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Orientation, thermal characteristics and structural dimensions of Mangrove Kingfisher *Halcyon senegaloides* nest cavities in arboreal termitaria in central Mozambique

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The breeding ecology of the Mangrove Kingfisher *Halcyon senegaloides* (family Alcedinidae) remains poorly known. While the few nests recorded in southern and East Africa have been in tree hollows, a seasonal population in central Mozambique woodland breeds in cavities in arboreal termitaria. Despite this breeding strategy being widely recorded in many tropical kingfisher species, it has received little research attention in the Afrotropical realm. We report on the siting and structural characteristics of arboreal termitaria used as nesting sites by Mangrove Kingfishers in central Mozambique and document the thermal dynamics of a nesting cavity in an arboreal termitarium. Arboreal termitaria (average volume 40.1 ± 23.8 l) occurred at a density of 0.52 ± 0.22 termitaria ha^{-1} in large trees or shrubs, mostly of the families Fabaceae and Malvaceae. Termitaria containing nest cavities were situated 10.8 ± 3.1 m above the ground, and most nests (78.6%) faced north. Nest cavity temperatures averaged 31.4 ± 2.6 °C, which is warmer and more stable than the average ambient temperatures of 28.7 ± 4.0 °C. 'Carton' termitaria (comprising a mixture of faecal matter and wood fragments) are thus believed to confer a thermal advantage for summer-nesting Mangrove Kingfishers.

Orientation, caractéristiques thermiques et dimensions structurelles des nids du Martin-chasseur des mangroves *Halcyon senegaloides* dans des termitières arboricoles au centre du Mozambique

L'écologie de la reproduction du Martin-chasseur des mangroves *Halcyon senegaloides* (Alcedinidae) reste mal connue. Alors que les quelques nids observés en Afrique australe et de l'Est se trouvaient dans des creux d'arbres, une population saisonnière du centre du Mozambique se reproduit dans des cavités de termitières arboricoles. Bien que cette stratégie de reproduction ait été largement observée chez de nombreuses espèces tropicales de martin-pêcheurs/chasseurs, elle n'a fait l'objet que de peu de recherches dans les régions Afrotropicales. Nous rapportons l'emplacement et les caractéristiques structurelles des termitières arboricoles utilisées comme sites de nidification par les Martins-chasseurs des mangroves dans le centre du Mozambique et documentons la thermodynamique d'une cavité de nidification dans un termitière. Les termitières arboricoles (volume moyen 40.1 ± 23.8 l) étaient présentes à une densité de 0.52 ± 0.22 termitières ha^{-1} dans de grands arbres ou arbustes, principalement des familles Malvaceae et Fabaceae. Les termitières contenant les cavités des nids étaient situées à 10.8 ± 3.1 m au-dessus du sol et la plupart des nids (78.6 %) étaient orientés vers le nord. La température moyenne des cavités des nids était de 31.4 ± 2.6 °C, soit une température plus chaude et plus stable que la température ambiante moyenne de 28.7 ± 4.0 °C. Ces résultats suggèrent que ces termitières 'cartonnées' (construites avec un mélange de fragments de bois et matières fécales) confèrent un avantage thermique aux martins-chasseurs des mangroves qui nichent en été.

Keywords: Alcedinidae, breeding ecology, nest dimensions, nest temperatures

Introduction

The use of arboreal termitaria as nesting sites is widespread in tropical kingfishers (family Alcedinidae) and has been recorded in at least six genera and more than 40 species globally (Hindwood 1959; Fry et al. 1992). This strategy is rare in Africa, however, with only three kingfisher species recorded nesting in termitaria in Central and West Africa, and only the Mangrove Kingfisher *Halcyon senegaloides* recorded doing so in the southern African subregion (Brosset and Erard 1986; Fry et al. 1988, 1992; Clancey 1992; Davies et al. 2012). Although widely recorded, few studies have specifically investigated the use of arboreal termitaria as nesting sites for birds (Brightsmith

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2000, 2004; Kesler and Haig 2005a, 2005b; Sanchez-Martinez and Renton 2009; Davies et al. 2012).

The Mangrove Kingfisher has an extensive but patchy coastal distribution from southern Somalia to the Eastern Cape Province of South Africa (Fry et al. 1988, 1992; Turpie 2005). In central Mozambique the species ranges farther inland, extending at least 120 km inland along the Savé Valley (Allan et al. 2000) and approximately 150 km inland to the Inhamitanga–Caia region (Davies et al. 2012). The breeding biology of Mangrove Kingfishers remains poorly known, with fewer than 10 breeding records reported from South Africa, all of which are from the Eastern Cape province where this species was recorded to breed in holes in trees along large rivers inland of the coast (Boon 2000). Few data are available for East Africa, where it also appears to be primarily a tree-hole nester (Pakenham 1943; Fry et al. 1988). In central Mozambique, Mangrove Kingfishers were long suspected to breed in arboreal termitaria (Clancey 1971, 1992, 1996; Turpie 2005), as later confirmed (Davies et al. 2012).

The breeding biology of Mangrove Kingfishers was investigated in central Mozambique, and aspects of the basic natural history were subsequently reported (Davies et al. 2012). This article addresses the orientation, structural characteristics and thermal properties of the unusual nest sites used by this species in central Mozambique. We thus present an under-reported, and likely wider phenomenon, of birds using termitaria for nesting in the Afrotopics.

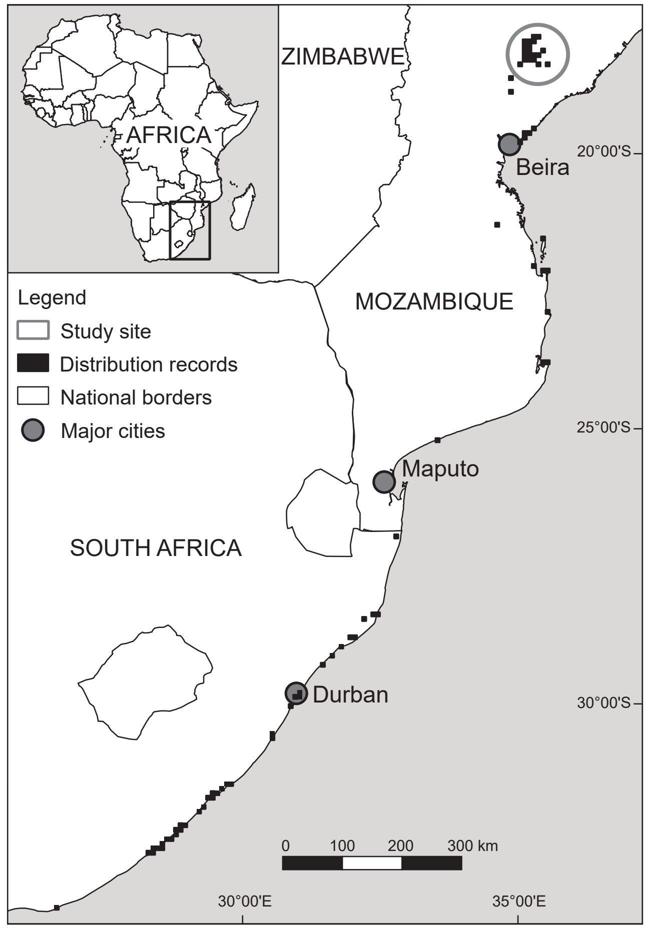

Figure 1: Pentad-resolution (5' × 5') distribution of Mangrove Kingfishers *Halcyon senegaloides* in southern Africa based on the Southern African Bird Atlas Project 2 (SABAP2) full protocol data from 2007–2018. The circle indicates the study site

Methods

Study site

Breeding site data were gathered in the Catapú Concession (17°55′–18°06′ S, 34°55′–35°5′ E; 100–200 m asl), Sofala Province, central Mozambique (Figure 1), during 2–21 December 2010, coinciding with the breeding season of Mangrove Kingfishers (Berruti 1997; authors pers. obs). Catapú is a 24 821-ha logging concession ~30 km south of the Zambezi River in the Inhamitanga-Caia region. The vegetation forms part of the *Flora Zambesiaca* area, and more specifically falls within the Swahili–Maputaland regional transition zone (Coates Palgrave et al. 2007). The habitat is a mosaic of dry deciduous lowland forests, deciduous thickets and open woodland, all on sandy soils (Coates Palgrave et al. 2007). Most rain falls in the austral summer, and ranges between 700–1 400 mm per annum (Coates Palgrave et al. 2007).

Nest site availability and characteristics

Three transects (of 7.40, 6.04 and 0.67 km) were walked along dirt tracks, and all arboreal termitaria belonging to *Nasutitermes* (Isoptera: Termitidae: Nasutitermitinae; Davies et al. 2012) either side of the transect were recorded. Each transect was walked only once, with the transect distance governed by the length of the dirt track that passed through suitable habitat. We recorded the perpendicular distance (m) between the transect and the observed termitarium, whereafter we approached the tree containing the termitarium to record the height of the termitarium (meters above ground level), height of the tree (determined using a forester's sextant), circumference at breast height (CBH, cm) of the main stem (or if multiple stems, the three largest stems), and aspect of the termitarium. We recorded the hierarchical limb number on which the termitarium was located, with main stems being assigned a value of '1', branches occurring after the first fork as '2', and so forth. Diameter at breast height was calculated using the formula CBH/π. We estimated the height, width and depth of each termitarium (using the average estimate of each measure across the three authors), and physically measured these dimensions whenever we could access the termitarium (including through the use of a ladder or climbing ropes). The volume of each termitarium was subsequently calculated using the formula for determining the volume of an ellipsoid (Lubin et al. 1977; Brightsmith 2000; Kesler and Haig 2005a; Sanchez-Martinez and Renton 2009). Termitaria were deemed to have a potentially suitable nest cavity if there was a visible cavity in the termitarium of the approximate size as those observed being used by Mangrove Kingfishers at the study site, and provided that such cavity did not show signs of decay (suggestive of an old, abandoned cavity and likely a dead or dying termite colony: Hindwood 1959). A note was also made

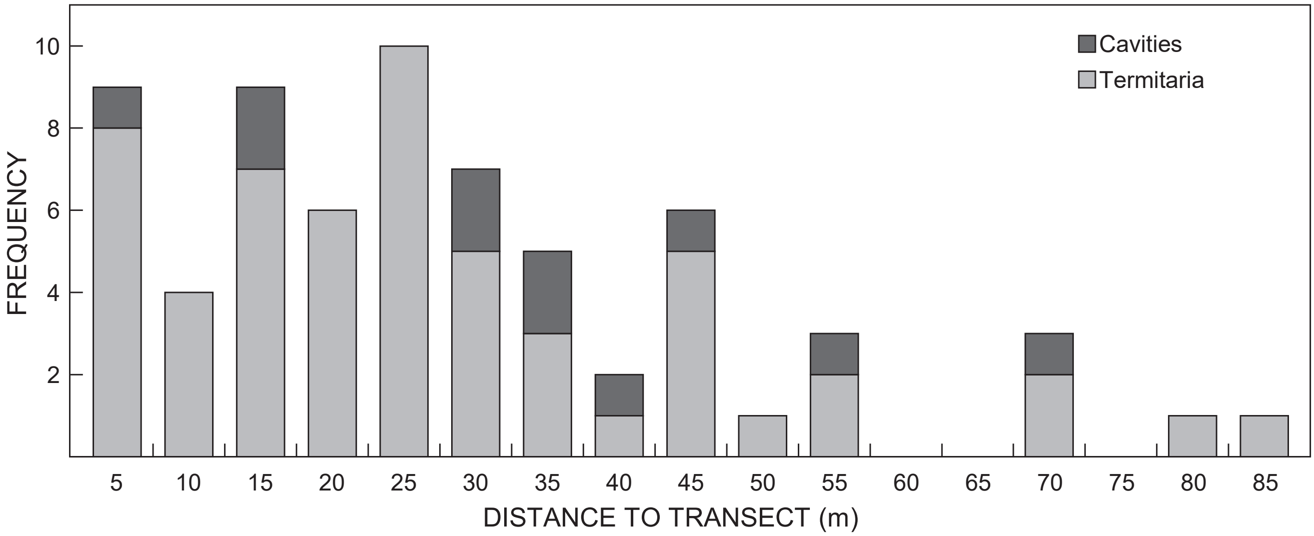

Figure 2: Perpendicular distance between the transect and observed arboreal termitaria as well as termitaria containing potentially suitable nesting cavities at Catapú logging concession, Caia, central Mozambique. Perpendicular distances were pooled into 5-m intervals, with the *x*-axis label indicating the maximum value of each interval

of Mangrove Kingfishers seen or heard in the immediate proximity (within ~30 m) of the potential nest cavity.

Termitaria and nest site densities

Arboreal termitaria and nest site densities were determined using the software package Distance version 7.3 release 1 (Thomas et al. 2010), with each transect treated as an individual layer. Perpendicular distance data were pooled into 17 intervals of 5 m each, extending to the maximum distance at which we detected an arboreal termitarium (82 m). The data were fitted with seven detection functions and adjustments (half-normal with no adjustment; half-normal with cosines; half-normal with simple polynomials; hazard rate with no adjustment; hazard rate with simple polynomials; hazard rate with hermite polynomials; and hazard rate with cosines) to assess the most appropriate detection model. The best model was selected on the basis of having the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2002). We excluded the terminal 5% of distances from the analyses to account for reduced detection probabilities at large distances (Thomas et al. 2010).

Thermal environment of nest cavities in termitaria

We deployed two Thermochron iButtons® (Dallas Semiconductors, Dallas, Texas) to record ambient temperature and the temperature within a single potential nest cavity in an arboreal termitarium. One iButton® was placed inside the cavity, while a second was attached to the tree immediately beneath the termitarium, with both loggers programmed to record temperatures at 10-min intervals for a period of 19 days.

Statistical analyses

Mann–Whitney *U*-tests were performed to evaluate whether there were differences in the median volume between termitaria containing nesting cavities and those lacking nesting cavities, while a paired two-tailed *t*-test was used to compare average hourly temperatures inside the nest to the corresponding ambient temperatures. All metrics are presented as mean ± standard deviation with the range in parentheses, unless stated otherwise. Statistical analyses were performed using the package *dplyr* (Wickham et al. 2023) implemented in R 4.0.2 (R Core Team 2020) through the RStudio interface (RStudio Team 2020), with $\alpha < 0.05$ considered to be statistically significant.

Results

Nest site availability

We located 59 arboreal termitaria along the three transects, 15 (25.4%) of which had potentially suitable nesting cavities. Mangrove Kingfishers were seen and/or heard calling in the immediate vicinity (≤30 m) of 13 (86.7%) of the termitaria that contained potentially suitable nesting cavities, while two nests were confirmed to be active by an adult bird seen entering one cavity and eggs being visible in a second cavity. The perpendicular distance between the transect and the observed termitaria ranged from 1 to 82 m, with the frequency at which termitaria were observed being negatively correlated with their distance from the transect (Figure 2). Termitaria containing potentially suitable nest cavities were infrequent and showed a relatively equal distribution across the transect width (Figure 2).

Nest densities

The half-normal detection function without any adjustments and with strict monotonicity constraints enforced had the lowest AIC value overall as well as when analysing just those termitaria containing nesting holes and was used to analyse the data. Arboreal termitaria occurred at a density of 0.52 ± 0.22 (95% confidence interval [CI]: 0.12–2.34) termitaria ha^{-1}. Arboreal termitaria with potentially suitable nesting cavities had an overall density of 0.07 ± 0.04 (95% CI: 0.02–0.30) termitaria ha^{-1}.

Nest site characteristics

Trees containing arboreal termitaria averaged 19.0 ± 5.7 (10–35) m in height and had a diameter at breast height of 60.2 ± 24.2 (29.3–161.1) cm. Termitaria were typically positioned at a height of 9.7 ± 3.0 (4–18) m on branches, with a hierarchical value of 3.5 ± 1.6 (1–8). Arboreal termitaria overall had an average volume of 30.1 ± 17.7 (5.2–94.3) l. The 15 termitaria that contained potentially suitable nest cavities had an average volume of 40.1 ± 23.8 (7.7–94.3) l and were situated 10.8 ± 3.1 (6–17) m above the ground. Termitaria containing potential nesting cavities were significantly larger than those not containing cavities (W = 213, $p < 0.05$), although there was no statistical difference between the heights of termitaria containing cavities and those that did not have visible cavities (W = 248.5, p = 0.13). The majority of arboreal termitaria had a north-easterly or south-westerly orientation (Figure 3), while most potential Mangrove Kingfisher nests had a northerly orientation (NW: n = 6; NE: n = 5; SE: n = 2; SW: n = 1). Five of the arboreal termitaria containing potential nests were in *Sterculia appendiculata* (Malvaceae), two were in *Albizia* sp. (Fabaceae), one each were in a *Senegalia nigrescens* (=*Acacia nigrescens*; Fabaceae) and a *Millettia stuhlmannii* (Fabaceae), while the tree species for the remaining cavity-containing nests were not determined.

Thermal characteristics

We recorded 2 693 temperature readings from each of the iButtons® placed inside and outside the potential nest cavity. Temperatures within the nest cavity (31.4 ± 2.6 °C, range 26.7–38.5 °C) were higher than ambient temperatures (28.7 ± 4.0 °C, range 22.9–40.0 °C) and displayed lower amplitudes (11.8°C for inside versus 17.1 °C for outside the nest cavity). Temperatures at both locations showed a cyclical diel pattern, with ambient temperatures peaking between 13:00 and 15:00, and cavity temperatures peaking between 17:00 and 18:00. Nest cavity temperatures remained higher than the ambient temperatures throughout the late afternoon, night and early morning (16:00–08:00) (Figure 4). Hourly temperatures inside the nest cavity were significantly different from the ambient temperatures ($p < 0.01$, t = 5.44, df = 23).

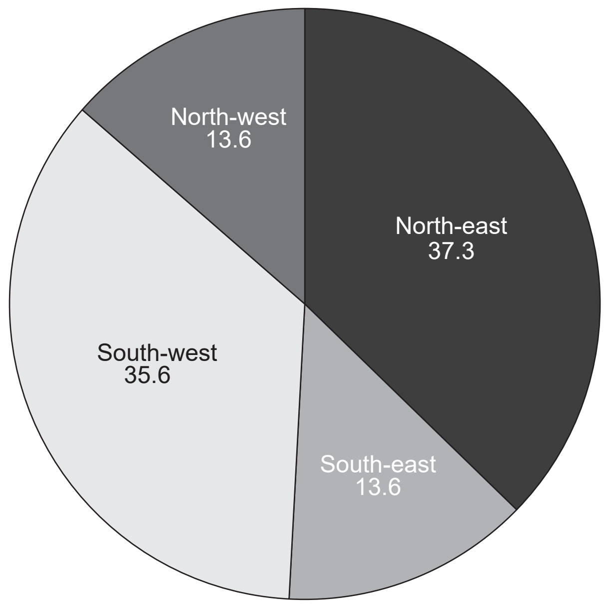

Figure 3: Proportional (%) orientation of the arboreal termitaria recorded at Catapú logging concession, Caia, central Mozambique

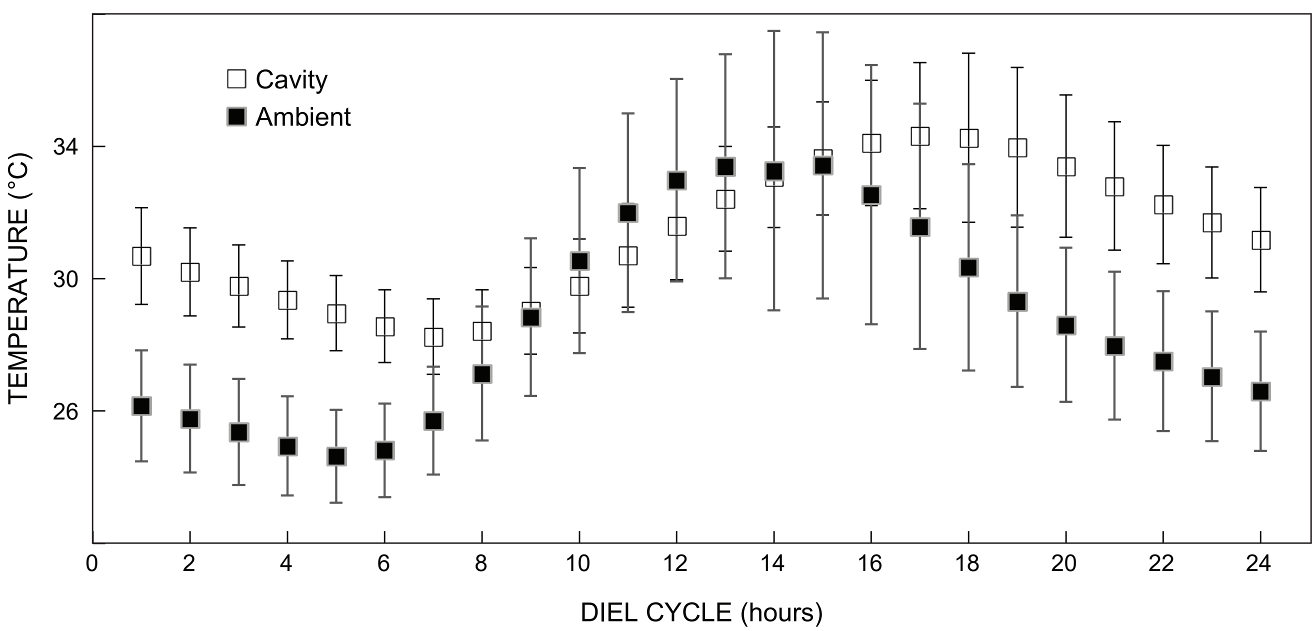

Figure 4: Hourly temperature variations within a nest cavity in an arboreal termitarium and ambient temperatures measured at the base of the same termitarium, measured at 10-min intervals during 2–21 December 2010 at Catapú logging concession, Caia, central Mozambique. Data are presented as mean ± 1 standard deviation

Discussion

We provide the first data on the siting, thermal characteristics and structural dimensions of Mangrove Kingfisher nests in arboreal carton termitaria in central Mozambique. Our findings indicate that Mangrove Kingfishers choose to nest in larger termitaria, but there was no significant difference between the heights of excavated and non-excavated termitaria. These results partially reflect those of studies in Australia and South America, where termitaria with active bird nests were situated higher and had a larger volume than those that did not contain active nests (Brightsmith 2000; Kesler and Haig 2005a; Sanchez-Martinez and Renton 2009). Larger termitaria are likely preferred as nesting sites as they provide sufficient space for the nesting chamber, are likely to be more stable (Hindwood 1959), and may confer a greater thermal advantage. The height of the excavated termitaria at our study site was likely limited by the height at which termitaria occur at the study site, with the height of excavated termitaria spanning nearly the entire height range of observed termitaria.

The volume of the termitaria used for nesting by Mangrove Kingfishers in this study was comparable to those used by Orange-fronted Parakeets *Eupsittula canicularis* in Mexico (14.9–140.9 l: Sanchez-Martinez and Renton 2009), but substantially smaller than those used by Tui Parakeets *Brotogeris sanctithomae*, Cobalt-winged Parakeets *B. cyanoptera* and Black-tailed Trogons *Trogon melanurus* in the Amazon (67–142 l: Brightsmith 2000, 2004), yet larger than termitaria used by Pohnpei Kingfishers *Todiramphus reichenbachii* (27.6–29.8 l) on Pohnpei Island, Micronesia (Kesler and Haig 2005a). These differences are likely partly driven by differences in average body mass, with the parakeets and trogons averaging 63–75 g and 90 g, respectively (Brightsmith 2000; Sanchez-Martinez and Renton 2009), Micronesian Kingfishers averaging 58 g (Kesler and Haig 2004) and Mangrove Kingfishers averaging 85 g (Turpie 2005). These differences may also reflect the sizes of the available termitaria at each study site.

The heights at which we recorded Mangrove Kingfishers nesting was similar to the mean heights at which parakeets and trogons were reported to nest in the Amazon (10.1 m: Brightsmith 2000), but was greater than the heights at which other termitarium-nesting Amazonian bird species nest (6.5–8.0 m: Brightsmith 2004) as well as the height at which Micronesian Kingfishers (4.3 m; Kesler and Haig 2005a) and Orange-fronted Parakeets (6.1 m: Sanchez-Martinez and Renton 2009) nest. These differences may be driven by the size and height of the available termitaria at each site, the sizes of the respective bird species, as well as the average foraging height and behaviour of the different species (Brightsmith 2000).

The densities of arboreal termitaria in our study (0.52 ± 0.22 termitaria ha^{-1}) was substantially lower than the average density of 15.8 ± 4.2 termitaria ha^{-1} recorded in the Amazon (Brightsmith 2000) and the 4.4 termitaria ha^{-1} recorded in Mexico (Sanchez-Martinez and Renton 2009). This low density of arboreal termitaria, and their being largely restricted to a relatively small geographical area, may explain why comparatively few southern African bird species have been recorded nesting in arboreal termitaria relative to birds in South and Central America and Australia (Hindwood 1959; Brightsmith 2000; Sanchez-Martinez and Renton 2009). Nest site availability appears not to be a limiting resource for these arboreal termitarium-nesting species (Brightsmith 2000; Kesler and Haig 2005a; Sanchez-Martinez and Renton 2009; this study), although the proximity of suitable cavities to each other may result in intraspecific competition, which could preclude the use of some apparently suitable nesting sites (Renton 2004; Sanchez-Martinez and Renton 2009). Mangrove Kingfishers actively harass and chase potential competitors within their home ranges, with this behaviour being more pronounced closer to nesting sites (Turpie 2005).

Our data suggest that Mangrove Kingfishers will preferentially nest in north-facing termitaria, although our sample size is too small to statistically investigate this possibility. The average temperatures within the potential nest cavity that we measured were less variable than the ambient temperatures, and peaked later in the day compared with the ambient temperatures. The temperatures that we recorded within the nest cavity are within the 33–37 °C range of incubation temperatures for many bird species (Drent 1975). Nesting sites in arboreal termitaria are believed to aid incubation in other avian taxa by maintaining a high relative humidity, a cooler temperature at midday and a higher average temperature at night (Noirot 1970; Wiebe 2001; Kesler and Haig 2005b; Ardia et al. 2006), thus decreasing the amount of energy required to be invested in incubation by the parents (Sanchez-Martinez and Renton 2009). We also recorded lower midday temperatures and higher nocturnal temperatures in the cavity that we studied, suggesting that termitaria in central Mozambique likely confer a similar thermal advantage on cavity-nesting bird species by providing an environment in which temperatures for developing eggs is moderated.

In addition to proffering a thermal advantage, termitarium nests likely also offer safety from predators (much as a tree-hole nest would), while being comparatively easier to bore into (Hindwood 1959). The shape and position of the termitarium on the tree probably renders it inaccessible to most mammalian predators, as well as some reptiles (cf. Hindwood 1959), while the termites themselves may also act as an additional deterrent to any would-be predators (Hindwood 1959). Termitarium nests may additionally stave off competition for tree cavity sites from aggressive sympatric hole-nesting species, such as the Broad-billed Roller *Eurystomus glaucurus* and woodpeckers.

It remains to be determined whether Mangrove Kingfishers excavate their own nests in the arboreal termitaria or whether they are secondary cavity nesters. The summer-nesting Green-backed Woodpecker *Campethera cailliautii* has been recorded nesting in arboreal termitaria (Short and Horne 1988; Davies and Boon 1999; Davies et al. 2012) as has the Black-backed Barbet *Pogonornis minor* (Short and Horne 1988), with those species presumably having excavated the cavities themselves. Green-backed Woodpeckers occur sympatrically with Mangrove Kingfishers on the Catapú Concession, with the former species having been observed investigating a cavity in an arboreal termitarium in this region (Davies et al. 2012). Several primary cavity nesters have been recorded from the Catapú Concession (Parker 2005; authors unpublished data) and it is possible that one or more of these species excavate cavities in the arboreal termitaria which are subsequently utilised by Mangrove Kingfishers. However, given the soft carton texture of these arboreal termitaria (Davies et al. 2012), it is equally plausible that Mangrove Kingfishers are weak cavity excavators in this region, and this possibility should be investigated further. In Australia, some kingfisher species excavate nests in arboreal *Nasutitermes* termitaria by repeatedly flying at the termitarium from a short distance to break its hard outer shell, whereafter they excavate a nesting chamber (Hindwood 1959).

Various aspects relating to the unique use of arboreal termitaria for breeding by Mangrove Kingfishers remain to be investigated. Indeed, the full suite of species that utilise arboreal termitaria as nesting sites in central Mozambique, and the related level of interspecific competition, merit investigation.

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Data availability — The datasets analysed during the current study are available from the corresponding author on reasonable request.

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