a weaver colony although the extent of this is not well documented. More broadly, falcons may impact interactions between the community of associate species at Sociable Weaver colonies (Lowney et al. 2020b), and may also indirectly have ecological impacts on communities of both animals and plants in the Kalahari. Therefore, a deeper knowledge of Pygmy Falcon biology is crucial to understand this system, their impact on Sociable Weavers and ultimately their potential influence in the ecological role of weavers and their colonies. Moreover, studying the life history of the falcons provides information on this poorly studied predator species and serves as a valuable baseline for investigating their evolutionary adaptations and ecological role.

We study the life history of Pygmy Falcons using a long-term marked-individual approach as this species is likely crucial to understanding the dynamics of between-species interactions around Sociable Weaver colonies, and the role of the colonies to the Kalahari animal community. Our broader study follows lifetime reproductive output and individual decisions, but our aim here is to provide information of the population level breeding decisions, densities, weaver colony choice and overall breeding biology of a population of Pygmy Falcons within the Southern African range of the species. Using data collected over 10 breeding seasons (2011–2020), we present a detailed overview of the main breeding parameters, including aspects of nest site selection, territory occupancy, spatial nest dispersion, number of breeding attempts, clutch size, number of fledglings and breeding success. Furthermore, we also investigate the annual and seasonal variation of these parameters throughout the study period.

Methods

Study site

We collected data at Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (−27.225, 22.478, Fig. 1). The reserve currently covers ~1200 km², but our main study area comprises c. 124 km² (Fig. 1). Data collection started in August 2011, the start of the 2011/2012 breeding season, and here we present data collected until the end of the 2020/2021 breeding season, 10 breeding seasons. The breeding seasons are presented as the year of the start of the season (i.e. 2011/2012 season = 2011). Our study area increased over time: 82.86 km² in 2011, 95.14 km² in 2012, 113.42 km² between 2013 and 2017, and remained 123.99 km² between 2018 and 2020. Tswalu Kalahari is in a semi-arid area near the southern border of the Kalahari Desert. Summer and winter temperatures may climb above 40°C and fall below 0°C, respectively (Lowney et al. 2020a). The mean annual rainfall is 361 mm (± SD 169.2 mm), the majority of which falls between December and March, with June to August being the driest months (Tokura et al. 2018). The two main tree species are camelthorn (*Vachellia erioloba*) and shepherd's tree (*Boscia albitrunca*).

Survey methods

In our study area, we have georeferenced a total of 362 Sociable Weaver colonies, and recorded the tree species or type of structure in which the colony was built. We assume this total are all colonies within the boundaries of our study area, and it is unlikely that colonies remain undetected. Some of these colonies have since collapsed or burnt, and some of these colonies have been newly built during the study period. Therefore, the true number of colonies are dynamic, and we continuously explore the study area and opportunistically add new colonies if they emerge. Since the size of our study area increased, the number of colonies checked/located also increased with time. Mapping of all weaver colonies was initiated in the first season in the core area, and colonies were added as they were found in subsequent seasons. Colony size was documented once each year (often during austral spring, August–October) by standing under the colony and counting the number of individual chambers. The numbers of chambers serve as a good proxy to the size of the colony (Leighton and Echeverri 2014).

At the start of each breeding season, we surveyed each Sociable Weaver colony in the study area to identify those occupied by Pygmy Falcons. Because falcons use weaver

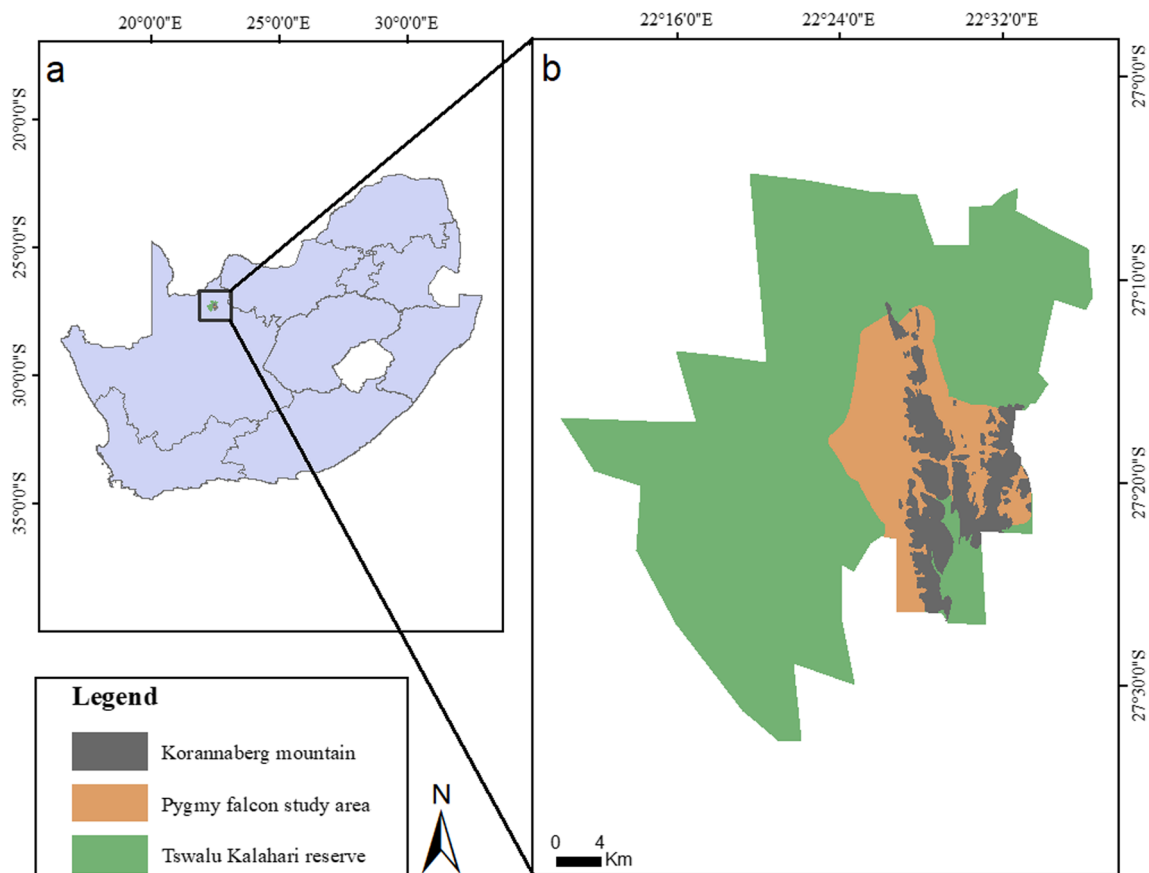


Fig. 1 Map of South Africa showing the location of Tswalu Kalahari reserve in the Northern Cape province (a) and the long-term Pygmy Falcon study area within the reserve which encompasses parts of the Korannaberg mountain range (b)

colonies year-round and they are obligate users of these colonies, this ensures that all active falcon sites in the study area are found each year. The chambers in a colony that are occupied by falcons are marked with an obvious white faecal mat, making them easily identifiable (Supplementary Fig. S1, Maclean 1970; Krochuk et al. 2018; Lowney et al. 2020a). At colonies that showed falcon presence, we monitored falcon occupied chambers using a telescopic mirror fitted with a LED light to determine if falcons were breeding. We checked falcon chambers at all colonies approximately every 7–10 days for most of the season until eggs or chicks were observed, and breeding was confirmed. In cases where we could not confirm eggs or chicks in active falcon chambers, we deemed these falcons as non-breeding individuals that did not initiate breeding in that year. However, it is possible that eggs were laid and were soon after predated.

After breeding was confirmed, we monitored nests to record clutch size, brood size, incubation length, number of fledglings and number of breeding attempts. We considered a nest successful if it fledged at least one individual, otherwise it was considered to have failed. If known, the cause

of failure was recorded. We classified a breeding event as being predated when the entire contents (eggs or nestlings) of the falcon chamber disappeared between checks. A nest was considered abandoned when its contents were found unattended, and adults were not observed around the nest after repeated visits.

At the start of the study, we suspected that two incubating falcons abandoned their clutch when flushed during nest inspection. Therefore, we minimised nest visits once a clutch was found and avoided inserting the mirror if we observed incubating individuals in a chamber. Therefore, we could not accurately determine the laying date, nor the exact clutch size of some nests. For these nests, we determined laying months by back calculating incubation (using 29 days, range 27–31 days detailed in Maclean 1970) and nestling periods (30 days, Maclean 1970).

Most falcons in the study area are marked. We captured individual falcons at their breeding or roosting chambers just before sunrise by placing a fabric bag sewn around a metal ring against the chamber entrance and gently nudging the underside of the nest with a blunt stick to encourage the bird out of the chamber. This method allows targeted

captures which is important given how many avian individuals use colonies. Between 2011 and 2014, we fitted falcons only with a uniquely numbered SAFRING metal ring. From 2015, each adult individual (> 10 months old) was fitted with a unique combination of a metal and three plastic colour rings allowing for individual identification without the need to re-trap. Nestlings and fledglings were first fitted with a metal ring, then with colour rings if they were recaptured in subsequent seasons; after surviving their first winter (Lowney et al. 2017; Bolopo et al. 2019). We used sightings or video cameras to monitor presence of colour ringed individuals and performed targeted capture of adults that are not colour ringed at their roosting or breeding chambers in the weaver colony. During captures and observations, we determined whether adults were in pairs, part of a group or as an individual (Bolopo et al. 2019). All captures and ringing of breeding birds were performed when chicks were within 1–2 weeks of fledging.

We aimed to determine all the ‘available’ falcon territories in our study area. Falcon pairs/groups often utilised multiple colonies within and across breeding seasons, and we, therefore, designated these colonies as one unique territory. These territories mostly remained consistent across years, even if different individual falcons comprised the pair/group. However, if a new pair/group occupied one of the colonies initially designated to an existing territory that was already occupied, we then split the territory into two unique territories due to this simultaneous occupation. We assigned each colony and territory with a unique identification. We computed the distance between each falcon occupied colony with the Geosphere R-package (Hijmans 2021) using the coordinates of these colonies.

Statistical analysis

We provide summary statistics for population level features and basic breeding parameters. Summary results are reported as mean \pm SD unless otherwise stated. We further explored how these parameters vary within seasons and across the years of this study. All data were analysed using the GLM-MTMB package because of its ability to handle zero-inflated models (Brooks et al. 2017). Residual distributions of the models were inspected to assess model fit, in cases where the data were not normally distributed, we log-transformed the response variables to satisfy the assumption of normality and fitted with a Gaussian distribution (Ives 2015). We conducted all analysis in the R statistical programme v 4.1.3 (R Core Team, 2022).

We investigated how population level dynamics and breeding at the territory level varied over the years by exploring several response variables linked to falcon nests or territories. First, we fitted a generalised linear mixed model (GLMM) with a binomial distribution to two

response variables; the likelihood that a territory would be occupied by falcons (yes/no), and the probability of falcons in an occupied territory initiating a breeding attempt (yes/no). Breeding season was included as an explanatory variable with territory ID as a random term. Second, we modelled the response variable of nearest neighbour distances (NND) between active falcon nests using a linear model (LM) with a Gaussian distribution. The breeding season was fitted as an explanatory variable. We excluded the 2011 season from the NND model because in this initial field season, some weaver colonies (and any active falcon nest in these colonies) were missed. In our dataset, of the 329 NND values calculated, 49% were duplicates of the same 2 nests being each other’s closest neighbours and we accounted for this by removing one of the NND values.

To determine whether colony size is explained by the tree species in which the colony is built, we fitted a LMM with the number of chambers as the response variable and the tree species as an explanatory variable. Due to the limited number of colonies built in silver cluster-leaf (*Terminalia sericea*) or man-made structure, these were removed from our statistical analyses. To determine whether breeding groups occupied more chambers than breeding pairs, we used the number of active chambers occupied as the response variable and whether the occupants were a pair or in a group as the explanatory variable. In both models, colony ID was used as a random term.

Within the study area and within each defined territory, there are multiple Sociable Weaver colonies available for falcon occupation. Colony occupation (yes/no) was analysed using a GLMM and binomial distribution with breeding season and colony size as the explanatory variables, and territory ID as a random term to explore if falcon occupation of a colony may be determined by colony size. Furthermore, to control for available colonies within a territory, we subset the data using only colonies within half the average NND (630 m) found during the study period and then ran the same model. This was to limit ‘available’ colonies for nest choice to those within the realistic active territory of each falcon nest.

The reproductive investment and output of nesting attempts were tested using a dataset of all nests where at least one egg was laid (all initiated nests). To investigate clutch size investment and output in terms of number of fledglings produced, we used a GLMM with binomial distribution with breeding season, egg-laying month, and colony size entered as explanatory variables, and territory ID as a random term. There were fewer data for the months of January and February, so we pooled both months to represent 1 month or completely removed from the models. For a full list of models, model terms and structure see the Electronic Supplementary Material.

Results

Population level metric density

We monitored a total of 356 active annual falcon territories throughout this study; an average of 35.4 ± 5.3 actively occupied territories each breeding season (range = 25 in 2011–43 in 2018). Each year between 11 and 20% of the weaver colonies were occupied by falcons (156–348 weaver colonies were monitored annually). Across the 10-year period, we recorded falcons breeding at least once in 120 of the 362 (33.1%) weaver colonies surveyed ‘annually’.

Overall, we identified 66 unique falcon territories in our study area, with 15 (22.7%) territories occupied 9 or 10 times ($\geq 90\%$) during the 10 seasons, 9 (13.6%) occupied 7 or 8 times, another 9 (13.6%) occupied 5 or 6 times, 22 (33.3%) occupied 3 or 4 times, and 11 (16.6%) occupied only once or twice through the 10 seasons. The overall probability of individual territory occupancy did not vary significantly with year ($\chi^2 = 8.75$, $df = 8$, $p = 0.36$).

The mean density of active falcon territories during a single season was 2.3/10 km². Falcon density was highest in 2015 (2.6 territories/10 km², Fig. 2a) and lowest in 2019 and 2020 (1.95 territories/10 km²). The NND between active falcon nests averaged $1.26 \text{ km} \pm 0.75$ (range 0.34–5.2 km; $n = 356$; Fig. 2b). We found 42.5% of nests, constituting 150 seasonal territories, were within 1 km of their nearest neighbour, and 41.9% were between 1 and 2 km of their nearest neighbours. Year did not explain significant variation in the NND of falcon nests throughout the study period ($F\text{-stat} = 0.64$, $df = 8$, $p = 0.73$).

Nesting structures and colony size

Weaver colonies in the study area were built on three tree species: camelthorn (68.2%, $n = 241$), shepherd’s tree (28%, $n = 99$) and silver cluster-leaf (1.7%, $n = 6$). Colonies were also built on manmade structures (1.9%, $n = 7$) including: thatched roofs, electric and telephone poles. Falcons roosted or nested in weaver colonies built on all these structures: camelthorn (78.3%, $n = 94$), shepherd’s tree (15.8%, $n = 19$), silver cluster-leaf (2.5%, $n = 3$) and manmade structures (3.3%, $n = 4$).

The annual average number of chambers in the monitored weaver colonies was $58.1 \text{ chambers} \pm 44.2$ (range = 1–302). On average, the biggest colonies were hosted on man-made structures (86.3 ± 70.6 , $n = 27$, range = 1–251). However, the biggest colony in the study area occurred on a camelthorn tree. Of the tree species, camelthorns hosted the largest colonies on average (61.2 ± 47.4 , range = 1–302), shepherd’s tree (41.7 ± 33.1 , $n = 489$, range = 1–165) and silver cluster-leaf (35.4 ± 23.6 , $n = 20$, range = 1–76). Colonies on camelthorn trees were on average 1.5 times bigger than colonies on shepherd’s tree ($\chi^2 = 14.26$, $df = 1$, $p < 0.001$).

The probability of falcons occupying a colony was significantly explained by the size of the colony (Table 1A). Occupation likelihood increased with increasing colony size (Fig. 3a). The smallest colony used by Pygmy Falcons for breeding had 12 chambers. In almost all cases, Pygmy Falcons occupied and initiated nests in colonies that were actively occupied by weavers, and the two species coexisted in these colonies. In only two separate cases were there falcon breeding attempts in colonies that were unoccupied by the weavers (abandoned by weavers one or more years before), and this occurred in different weaver colonies in 2011 and 2014. Both resulted in a successful falcon breeding attempt.

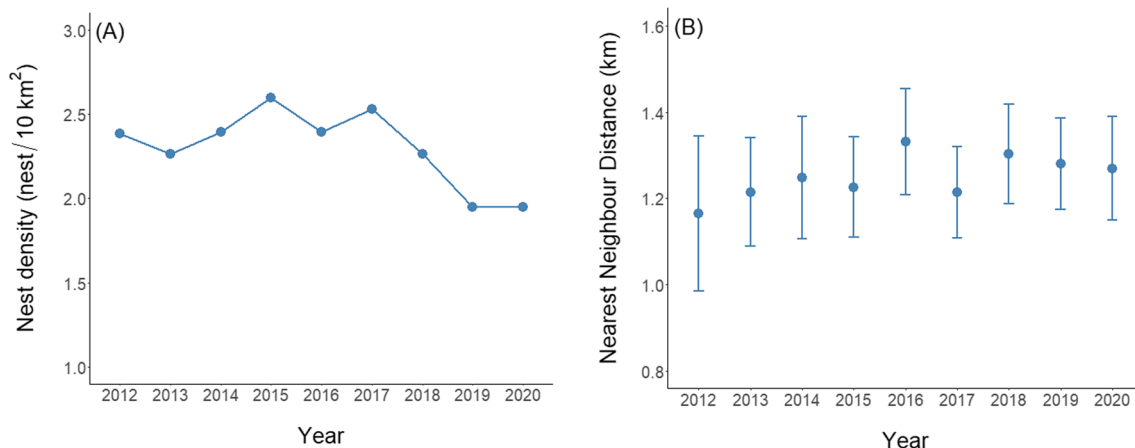
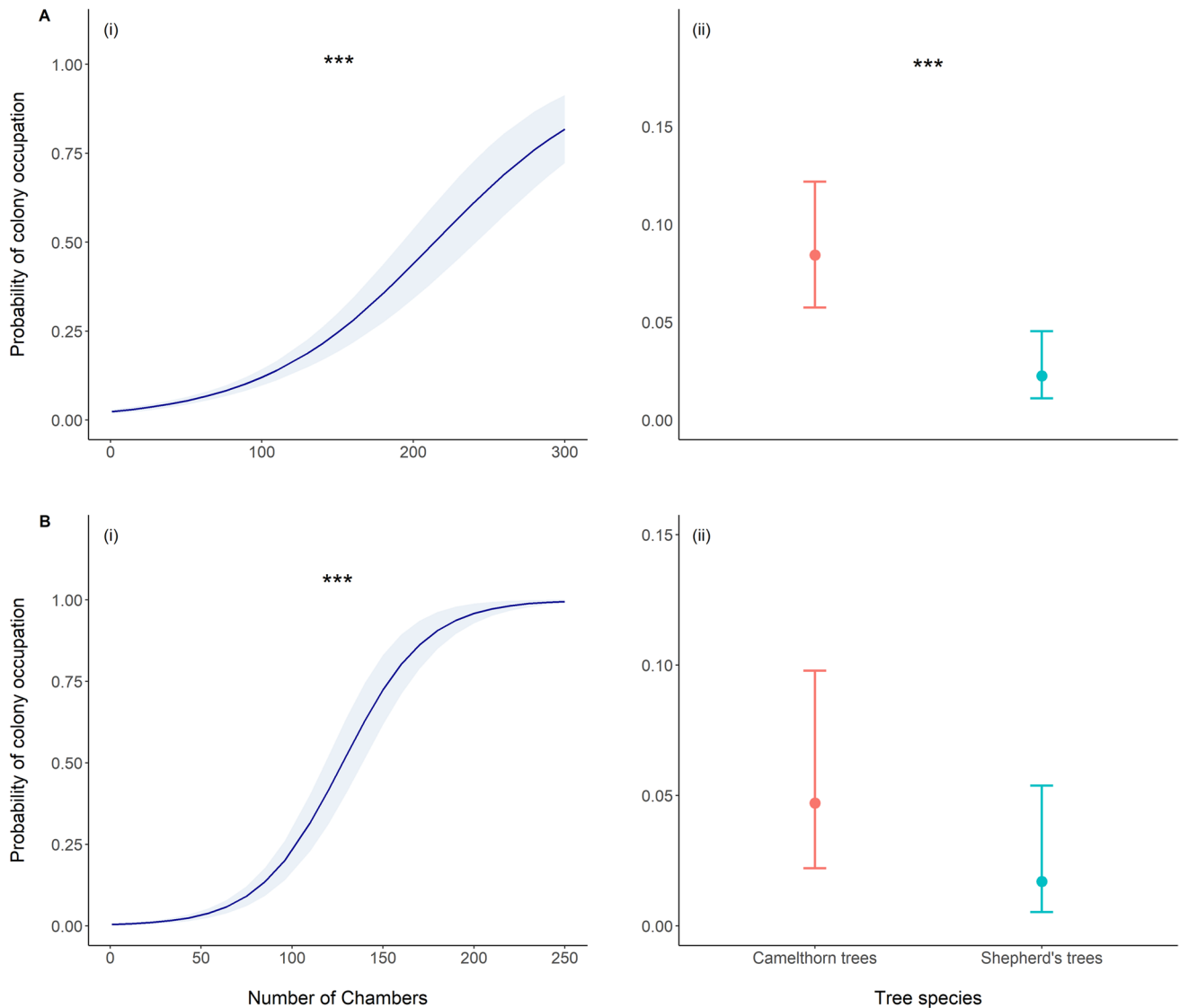


Fig. 2 Average annual nest density during the breeding seasons (a) and nearest neighbour distance (NND) between active nest colonies (b) of a population of Pygmy Falcons at Tswalu Kalahari, South Africa

Table 1 Falcon occupation of weaver colonies, using all the colonies within the study site (A) and probability of occupation using a subset of colonies within 630 m of each falcon territory (B)

Response variables	Explanatory variables	Estimate \pm SE	χ^2	<i>p</i>
(A) Falcon occupation, yes/no (using all colonies)	Year		12.4	0.13
	Colony size	0.017 \pm 0.002	43.9	<0.001
	Tree species		13.8	<0.001
(B) Falcon occupation, yes/no (using subset of colonies within 630 m of each falcon nest)	Year		5.8	0.66
	Colony size	0.043 \pm 0.005	63.6	<0.001
	Tree species		3.3	0.06

**Fig. 3** Falcon choice of colony depending on the size of the colony (i) and tree species (ii) within the whole study area (a) compared to with 630 m of a falcon-occupied colony (b). Falcons preferred larger colonies built in camelthorn trees (*** $p < 0.001$)

With colony size controlled for, year did not explain variation in the probability of a colony being occupied, although tree species did. Falcons were four times more likely to occupy colonies in camelthorn trees than in shepherd's trees ($p < 0.001$; Fig. 3a, Table 1A). When we used

a subset of colonies within 630 m of each active falcon occupied nest, a slightly different result was obtained (Table 1B). Colony size still strongly explained variation of the probability of occupation ($p < 0.001$; Fig. 3b, Table 1B), but tree species had no significant effect

($p=0.06$; Table 1B). The effect of year was still not significant ($p=0.66$; Table 1B).

Falcons occupied on average 2.9 ± 1.9 ($n=276$, range=1–9) chambers per weaver colony. We did not find a difference between the number of chambers occupied by breeding groups of falcons (4.0 ± 2.1 , $n=44$) and by breeding pairs (2.7 ± 1.6 , $n=232$; $\chi^2=0.57$, $df=1$, $p=0.4$).

Breeding attempts

Not all active falcon territories were found to initiate breeding. We found on average 16% of active territories per year did not breed (range 8.3% in 2014–38.5% in 2015). The probability of falcons initiating a breeding attempt was explained by year ($\chi^2=19.0$, $df=9$, $p=0.02$), but this was mainly driven by a far lower probability of initiating breeding in 1 year (2015), which tended to be lower than initiation probabilities in 2014 ($t=2.95$, $p=0.09$) and 2020 ($t=-2.99$, $p=0.08$), although these were not statistically different in post hoc analysis.

We followed a total of 326 breeding attempts during the study period (32.6 ± 7.3 per season). Breeding was initiated during August in early spring and lasted until late summer in some years (Fig. 4). We detected the earliest and latest first breeding attempts (time of laying the first egg), respectively, on 14 August and 08 February. The peak of initiation of breeding attempts was in September (Fig. 4) when we detected 33% of egg laying events with an annual average of 13.5 ± 5.7 attempts ($n=8$ seasons). On 12 occasions, we were unable to accurately estimate the laying month, and these occasions are excluded from this data.

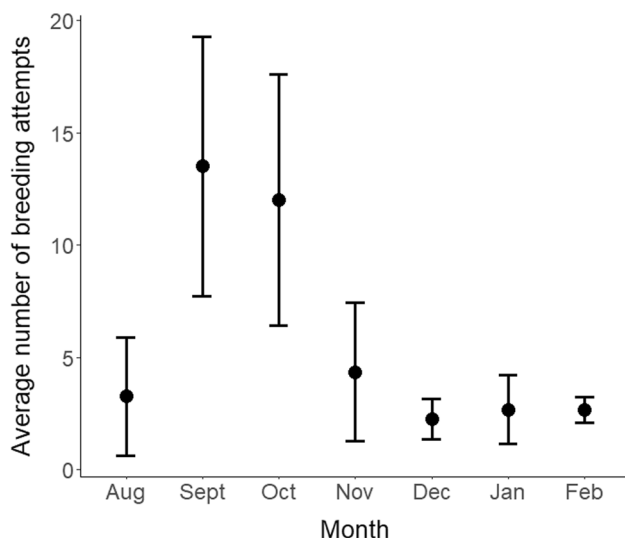


Fig. 4 Average number of breeding attempts (egg laying events) initiated by month with 95% confidence intervals in our study population of Pygmy Falcons, pooled for the 10 years of data collection

We found evidence of multiple breeding attempts in the same season, with 8.4% ($n=29$) of breeding attempts being a follow-up attempt. Falcons initiated breeding twice ($n=26$) and a maximum of three times ($n=3$) in a breeding season. We found that on occasions when the initial attempt was predated, abandoned or successful, falcons laid replacement clutches on nine, two and eight occasions, respectively. The same falcon pair/territory successfully raised two full broods in a season only on four occasions.

Clutch size and brood size

Incubation lasted an average of 33 ± 4 days (range=22–43 days, $n=57$) while the nestling period was 37 ± 5 days (range=26–48 days, $n=51$). Clutch size ranged from one to three eggs ($n=280$), with three eggs (48%) being the modal clutch size followed by two egg clutches (42%) and one egg clutches (10%). Of the 254 clutches we recorded as first breeding attempts per season, only 12% were one egg clutches, while 1 egg clutches accounted for 31% of replacement clutches ($n=26$). We recorded a mean clutch size of 2.38 ± 0.66 with the largest mean clutch size recorded in 2011 (2.75 ± 0.44 ; $n=20$) and the smallest in 2019 (2.04 ± 0.35 ; $n=24$).

When we explored the likelihood of falcons laying the maximum (and modal) clutch size of three eggs (as opposed to clutches of one or two eggs), we found it varied significantly across years (Fig. 5) but not with laying months or colony size (Table 2a). This significant variation across years was driven by the low probability of three egg clutches in

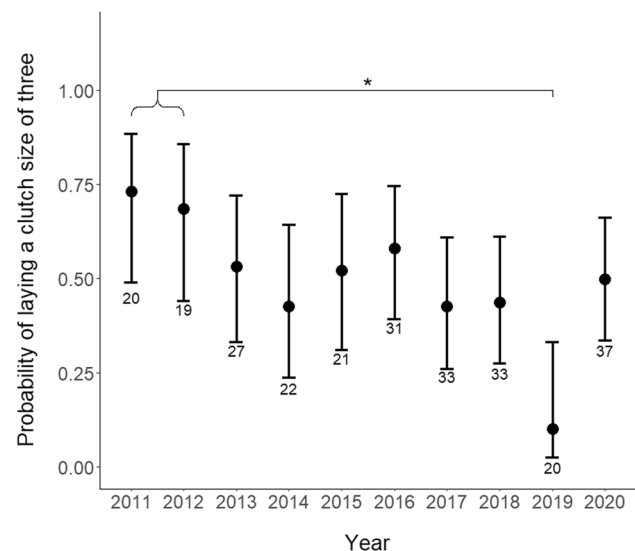


Fig. 5 Likelihood of falcons laying a clutch size of three with 95% confidence intervals with the year, the egg-laying month and size of colonies controlled. Sample sizes are presented below bars. Horizontal lines connect years that differ significantly, $*p < 0.05$

Table 2 A generalised linear mixed model exploring (A) the probability that falcons lay a clutch size of three, (B) the probability to produce a fledgling per egg laid, (C) the number of fledglings produced and (D) the probability of nest success (at least one fledgling from a nest), with Territory ID used as random effect for each model

Response variables	<i>n</i>	Explanatory variables	Estimate \pm SE	χ^2	<i>p</i>
(A) Clutch size of three (yes/no)	263	Year		16.5	0.05
		Colony size	0.002 \pm 0.002	0.5	0.46
		Laying month		8.2	0.08
(B) Fledglings per egg laid	283	Year		24.7	0.003
		Colony size	0.001 \pm 0.003	0.1	0.71
		Laying month		12.7	0.01
(C) Number of fledglings produced	292	Year		48.6	<0.001
		Colony size	<0.001 \pm <0.001	0.5	0.5
		Laying month		41.8	<0.001
(D) Success (yes/no)	291	Year		19	0.02
		Colony size	<0.001 \pm 0.001	0.1	0.69
		Laying month		28.8	<0.001

2019, which were approximately seven times less likely than in 2011 ($p=0.01$) and 2012 ($p=0.02$). Overall, 73% of clutches hatched and reached the brood stage; therefore, brood size averaged 2.25 ± 0.67 (range = 1–3). The hatching outcome of 4% clutches was unknown while 22% remained unhatched.

Breeding success

Of the 326 breeding attempts, 61% were successful (at least one chick fledged), including 8 successful second attempts. On average, 1.99 ± 0.71 ($n=199$) fledglings were produced with 2015 producing the lowest mean of 1.64 ± 0.74 fledglings ($n=14$), and 2013 producing the highest mean of 2.45 ± 0.60 fledglings ($n=20$).

In total, 31.3% of breeding attempts failed including all third breeding attempts within a season. Predation and abandonment accounted, respectively, for 50% and 25% of the 127 failed nests. Other events attributed to nest failure include nest collapse/breakage (8%), human interference (2%) and fire (1%). The reason for 15% of failed attempts was unknown. Known breeding failure occurred at the incubation (60.8%, $n=62$ of which 27 were predation events and 24 were abandoned) and nestling stages (38.5%, $n=29$ of which 18 were predation events and only one was abandoned). We could not determine the outcome of 7.6% breeding attempts.

The probability of Pygmy Falcons fledgling all eggs laid per nest was explained by year ($\chi^2=47.6$, $p<0.001$) and egg laying month ($\chi^2=39.2$, $p<0.001$) but not by colony size (Fig. 6a, Table 2B). This probability was at least 1.9 times higher in 2011 (t ratio > 3.22 , $p<0.05$) than in every other year between 2015 and 2018. Similarly, falcons were at least 1.9 times as likely to fledge all eggs laid per nest in 2013 (t ratio > 3.36 , $p<0.05$) than in each year between 2015 and 2019. Falcons were also at least two times less likely to fledge all eggs in 2016 (t ratio > 3.27 , $p<0.05$) than in

2012, 2014, 2020. We recorded within-season variation with the month of August having almost three times more likelihood to fledge all eggs laid per nest than in November (t ratio = 3.23, $p=0.01$). All eggs laid per nest in September (t ratio > 3.03 , $p<0.05$) were at least 1.7 times more likely to fledge compared to those laid each month between October and December.

We found that the number of fledglings varied across years ($\chi^2=48.6$, $p<0.001$) and egg laying month ($\chi^2=41.8$, $p<0.001$) but colony size had no effect (Fig. 6b, Table 2C). The number of fledglings produced in 2011 (t ratio > 3.71 , $p<0.01$) and 2013 (t ratio > 3.18 , $p<0.05$) was, respectively, at least 2 and 1.8 times higher than those produced each year between 2015 and 2019. The number of fledglings also showed within-season variation as clutches laid early in the season, August–September, produced significantly higher numbers than those laid later in the season, October–January. Clutches laid in September produced at least 1.5 times more fledglings (t ratio > 3.19 , $p<0.001$) than those laid each month between October and January. Furthermore, clutches laid in the month of August produced three times more fledglings than those laid in November (t ratio = 3.28, $p=0.01$).

We recorded the highest proportion of successful attempts in 2011 (86%, $n=18$ of 21 attempts) and the least in 2019 (42%, 13 of 31 attempts). Breeding success was significantly explained by year ($\chi^2=18.7$, $df=9$, $p<0.05$) but this was mainly driven by a lower probability of success in 2016, which tended to be lower than success probabilities in 2012 ($t=3.02$, $p=0.08$) and 2020 ($t=3.04$, $p=0.07$), although these were not statistically different in post hoc analysis. Breeding success was also explained by the month a breeding attempt was initiated ($\chi^2=28.7$, $df=5$, $p<0.001$; Fig. 7) but not by the size of the colony (Table 2D). Post hoc analysis revealed that the success of attempts initiated in September (11.5 ± 3.2 , $n=8$ seasons, sum = 88) was 1.4, 3.4 and 6 times higher (t ratio > 2.86) than those initiated in October

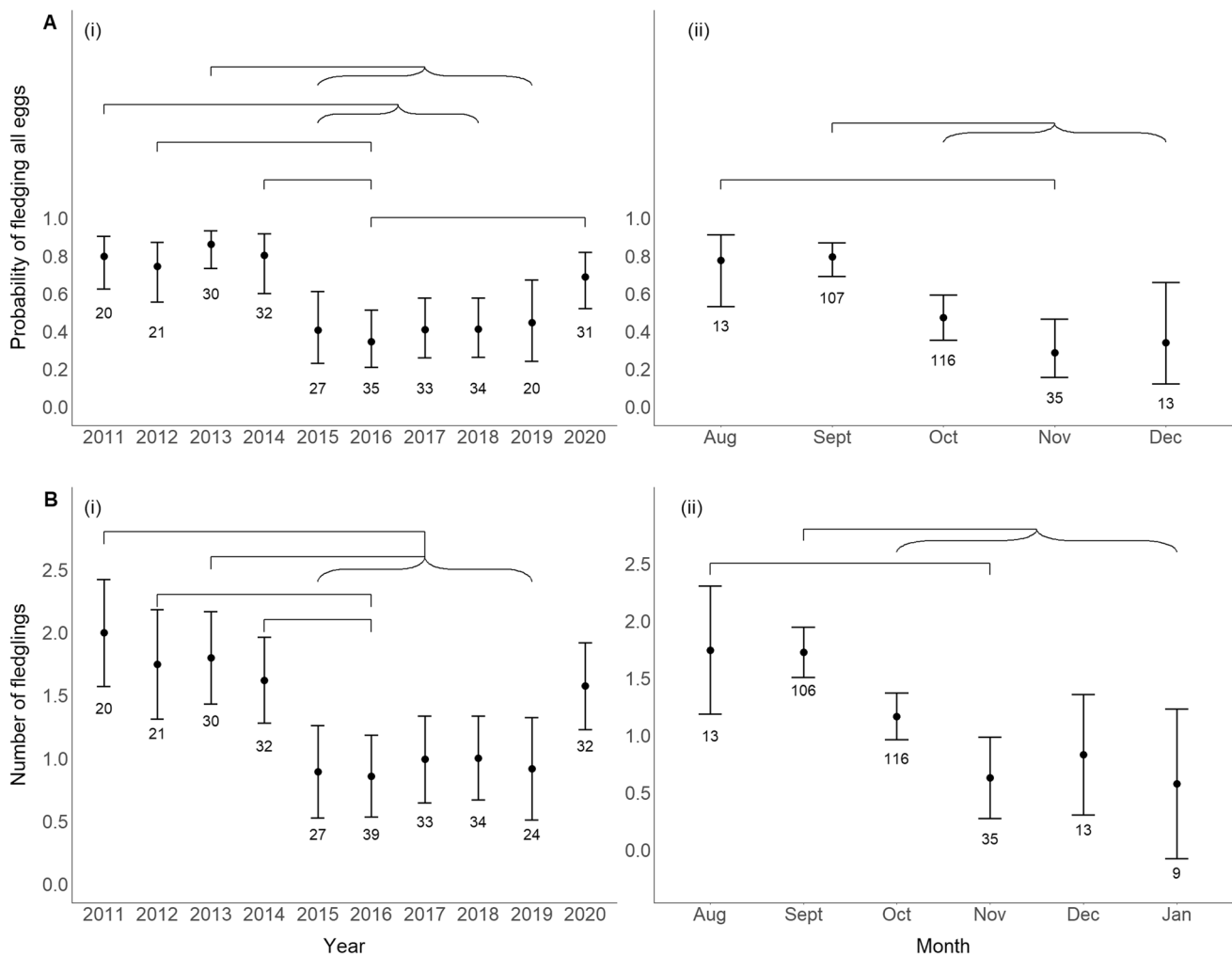


Fig. 6 Probability ($\pm 95\%$ confidence intervals) **(a)** of all eggs laid in a given clutch developing into chicks and fledge, and **(b)** the number of fledglings produced per nest with the year **(i)** and with the month

(ii) breeding was initiated with size of colonies controlled. Sample sizes are presented below bars. Horizontal lines connect years/months that differ significantly

($p < 0.01$), November ($p < 0.001$) and January ($p = 0.05$) respectively. Moreover, attempts initiated in October were 2.4 times more likely to be successful than those initiated in November (t ratio = 2.95, $p = 0.05$).

Discussion

Our findings reveal detailed long-term breeding parameters of a Pygmy Falcon population. Clutch size, number of fledglings and breeding success of the falcons varied significantly between and within seasons in the 10-year period. We found that falcons selected larger colonies for breeding, but the colony size did not explain variation in breeding investment and output. The breeding season occurred during the austral spring and into early summer, and we found that breeding success was influenced by laying date, with those

birds breeding earlier being more successful. We found that nearly two-thirds of all breeding attempts were successful, and an average of two chicks per nest fledged. Of the nesting attempts that failed to produce any chicks, predation was likely the reason for failure.

The average nest density of the Pygmy Falcon was 23 nests/100km² which suggests far higher population density than the 0.5 individuals/100 km² estimated by Krüger et al. (2002) using transect data. We found that falcons occupied 11–20% of the weaver colonies monitored each year through the study period, which is similar to the 23% and 25% occupation, respectively, reported by Hoesch (1936) and Maclean (1970). This value would be partly determined by the density of Sociable Weaver colonies, which is likely higher in our study area. The annual average distance of 1.26 km between two falcon occupied colonies recorded for this study was almost double the distance of 0.8 km reported by Maclean

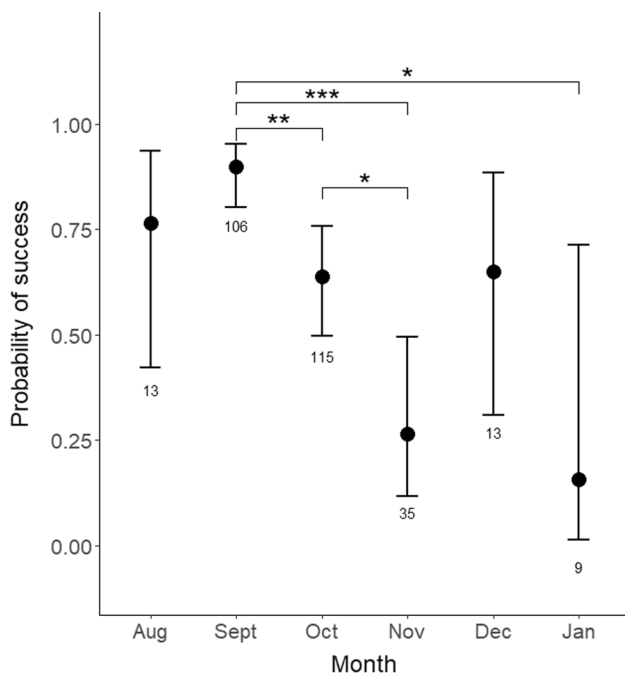


Fig. 7 Probability of breeding success ($\pm 95\%$ confidence intervals) for nests depending on the month a breeding attempt was initiated between 2011 and 2022. Sample sizes are presented below bars. Horizontal lines connect months that differ significantly, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

(1970). This discrepancy likely owes to our considerably larger study area covering a diverse habitats (Tokura et al. 2018) and the small sample size and study area of Maclean (1970), focussed along a single riverbed. Nest spacing in raptors is partly dictated by habitat diversity which can hold higher prey availability, and hence preferred for foraging and nesting (Poirazidis et al. 2007; Rodríguez et al. 2018).

Our results show that falcons preferred to nest in larger colonies. Larger colonies were likely preferred by Pygmy Falcons because they are better thermoregulatory hubs, with intermediate and centre chambers being more insulated than chambers at the edge of the colony (van Dijk et al. 2013; Lowney et al. 2020a). Furthermore, the falcons probably preferred larger colonies because they provide more readily available prey, potentially insects and birds (Lowney and Thomson 2021, 2022; Brown et al. 1992) and intuitively more individual Sociable Weaver nests (Covas 2002). However, despite preferring larger colonies, we found no clear evidence that colony size was correlated with Pygmy Falcon reproductive output. Nest characteristics such as nest size have been linked to reproductive performance in some passerines, including sociable weavers (Covas 2002, Vergara et al. 2010, Møller et al. 2014 but see Alabrudzińska et al. 2003, Lambrechts et al. 2012, 2016). We found that falcons favoured colonies built in camelthorn trees to those in shepherd's trees probably because the former contained,

on average, larger colonies than the latter. It is beyond the scope of this study to determine why weavers preferred to build their colonies in camelthorn trees, but we suggest that it is because this tree is relatively the more abundant species around the Korannaberg mountains, an area of the study site that receives higher amount of rainfall than other parts of the study area (Tokura et al. 2018) and that holds higher densities of Pygmy Falcons.

The earliest breeding attempts were recorded in August and the latest in February. Maclean (1970) reported a similar timeline extending into March but describes this as the length of the falcon's "breeding season". It is unclear if this included the entire breeding behaviour from courtship to complete brood rearing. Spring to early summer breeding is common for austral raptor species (Olsen and Marples 1993). Prolonged breeding season can have implications for reproductive investment (Griebeler et al. 2010). We found evidence of multiple breeding attempts within a season and falcons in our study population did not raise more than two broods in a season which is in line with Maclean (1970). All third reproductive attempts that we monitored failed during incubation. Breeding strategies such as single and multiple breeding are employed by birds to maximise offspring fitness within a season (Verhulst et al. 1997). Single-brooded species, which generally have a short breeding season, express an initial increase in clutch size before a subsequent decline during the season while multiple-brooded species tend to peak clutch size at mid-season (Lack 1947; Crick et al. 1993; Gil-Delgado et al. 2005). Pygmy Falcon breeding exhibited a pattern of steady decline in clutch size within a season often typical of single-brooded species. Multiple breeding is infrequent in raptors because of their prolonged breeding season but the exceptions are with small-sized (Newton 1979), and cooperative breeding species (Malan et al. 1997) like the Pygmy Falcon (Bolopo et al. 2019). Hence, it is expected that the falcons be multiple-brooded species in seasons with suitable conditions.

The average clutch size (2.4 eggs) reported here is smaller than the average (3.1 eggs) reported by Maclean (1970). We never recorded a clutch size of more than three eggs in our study area, but Maclean (1970) reported four eggs for the same species in Kgalagadi, c.310 km west of our study site. However, the modal clutch size of three eggs reported in this study was the same as in Maclean (1970). Clutch size typically varies with laying dates (Klomp 1970), and we found evidence that falcons were less likely to lay a three egg clutch size depending on the month they initiated breeding. Moreover, significant variation in clutch size across the 10-year period of the study was strongly driven by lower likelihood of falcons laying three egg clutches in 2019. Annual variation in clutch size is linked to environmental stochasticity (Lepage and Lloyd 2004). In desert environment where productivity

is strongly associated with the extremely varied weather conditions (Dean and Milton 2001), species are known to vary reproductive investment (clutch size) with resource availability (Lepage and Lloyd 2004; Lloyd 2008; Mares et al. 2017). Daily rainfall data collected between 2001 and 2021 from 38 rain gauges in Tswalu Kalahari showed that an average of 117 mm and 202 mm of rainfall was recorded, respectively, in 2018 and 2019 seasons which is the lowest for the entire period of this study.

The maximum number of fledglings produced was in line with reports in Maclean (1970); however, both hatching and fledgling success were markedly higher in our study. There was seasonal decline in reproductive output of the falcons which is similar to reports by Garcia-Heras et al. (2016) for an arid zone raptor—the Black Harrier (*Circus maurus*). This reduction in reproductive performance typically occurs during the course of the breeding season (Öberg et al. 2014; Pärt et al. 2017) in seasonally breeding species (Price et al. 1988; Svensson 1995). Decline in reproductive outcomes within the season is usually a response to a deteriorating environmental quality as the breeding season progresses (Perrins 1970; Daan and Tinbergen 1997; Gruebler and Naef-Daenzer 2010) or/and due to individuals' phenotypic quality, with early breeders having better quality (Price et al. 1988; Verhulst and Nilsen 2008; Reed et al. 2009; Harriman et al. 2017).

More than 30% of breeding events failed to reach the fledgling stage. In our study, nest predation was the principal cause of failure, but Maclean (1970) reported abandonment as the main cause of nest failure. The Cape cobra and boomslang are the main nest predators associated with Sociable Weaver colonies causing up to 75% loss in weaver nests (Maclean 1973b; Covas 2002). We often encountered both of these snake species predated the weaver nests, and the Pygmy Falcon nests suffer too (Lowney et al. 2022) since they exclusively use the weaver colonies. Nest predation is the dominant cause of nest failure in most birds (Ricklefs 1969; Martin 1993; Newton 1998; Remeš et al. 2012) and snakes have been identified as the principal predators of avian nests (Best and Stauffer 1980; Stake et al. 2004; Degregorio et al. 2014; Chen et al. 2020 but see Miller et al. 2015). Maclean (1970) identified human interference as the event leading to nest desertion by the falcons, but to reduce this likelihood, we avoided investigating nests chambers when an adult falcon was in the chamber. Overall, 25% of nest failures in our study were still due to abandonment and we could not determine the cause. However, we observed fatal competition between Pygmy Falcon males which resulted in a nest abandonment

(Lowney et al. 2017). Predation of adult Pygmy Falcons have been reported by Engel (2011) and we have observed predation of breeding adults by Pale-chanting Goshawks (*Melierax canorus*), which are common in the study area. Such adult predation would show as abandoned nests in our study.

Our results highlight long-term variation in the breeding biology of the Pygmy Falcon and adds to the growing body of knowledge on their life history (Hoesch 1936; Maclean 1970; Covas et al. 2004; Spottiswoode et al. 2004; Lowney et al. 2017; Krochuk et al. 2018; Bolopo et al. 2019; Lund et al. 2020; Oschadleus 2022). While further studies are needed to understand the drivers of these variations, we theorise that they might be strongly linked to rainfall. This is very plausible because the Kalahari is characterised by pulsed rainfall which result in sporadic eruption of resources that become available to the falcons. Hence, it is expected that the falcon's reproductive investment and output will vary with the infrequent resource availability such that falcons perform better in productive years. These results might have implications for the weavers and other associates of these colonies. Sociable Weavers in larger colonies have been shown to have a greater reproductive output than those in smaller colonies (Covas 2002). However, these results were derived from a study population that only rarely host Pygmy Falcons. Therefore, our results demonstrate that falcon preference for larger colonies may have knock on effects to the breeding performance of the weavers, particularly as the falcons have been shown to predate on the weavers (Covas et al. 2004). Long-term studies like this show decadal trends and offer critical insight in ecology and are useful for informing conservation management plans (Franklin 1989; Franklin et al. 1990; Lindenmayer et al. 2012).

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Author contribution All authors contributed to conceiving the idea of this project and data collection. OPO wrote the article. OPO and AML analysed the data. Specific contribution for each author, following the CRediT contribution roles are highlighted below. OPO:

conceptualization-equal, data curation-equal, formal analysis-equal, writing—original draft-lead; AML: conceptualization-equal, data curation-equal, formal analysis-equal, writing—review and editing-equal; DB: conceptualization-equal, data curation-equal, writing—review and editing-supporting; RLT: conceptualization-Lead, data curation-lead, formal analysis-supporting, funding acquisition-lead, methodology-lead, supervision-lead, writing—review and editing-lead.

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Data availability statement The datasets will be archived in at the University of Cape Town's open-access institutional data repository, ZivaHub, and made available to the public upon request following acceptance and publication of this article.

Declarations

Conflict of interest All authors certify that they have no competing interests to declare regarding the content of this article.

Ethics approval The project conformed to the legal requirements of South Africa and has received annual research permits from the Northern Cape Province Department of Tourism and Environment and Conservation, and it is covered by ethics approvals from the University of Cape Town, South Africa.

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