Camelthorn and blackthorn trees provide important resources for Southern Pied Babblers (*Turdoides bicolor*) in the Kalahari

KIM HUNT,[1] LIAM É MARAIS,[2,3] SUSAN J. CUNNINGHAM,[1] AMANDA R. RIDLEY,[1,4] LESEDI MOAGI,[3,5] SANJO ROSE,[1] ANDREW E. MCKECHNIE[2,3] & AMANDA R. BOURNE*[1,6]

[1]DSI-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

[2]Department of Zoology and Entomology, DSI-NRF Centre of Excellence at the FitzPatrick Institute, University of Pretoria, Pretoria, South Africa

[3]South African Research Chair in Conservation Physiology, South African National Biodiversity Institute, Pretoria, South Africa

[4]Centre for Evolutionary Biology, School of Biological Sciences, University of Western Australia, Crawley, Australia

[5]Department of Nature Conservation, Tshwane University of Technology, South Africa

[6]Australian Wildlife Conservancy, Subiaco, Australia

*Corresponding author. Email: abourne.uct@gmail.com. Twitter ID: @manda_babbler

ABSTRACT

In the southern Kalahari Desert, cooperatively breeding Southern Pied Babblers *Turdoides bicolor* frequently build their nests and forage in camelthorn trees *Vachellia erioloba*, a keystone species in the region, and blackthorn trees *Senegalia mellifera*, a widespread early successional shrub. Using Ivlev's electivity indices (Ei), we show that Southern Pied Babblers preferentially nest in camelthorn trees and preferentially forage in or under camelthorn and blackthorn trees. Southern Pied Babblers primarily forage on the ground; however, they will make use of arboreal resources when these are available. We observed the birds spending the highest proportion of foraging time off the ground during October, when breeding is also most common, compared with all other months within the austral summer breeding season. They are most likely to be observed foraging in camelthorn trees earlier in the breeding season and blackthorn trees later in the breeding season. We demonstrate that Southern Pied Babblers have a strong relationship with camelthorn trees, in which they prefer to both nest and forage. We highlight the importance of protecting camelthorn trees, a keystone species in the region, as part of the conservation and management of endemic Kalahari fauna such as the Southern Pied Babbler. In addition to contributing to the literature on keystone species, our observations raise questions about the ways in which avian reproduction in the arid zone could be decoupled from rainfall via the phenology of deep-rooted tree species.

Keywords: arid ecosystems, environmental cues, Ivlev's electivity index, keystone species, nesting preference, reproductive behaviour.

The Kalahari Desert in southern Africa is a summer-rainfall arid-savannah dune-field habitat characterized by open grassy plains and sparse trees and shrubs (Kong *et al*. 2015) supporting a diverse bird community (Dean *et al*. 2002, Hudson & Bouwman 2007, Seymour & Dean 2010). Rainfall is erratic and relatively low (100–400 mm per year), falling primarily during the austral summer (November–March) in spatially and temporally unpredictable thunderstorms (Lovegrove 1993, MacKellar *et al*. 2014, van de Ven *et al*. 2019). Natural surface water resources are limited to calcrete pans and fossil riverbeds which become inundated for short periods after heavy rains (Smit 2013). The dominant plant species are camelthorn trees *Vachellia erioloba* and sour grass *Schmidtia kalahariensis* (Steenkamp *et al*. 2008). Other common plant species include blackthorn *Senegalia mellifera*, driedoring *Rhigozum trichotomum*, grey camelthorn *Vachellia haemotoxylon* and shepherd's tree *Boscia albitrunca*.

Camelthorns are the largest trees in the Kalahari, growing up to 16 m tall (Krug 2017) with canopy diameters up to 22 m (Carr 1976, Moustakas *et al*. 2006). Once established, they have a very deep tap root that can reach ground water up to 60 m below the surface (Canadell *et al*. 1996, Krug 2017). As a result, they can have near-permanent access to ground water and can grow largely independent of annual rainfall, impervious to all but the most severe droughts (Barnes *et al*. 1997, Timberlake *et al*. 1999, Barnes 2001, Moustakas *et al*. 2006). They bud, flower and fruit predictably between August and October each year (Barnes *et al*. 1997), prior to summer rainfall. As such, they are an important source of food for herbivores towards the end of the dry season, including the moth and butterfly larvae on which bird species such as Southern Pied Babblers *Turdoides bicolor* and Crimson-breasted Gonoleks *Laniarius atrococcineus* feed their young (Steenkamp *et al*. 2008, Ridley & van den Heuvel 2012, Ridley 2016). Similar to the Saguaro Cactus *Carnegiea gigantea* in the Sonoran Desert (Wolf & Martinez del Rio 2000, Wolf *et al*. 2002, Wolf & Martínez del Rio 2003), the camelthorn is a keystone species (Mills *et al*. 1993, Cottee-Jones & Whittaker 2012, Lindenmayer & Westgate 2020). The life cycles of many Kalahari plants and animals are intimately tied to camelthorns (Leistner 1967, Milton & Dean 1995, Dean *et al*. 1999, Eccard *et al*. 2006, Steenkamp *et al*. 2008, Lerm 2014, Campbell *et al*. 2015, Lowney & Thomson 2021, 2022), which provide predictable resources such as shade, food and shelter in an otherwise highly stochastic environment (Gubb 1988, Milton & Dean 1995, Barnes *et al*. 1997, Dean *et al*. 1999, Krug 2017). Camelthorn trees are slow to grow from saplings into larger size classes (Seymour 2008), which can be as gradual as only a 4.5-cm increase in average height over 15 years (Seymour *et al*. 2022).

Southern Pied Babblers are medium-sized (60–90 g), monomorphic (Bourne *et al*. 2021a), cooperatively breeding passerines endemic to the Kalahari (Hockey *et al*. 2005). They build open cup grass nests (Fig. 1) and breed during the austral summer (Ridley 2016, Bourne *et al*. 2020a). They are primarily terrestrial foragers, searching the ground under trees and shrubs for invertebrate prey (Thiele *et al*. 2008), mainly Coleoptera, Lepidoptera and Orthoptera (Ridley 2016). Previous studies provide a good understanding of their reproductive ecology (Raihani & Ridley 2007, Ridley & Raihani 2008, Nelson-Flower *et al*. 2011, Thompson *et al*. 2013, Wiley & Ridley 2016, Bourne *et al*. 2020a, 2020b, 2020c, 2021a, 2021b, 2021c) and foraging behaviour (du Plessis *et al*. 2012, Golabek *et al*. 2012, Ridley 2016). For example, Southern Pied Babblers in the southern Kalahari start breeding predictably in September or October each year, at the beginning of the austral summer and well ahead of typical summer rainfall (Bourne *et al*. 2020a). Southern Pied Babblers are known to nest and forage in camelthorn and blackthorn trees (Wiley 2017) but the extent of their reliance on these species has not been specifically evaluated. To determine the overall importance of

camelthorn and blackthorn trees for Southern Pied Babblers in the southern Kalahari, we observed breeding and foraging behaviour and identified nesting site and foraging site preferences for the first time. To achieve this, we determined (i) the relationship between the timing of breeding in Southern Pied Babblers and rainfall, (ii) which tree species Southern Pied Babblers preferentially use for both breeding and foraging, and (iii) the seasonal patterns of preferential use, to determine an overall picture of important tree resources for a species endemic to the Kalahari semi-arid savanna region.

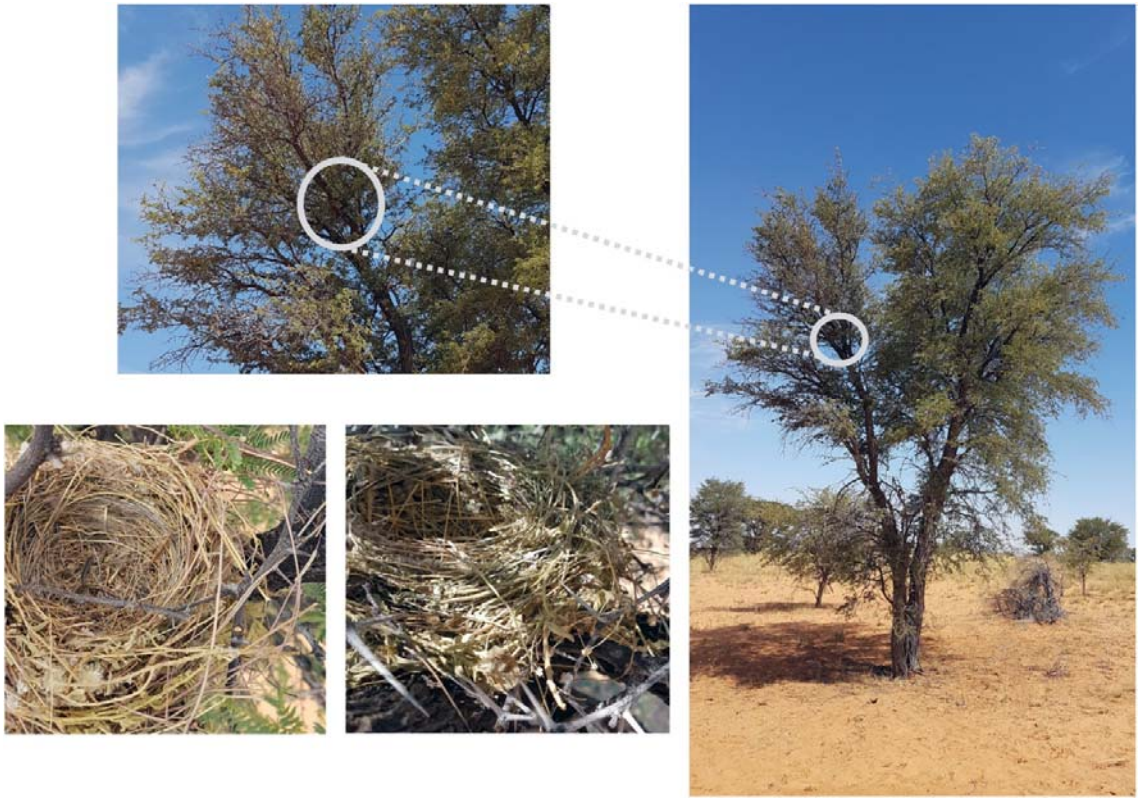

Figure 1. Southern Pied-Babblers *Turdoides bicolor* build open-cup grass and leaf nests in thorn trees, such as this camelthorn tree *Vachellia erioloba*.

METHODS

Data were collected at the 33-km^2 Kuruman River Reserve (KRR; 26°58′S, 21°49′E) and neighbouring properties in the southern Kalahari, where a habituated population of Southern Pied Babblers was established in 2003 (Ridley & Raihani 2007, Ridley 2016). During the study, daily maximum air temperature (T_{max} in °C) and rainfall (mm) data were collected from an on-site weather station (Vantage Pro2; Davis Instruments, Hayward, CA, USA). The region primarily receives summer rainfall, with 72% of annual rainfall occurring between December and February each year (Bourne *et al*. 2020a). Average daily summer maximum temperature from 2003 to 2020 was 34.3 ± 0.8 °C (range: 32.8–35.6 °C) and summer rainfall averaged 150.9 ± 63.5 mm (range: 49.8–262 mm).

Nest observations

To determine the relationship between the timing of breeding and rainfall, nests were located by observing the nest-building and nest attendance behaviour of breeding Southern Pied Babbler groups (Ridley & van den Heuvel 2012, Bourne *et al*. 2020a). Each group in the population was observed at least once per week to determine the presence of breeding activity. Breeding attempts were included in the study once nest-building was completed, a clutch was laid and incubation was initiated. Initiation date was recorded as the first day of observed incubation, using data published by Bourne *et al*. (2020a) for the period September 2005 through February 2019 and supplemented with additional unpublished data collected for the 2019–2020 breeding season (C. Soravia unpubl. data). Due to the remote location of the field site and related difficulties collecting data year-round, breeding data were collected between September and March only. We consider this reasonable, as determination of the breeding season was based on several years of fieldwork (Ridley 2016) during which only 5% of breeding attempts occurred outside the austral summer breeding season.

To determine which tree species Southern Pied Babblers prefer for nesting in, we characterized nesting sites ($n = 58$, initiated by 20 different Southern Pied Babbler groups) immediately following the end of a breeding attempt due to fledge or failure. Nesting site characterizations were conducted between October 2016 and March 2017, on clear afternoons, between 14:00 and 16:00 h, within a maximum of 5 days of the end of the breeding attempt (Griffith *et al*. 2016). Data were captured using Cybertracker v3.448 (www.cybertracker.org) installed on a Mobicel TRENDY Android smartphone. For the purpose of this study, the focus was on recording the tree species in which the nest was located. Additional characteristics that were measured, including nest orientation, height above the ground, distance of the nest from the canopy edge and from the centre of the tree and canopy cover above the nest, are discussed in more detail in the Supporting Information.

Behaviour observations

As part of an ongoing study of the behaviour of wild Southern Pied Babblers, birds in the study population have been observed under natural conditions since 2003 (Ridley 2016, Ridley *et al*. 2021). Habituation of the birds allows human observation from distances of 1–5 m (Ridley & Raihani 2007), enabling collection of detailed behavioural data (du Plessis *et al*. 2012, Wiley & Ridley 2016, Bourne *et al*. 2021b, 2021c). All individuals are uniquely marked with one metal and two to three colour leg rings for individual identification.

To determine which tree species Southern Pied Babblers prefer foraging in, and to identify any seasonal patterns in foraging site preferences, data on foraging behaviour of breeding Southern Pied Babblers were obtained from 118 individuals across 15 different babbler groups and were collected over 130 days between September 2016 and February 2019. On all observation days, groups were either incubating clutches of eggs or provisioning nestlings. Behavioural observations were conducted during six discrete observation sessions between 07:00 and 19:00 h on each observation day, as described in detail by Bourne *et al*. (2021c), and involved scan sampling, noting the behaviour of all individuals in the group at regular 15- to 25-min intervals (Altmann 1974).

Scan sample data ($n = 16\,141$ behaviour scans) were captured using Cybertracker v3.448 installed on a Mobicel TRENDY Android smartphone. Scan samples included all visible birds in the observed group. Data collected were the date, group identity, vegetation used

(camelthorn, blackthorn, driedoring, other plant species, open ground (away from the canopy of a tree or shrub)) and location (on or off the ground). Observations of nest attendance and foraging are not confounded because Southern Pied Babblers do not forage while arriving at, attending or leaving a nest. The observer also recorded location data every 15–25 min using a handheld Garmin eTrex 20× GPS. These locations were used to map Southern Pied Babbler territories at the study site.

The availability of nesting sites (camelthorn, blackthorn, other species) and foraging sites (camelthorn, blackthorn, driedoring, other species, open ground) within mapped territories was measured during a structured vegetation survey undertaken in October 2018 following the method described by Cunningham *et al*. (2015). Briefly, we estimated availability of each nesting and foraging site for each of 10 representative Southern Pied Babbler territories. The structured vegetation survey was undertaken over 10 consecutive days using a 30 × 30 m grid. At each grid point ($n = 1229$; mean = 122 ± 46 points per territory, range = 42–196), we recorded the presence or absence of plants and the name of the plant species where present. Data were captured by two observers using Cybertracker v3.448. One observer navigated to each grid point and placed the pole while the other identified the plant species and entered the data ($n = 5299$ observations). For non-surveyed territories included in this study ($n = 8$), the average was used.

Statistical analysis

Statistical analyses were conducted in R version 4.0.2 (R Core Team 2020). Unless otherwise indicated, summary statistics are presented as mean ± one standard deviation and statistical significance taken as $P < 0.05$. We used Ivlev's electivity index (Ei; Ivlev 1964, Strauss 1979, Cunningham *et al*. 2015) to estimate degree of preference or avoidance of different tree species by nesting Southern Pied Babblers. The index evaluates choice relative to availability in the environment in the following manner:

$$\mathrm{Ei} = (r_i - P_i) / (r_i + P_i)$$

where r_i = proportion of times a particular tree species was used for nesting and P_i = proportion of available trees of each species in the nesting Southern Pied Babbler group's territory. Ei values range from −1 to 1, with positive values indicating preference and negative values indicating avoidance.

We took the mean of individual Ei values for each tree species category per territory and used non-parametric one-sample Wilcoxon signed rank tests with continuity correction (V) to assess whether these means were significantly different from zero, indicating significant preference for or avoidance of the corresponding tree species. Other tree species made up 4% of the available trees in the landscape. However, because the characteristics of the less common tree species included in the 'Other' category vary considerably, other trees were not included in the analyses presented.

We used Ei as described above to estimate degree of preference or avoidance of particular foraging sites, with r_i = proportion of time a particular site was used for foraging in, and P_i = proportion of available foraging sites in that territory. One-sample t-tests were used to assess whether means differed significantly from zero. To investigate whether the probability of observing breeding Southern Pied Babblers foraging off the ground differed between early and late breeding season, we used a binomial generalized linear mixed model (GLMM) with

the proportion of observations in which foraging off the ground was recorded as the response and season (early vs. late) as the predictor, and included group identity as a random term to account for repeated measures of Southern Pied Babbler groups at the study site (Harrison *et al*. 2018).

RESULTS

Most rainfall (86.5%) between 2005 and 2020 occurred between December and March (Fig. 2), whereas Southern Pied Babblers initiate breeding predictably in September. On average, more nests were initiated in October, before substantial rain, than in any other month during the breeding season (Fig. 2). Winter rainfall at the study site is negligible, with June rainfall averaging 4 mm and July and August rainfall averaging 0.7 mm (data not shown). Rainfall never exceeded 12 mm in the 2 months leading up to the start of the breeding season and no rainfall at all was recorded in July, August or September in half of all years included in this study.

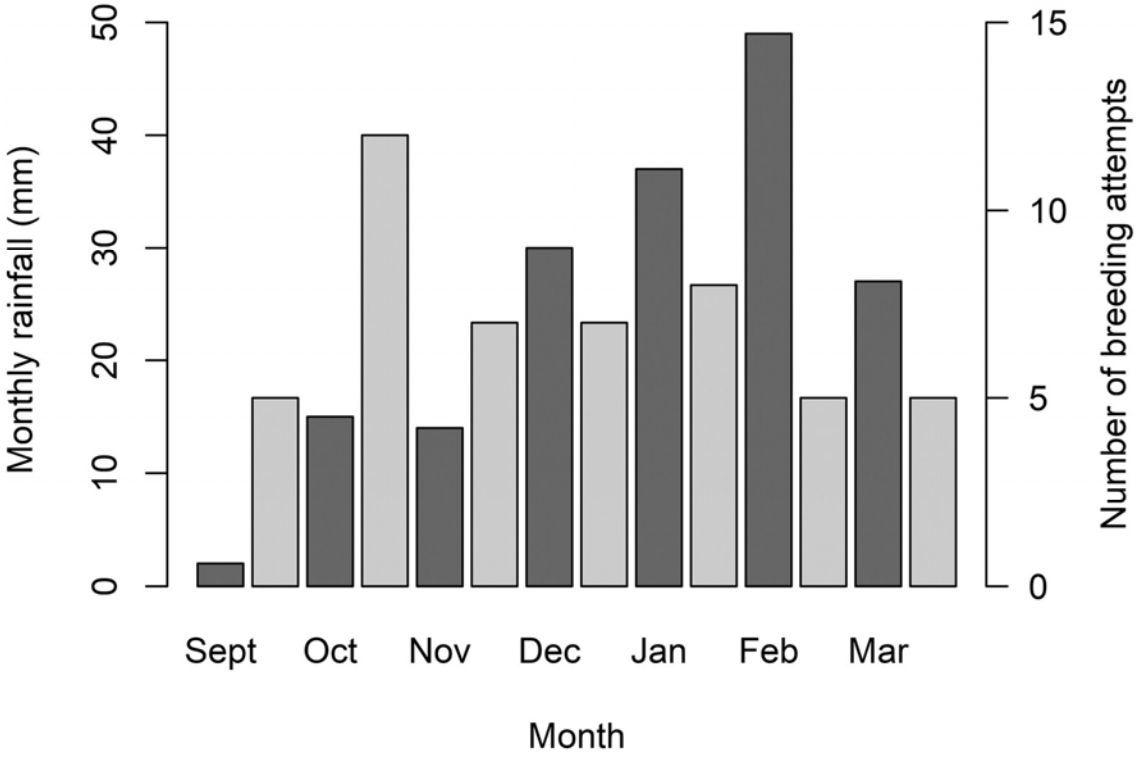

Figure 2. Most rain falls in the study area between December and March (dark grey bars), whereas Southern Pied Babblers initiate most nests in October each year (light grey bars).

Of the 58 nests characterized, 18 successfully fledged young. Fifty-one were constructed in camelthorn, six in blackthorn and one in buffalo thorn *Ziziphus mucronata*. Of the 18 fledged nests, 17 were constructed in camelthorn and one in buffalo thorn. Southern Pied Babblers preferred to build their nests in camelthorn trees (Fig. 3), selecting camelthorns 87.9% of the time, even though they only made up 65 ± 1.3% of available trees (Ei = 0.18 ± 0.14; $V = 163$, $P < 0.001$). Blackthorns, which make up 31% of available trees in the landscape, were avoided (Ei = −0.75 ± 0.51; $V = 7$, $P < 0.001$) and account for only 10% of nests. We only observed a single instance of Southern Pied Babblers nesting in one of the other species, a buffalo thorn.

More information on the remaining measured characteristics of Southern Pied Babbler nests, e.g. preferred branch heights, nest orientation and exposure to direct sunlight, is provided in the Supporting Information.

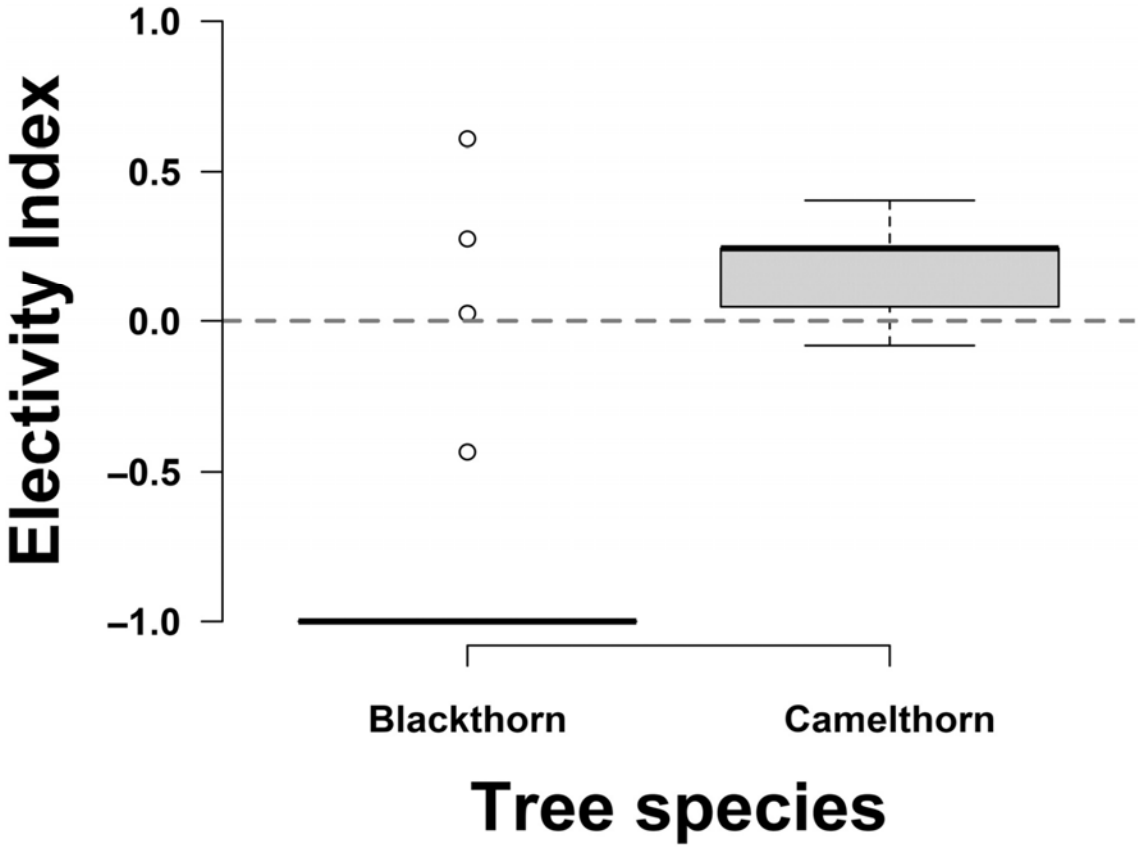

Figure 3. Southern Pied Babblers built nests in camelthorn trees more often than expected based on the availability of camelthorn trees in the landscape. Data were collected for 58 nests during one breeding season (September 2016 to March 2017).

Southern Pied Babblers foraged on the ground in 94.4 ± 0.1% of foraging observations (n = 7259 observations of foraging). Southern Pied Babblers were significantly more likely to be observed foraging off the ground, in tree canopies, earlier in the breeding season (between September and November) compared with later in the breeding season (Est = −1.269 ± 0.109, z = −11.67, P < 0.001). They were observed foraging off the ground in ~10% of observations early in the breeding season, compared with only ~3% of observations on average later in the breeding season (Fig. 4).

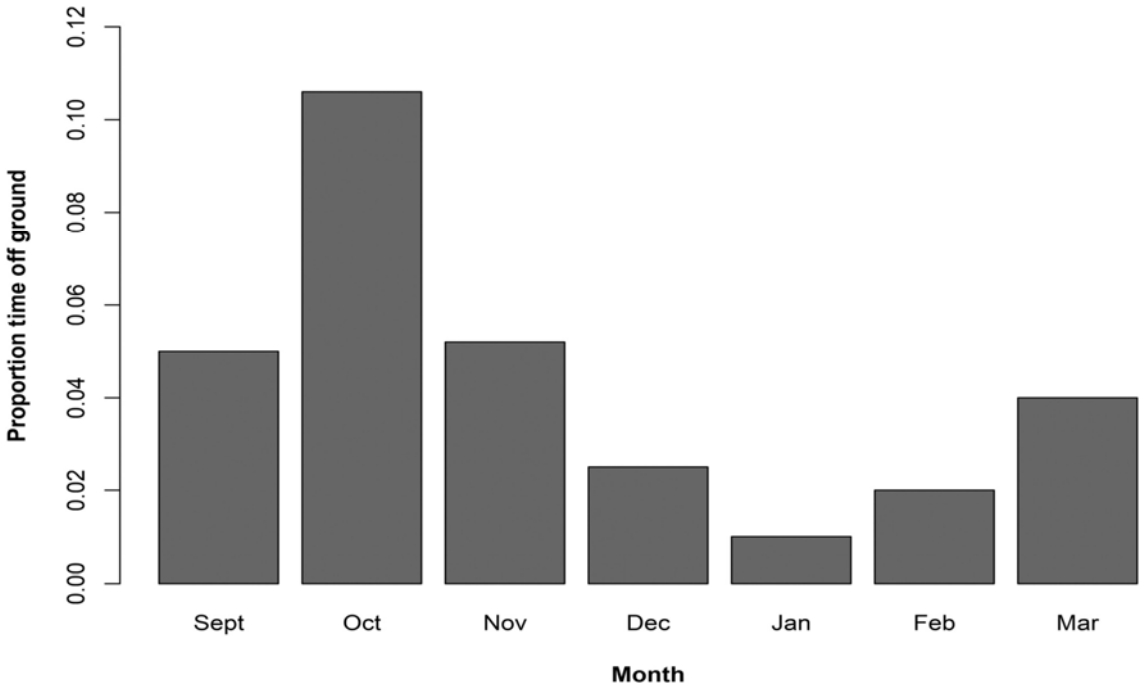

Figure 4. Southern Pied Babblers spend the highest proportion of time foraging off the ground during October, which is also when breeding is most commonly initiated and when breeding activity peaks (Fig. 2), compared with all other months within the breeding season.

Throughout the breeding season, Southern Pied Babblers avoided foraging in exposed open ground areas (Ei = −0.68 ± 0.17; $t = -12.9$, $P < 0.001$), used driedoring in keeping with its availability in the environment (Ei = 0.22 ± 0.59; $t = 1.12$, $P = 0.292$), and showed a clear preference for foraging in or under camelthorn (Ei = 0.24 ± 0.19; $t = 3.76$, $P = 0.004$) and blackthorn (Ei = 0.53 ± 0.24; $t = 6.74$, $P < 0.001$; Fig. 5). Camelthorns were used for 39% of foraging observations overall, blackthorns 28% and open ground areas 10%. The remaining 23% of foraging observations were recorded in a variety of other trees, shrubs and grasses. Southern Pied-Babblers showed a preference for foraging under both blackthorn and camelthorn (Fig. 5).The proportion of observations in which Southern Pied Babblers were observed foraging in or under camelthorn canopies was significantly higher early in the breeding season compared to later (Fig. 6; early = 48% of foraging observations, late = 30%; Est = −0.484 ± 0.046, $z = -10.41$, $P < 0.001$). On the other hand, we were more likely to observe Southern Pied Babblers foraging in blackthorn later in the breeding season (38% of observations) compared to earlier (15%; Fig. 6; Est = 0.822 ± 0.052, $z = 15.79$, $P < 0.001$). Additionally, Southern Pied Babblers were more likely to forage in camelthorn early in the season compared to blackthorn ($\chi_1^2 = 813.7$, $P < 0.001$) and more likely to forage in blackthorn compared to camelthorn later in the season ($\chi_1^2 = 89.7$, $P < 0.001$).

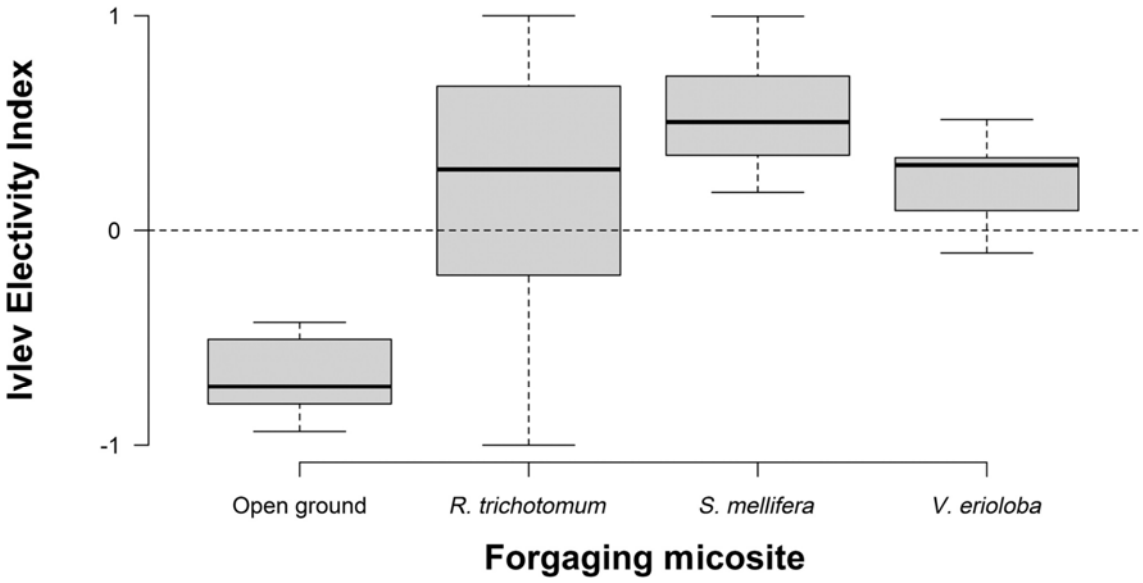

Figure 5. Southern Pied Babblers avoided foraging in open ground, used driedoring shrubs *Rhizogum trichotomum* in keeping with their availability in the environment, and preferentially foraged in blackthorn *Senegalia mellifera* and camelthorn *Vachellia erioloba*. Data were collected from 118 individuals across 15 different groups during observations conducted over 130 days between September 2016 and February 2019.

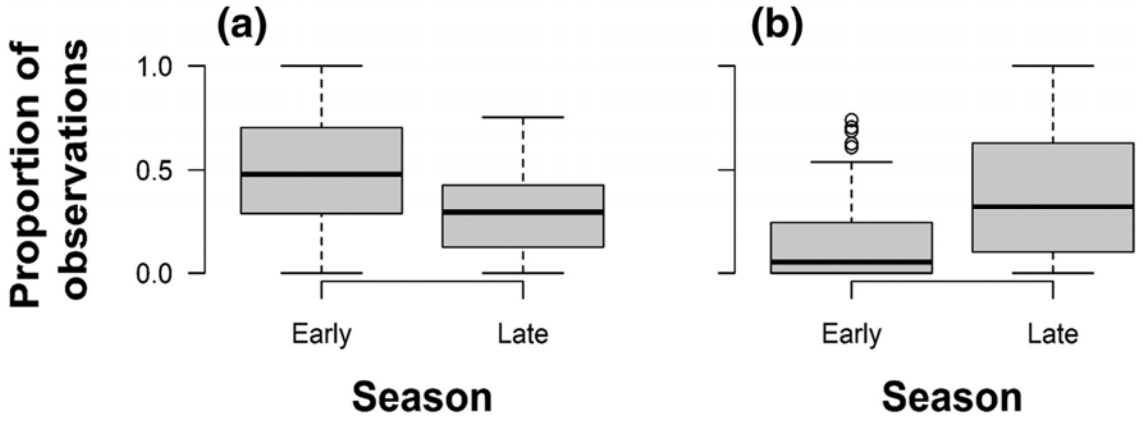

Figure 6. Proportion of foraging observations in (a) camelthorn trees *Vachellia erioloba* and (b) blackthorn trees *Senegalia mellifera* early and late in the breeding season. Southern Pied Babblers were more likely to be observed foraging in camelthorn trees earlier in the breeding season than later in the breeding season, whereas the reverse is true for blackthorn.

DISCUSSION

Our data confirm that the onset of breeding in Southern Pied Babblers does not occur in response to the onset of summer rainfall (Bourne *et al*. 2020a), as has often been assumed for this and other arid-zone bird species (Cumming & Bernard 1997, Dean *et al*. 2009, Cavalcanti *et al*. 2016, Ridley 2016, Wiley & Ridley 2016). Instead, Southern Pied Babblers initiate and reach peak breeding predictably in September and October each year, before the onset of the wettest part of the annual cycle between December and March (also see Bourne *et al*. 2020a). Although small amounts of early season rainfall are known to stimulate breeding in some arid-

zone birds (Lloyd 1999), Southern Pied Babblers in this study population initiated breeding before any rainfall at all, in half of the years included in this study. Whereas summer rainfall can extend the breeding season and result in Southern Pied Babbler groups producing multiple clutches during each breeding season (Ridley & Raihani 2008, Ridley 2016, Bourne *et al*. 2020a), the timing of the start of the breeding season and peak breeding appears to be independent of rainfall.

Behavioural observations of breeding individuals showed that Southern Pied Babblers preferentially use camelthorn trees for nesting, and camelthorn and blackthorn trees for foraging. We were more likely to observe the birds foraging off the ground and, specifically, in camelthorn canopies earlier (September and October, coinciding with the onset of breeding and peak Southern Pied Babbler nest initiation) compared with later in the breeding season (November onwards, coinciding with peak rainfall). Southern Pied Babblers are primarily a ground-foraging species. Our observation that 10% of foraging observations were recorded off the ground in camelthorn canopies early in the season, which is unusual behaviour for this species, therefore suggests that they make use of a very specific seasonal food resource during that time. We were more likely to observe the birds foraging under blackthorn trees later in the breeding season, indicating that both camelthorn and blackthorn trees are important, preferred foraging sites for Southern Pied Babblers at different times.

Nesting preferences are probably related to the architecture of the available trees in the landscape (Mainwaring *et al*. 2014) and foraging preferences are probably related to plant and invertebrate phenology and the food resources that different tree and shrub species support at different times (Hidalgo Aranzamendi *et al*. 2019, Gallinat *et al*. 2021). Both camelthorn and blackthorn fruit and flower towards the end of the cool, dry season (Milton 1987, Sekhwela & Yates 2007) and are likely to be important for food resources. However, taking our nesting and foraging observations together, we suggest that camelthorn trees are a crucial part of Southern Pied Babbler reproductive cycles. They are preferred for both nesting and foraging. The adjustment in foraging behaviour from ground foraging to foraging off the ground in camelthorn canopies for a short period of time overlapping with the onset of breeding in Southern Pied Babblers at the study site could indicate that the birds make use of a seasonal arboreal food resource associated with camelthorns to cue breeding.

The onset of breeding, breeding effort and breeding success in birds depends on the quantity and quality of available food (Drent & Daan 1980, Kotler *et al*. 1998, Chmura *et al*. 2018) and is often directly linked to rainfall (Hidalgo Aranzamendi *et al*. 2019). Rainfall is a particularly important driver of avian reproductive phenology in arid and semi-arid environments, where it activates several crucial biological processes (Noy-Meir 1973). As a result, various authors have demonstrated or assumed a strong predictive relationship between rainfall and the onset of breeding in arid-zone birds (Maclean 1969, Dean *et al*. 2009, Cavalcanti *et al*. 2016, Ridley 2016, Wiley & Ridley 2016).

However, the availability of good quality food resources is not always linked directly to rainfall. Birds in arid environments also respond to rainfall-independent resource pulses related to the effects of changes in photoperiod or temperature on plant phenology and invertebrate life cycles. For example, White-winged Doves *Zenaida asiatica mearnsii* arrive in the Sonoran Desert and initiate breeding to coincide with flowering of the Saguaro Cactus *Carnegiea gigantea* (Wolf & Martinez del Rio 2000), using it as a source of both water and nutrients (Wolf & Martinez del Rio 2000, Wolf *et al*. 2002). This keystone Sonoran Desert plant is resistant to drought and known for flowering and fruiting predictably during the hottest and

driest months of each year. In southern Africa, resident insectivores such as Sclater's Lark *Spizocorys sclateri* and Tractrac Chat *Emarginata tractrac* are also known to breed predictably in the early summer months, before substantial rainfall (Lloyd 1999).

In the other arid-zone bird species that breed before substantial rain, breeding is associated with food availability linked to local plant phenology (Lloyd 1999, Wolf & Martínez del Rio 2003). It seems likely that the onset of breeding in Southern Pied Babblers is also stimulated by a predictable annual pulse in food resources, in this case associated with the rainfall-independent phenology of at least one southern Kalahari tree or shrub. Given the early-season foraging behaviour we have observed, it is likely that this resource is associated with camelthorn trees. Irruptive herbivorous invertebrates feed on the new leaf growth, flowers and fruits produced by camelthorn trees during August and September (Steenkamp *et al*. 2008, Raath *et al*. 2017, Seymour & Joseph 2019) and provide a plentiful and reliable food source for breeding Kalahari animals, including the moth and butterfly larvae (e.g. *Gonometa postica*) Southern Pied Babblers favour for feeding young (Campbell *et al*. 2013, Ridley 2016). Although invertebrates, particularly aerial species, will be plentiful around camelthorn trees and in the habitat as a whole after rain (Noy-Meir 1973, Lowney & Thomson 2022), the herbivorous insects feeding on new camelthorn leaf growth are independent of rainfall. This is because established camelthorn trees have year-round access to ground water via deep tap roots (Canadell *et al*. 1996, Barnes *et al*. 1997, Krug 2017), enabling them to fruit and flower reliably in the spring, independent of rainfall.

Interestingly, we found that the proportion of foraging observations recorded alternated between the two tree species over the breeding season. Birds were more likely to be observed foraging in or under camelthorn trees early in the breeding season, whereas they were more likely to be observed foraging in or under blackthorn later in the breeding season. Blackthorns produce leaves later into the austral summer and can develop a second shoot generation after late rains (Skarpe & Bergström 1986). This may explain in part why foraging activity shifts to blackthorn later in the breeding season. Regardless of the mechanism involved, it is clear that both of these species are important forage resources for Southern Pied Babblers.

There is mounting evidence of recruitment and regeneration failure and population declines in long-lived arid-zone tree species (Read 1995, Liversidge 2001, Tolera *et al*. 2013, Ismail *et al*. 2014, Lindenmayer *et al*. 2014, Auld *et al*. 2015, McLellan *et al*. 2021), due to a range of threats including over-harvesting, climate change, over-extraction of groundwater, and poorly managed grazing by livestock and feral herbivores. Long-term monitoring of the size structure of camelthorns in the Kalahari, which can live up to 300 years and are sporadic recruiters (Schweiger *et al*. 2020), demonstrated poor survival of seedlings and an almost complete recruitment failure (no juvenile plants) as early as the 1990s (Van Rooyen *et al*. 1990, Steenkamp *et al*. 2008). It is also extremely slow-growing (Seymour *et al*. 2022). Given the important role that camelthorn plays in the ecology of many Kalahari animal communities (Eccard *et al*. 2006, Lowney & Thomson 2021), including Southern Pied Babblers, its status in the wild must be closely monitored. Camelthorns are a legally protected species in South Africa; however, the species continues to be commercially harvested for firewood and cleared for agriculture (Anderson & Anderson 2001, Powell 2005, Seymour 2008). While blackthorn trees are also a preferred foraging resource for Southern Pied Babblers, and a potentially important indicator of suitable available habitat for Southern Pied Babbler populations, blackthorn trees are common early successional plants and are not experiencing the same observed decline as camelthorn trees (Joubert *et al*. 2008, Oldeland *et al*. 2010).

CONCLUSION

Our results demonstrate that camelthorn and blackthorn trees are important resources for Southern Pied Babblers, in which they prefer to nest and forage. The effective conservation and management of the declining population of camelthorn trees, previously identified as a keystone species in the Kalahari region (Milton & Dean 1995, Seymour *et al*. 2022), will be an important part of the conservation and management of endemic Kalahari species such as the Southern Pied Babbler. Our behavioural observations also raise the possibility that reproduction in Southern Pied Babblers may be decoupled from rainfall via the phenology of deep-rooted tree species on which they rely for foraging and breeding sites, as has been observed in some other arid-zone bird species (Lloyd 1999, Wolf & Martínez del Rio 2003). Peak breeding initiation occurs early in the austral summer before substantial rainfall, or any rainfall at all in many years. The birds are more likely to be observed foraging in camelthorn canopies at this time than at any other time during the breeding season. The onset of breeding in Southern Pied Babblers is independent of rainfall and, because of their deep tap roots, the phenology of camelthorn trees is also independent of rainfall. A valuable next step for future research would be to test directly for the presence of an arboreal food resource associated with camelthorns at the time that Southern Pied Babblers initiate breeding.

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AUTHOR CONTRIBUTIONS

Kim Hunt: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Liamé Marais:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Susan Cunningham:** Conceptualization (equal); writing – review and editing (equal). **Amanda Ridley:** Conceptualization (equal); data curation (equal); writing – review and editing (equal). **Lesedi Moagi:** Data curation (equal); investigation (equal); writing – review and editing (equal). **Sanjo Rose:** Data curation (supporting); methodology (supporting); writing – review and editing (equal). **Andrew McKechnie:** Conceptualization (supporting); writing – review and editing (supporting). **Amanda Bourne:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (lead).

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

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ETHICAL NOTE

All data were collected under animal ethics permit numbers R2012/2006/V15/AR and 2016/V6/SC from the University of Cape Town and 1216/2016 from the Department of Environment and Nature Conservation. Birds were banded by licensed professionals and bird ringing licences were issued by SAFRing (11663).

Data Availability Statement

The data underlying all analyses presented in this study are archived at the University of Cape Town's open access institutional data repository, ZivaHub (a figshare platform), where they are publicly available (DOI: https://doi.org/10.25375/uct.20444610).

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