At home with the birds: Kalahari tree skinks associate with sociable weaver nests despite African pygmy falcon presence

Running head: Skinks associate with weaver nests

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Abstract

The way in which animals use habitat can affect their access to key resources or how they are buffered from environmental variables such as the extreme temperatures of deserts. One strategy of animals is to modify the environment or to take advantage of structures constructed by other species. The sociable weaver bird (*Philetairus socius*) constructs enormous colonial nests in trees. These nests are frequented by Kalahari tree skinks (*Trachylepis spilogaster*) and the two species coexist over a large portion of the Kalahari Desert in South Africa. We tested whether lizards were more abundant in trees containing sociable weaver nests and asked whether the physical features of trees were important predictors of skink abundance. We then focused on potential costs of this association by examining the relationship between skink abundance and the presence of a potential predator, the pygmy falcon (*Polihierax semitorquatus*), which exclusively **uses** weaver nest colonies for roosting and nesting. Finally, we simulated a predatory threat to determine if skinks assess risk differently if a weaver nest is present. We found a significant positive association between the presence of weaver nests and skink abundance. In the absence of nests, the type of tree did not influence skink abundance. Skinks used weaver nests and were more likely to perch on the nest than the tree. When threatened with predation, skinks preferred to take refuge in nests. Surprisingly, the presence of nesting pygmy falcons in nests did not influence skink abundance, perhaps because of the abundance of nearby refuges within nests, tree crevices, or in debris at the tree base. We suggest that sociable weaver nests provide multiple benefits to skinks including lowered predation risk, thermal refuges and greater prey availability, although this requires experimental testing. In the current era of global climate change, sociable weaver nests may become a crucial resource for lizards seeking refuge as the Kalahari climate warms.

Keywords: Arid environments, Ecosystem engineer, Flight initiation distance, Interspecies associations, Predation risk

Introduction

An animal’s habitat exerts selection pressure for traits conferring a fitness advantage in that particular environment (Schluter 2000). However, animals have the capacity to choose specific habitat types and this is influenced by the availability of essential resources (Thompson *et al.* 2001), protection from predators (e.g. availability of refuges, Caley & St John 1996) and the physical structure of the environment (Ward & Lubin 1993). Furthermore, inappropriate selection of specific habitats may have severe fitness and survival consequences (Schlaepfer *et al*. 2002). Harsh, ‘stressful’ environments, such as deserts, may exacerbate the potential negative consequences of selecting sub-optimal habitat, due to the interaction between an animal’s behaviour and its physiology (Sapolsky 2004).

In the case of heliothermic animals (i.e. animals that bask to raise their temperature) living in deserts, the thermoregulatory priority is to minimise overheating (Corbalán *et al*. 2013) by reducing exposure to conditions of high thermal stress (Cowles & Bogert 1944; Huey 1982). To ameliorate thermal constraints, many lizards seek refuge in vegetation clumps, which not only reduces thermal stress, but may also afford protection from predators. Therefore, the distribution and type of vegetation may influence local lizard abundance (Steffen & Anderson 2006) and diversity (Pianka 1966). For example, in North American flatland deserts, lizard species diversity is correlated with vegetation incorporating both horizontal (plant volume diversity) and vertical (percentage cover and standing crop) components (Pianka 1966). In the case of arboreal lizards, particular physical characteristics, such as tree circumference and canopy cover (Cooper & Whiting 2000a; Reaney & Whiting 2003), may also influence habitat selection.

In extreme environments, ‘ecosystem engineers’ may provide additional crucial habitat for animals through modification of the environment (Crain & Bertness 2006). Many ecosystem engineers live in colonies (e.g. black-tailed prairie dogs *Cynomys ludovicianus*) in which physical structures made from sand/mud or vegetation (e.g. burrows) gradually increase in dimension as social group size increases (Whicker & Detling 1988). These prominent structures are frequently more thermally stable than external air temperatures and potentially offer both foraging opportunities and refuge from predators (Kinlaw & Grasmueck 2012), for the builders themselves, as well as commensal organisms. Empirical studies in plant and intertidal animal communities suggest that in stressful environments, the probability of positive interactions or positive associations between species should increase (Bruno *et al*. 2003; Maestre *et al*. 2009). Documenting the associations between these ecosystem engineers and other species is important for understanding how communities persist in these environments.

A potential ecosystem engineer is the sociable weaver (*Philetairus socius*), a Kalahari Desert endemic bird of southern Africa. Sociable weavers build massive thatched nest colonies in trees and these nests are prominent physical structures throughout much of the Kalahari (Fig. 1). While colony size is variable, over 300 individual birds can reside in a single nest, in which individual nest chambers are embedded (van Dijk *et al.* 2013). These nests effectively buffer external environmental temperatures (Bartholomew *et al.* 1976; Broadley 2000) and reduce temperature variability within individual nest chambers (van Dijk *et al.* 2013). Anecdotal evidence suggests that sociable weaver nests may form an important resource to animals of several taxa, including reptiles. For example, striped skinks (*Trachylepis sparsa*) appear to be associated with weaver nests (Maclean 1973). However, few studies have tested for associations of animals with these nests.

Fig. 1 Sociable weaver *Philetairus socius* nest in the Tswalu Kalahari, South Africa.

Here, we investigated if there is an association of the Kalahari tree skink (*Trachylepis spilogaster*) with sociable weaver nests. Skinks are often found in trees with sociable weaver nests and are also frequently observed basking on weaver nests, but whether these nests represent a crucial habitat is not known. Kalahari tree skinks are arboreal lygosomine scincids occurring in the xeric regions of southern Africa (Broadley 2000). Brain (1969) suggested that they primarily forage on the ground but retreat into trees when disturbed. Skinks primarily feed on beetles, ants and termites (Huey & Pianka 1977a), all of which occur on the ground and in trees, suggesting that foraging opportunities may also be present in trees.

Several bird species also use sociable weaver nests (Maclean 1973), the most noteworthy being the African pygmy falcon (*Polihierax semitorquatus*). It is an obligate user of sociable weaver nests (Maclean 1973), with a distribution range within the range of sociable weavers in southern Africa. Pygmy falcons breed and roost exclusively in the physical nest chambers of sociable weaver nests, occupying these chambers throughout the year simultaneously with the weavers (Maclean 1973). However, this close association between falcons and weavers may have implications for small reptiles in this system. Small lizards (in general) comprise the second most important food item of a pygmy falcon’s diet (Maclean 1970) and Kalahari tree skink remains have been found in and below pygmy falcon nests (R. Thomson unpublished data). Therefore, while associating with sociable weaver nests may provide benefits related to basking, foraging and refuges for skinks, this relationship could also entail significant costs for skinks.

The life history and behavioural decisions (basking, foraging and escape) of small lizards are significantly influenced by predation risk (Williamson *et al.* 1989; Cooper 2000; Lima & Dill 1990). How long an individual remains exposed to a predation threat while engaged in other behaviours is influenced by the availability of, and nearest distance to, refuges (Cooper 1997). Escape decisions are a trade-off between the actual threat of predation (impacted by refuge availability) and the energetic cost of escaping (Ydenberg & Dill 1986; Cooper 1997). These decisions can be measured in terms of flight initiation distance (FID), which is the distance at which an animal starts fleeing from a potential predator (Bonenfant & Kramer 1996). To trade-off the fitness costs of lost foraging opportunities or actual predation with the benefit of future survival, individuals should adjust their behaviour to maintain a margin of safety and to minimize exposure (Carrascal *et al.* 1992; Cooper 2000).

Here, we first tested if Kalahari tree skinks occur at higher abundance on trees with sociable weaver colonies and then determined what tree features best explain skink abundance. We then examined the role of predation risk on habitat selection by first asking whether skinks differed in their flight initiation distance depending on the presence of sociable weaver nests. Finally, we investigated whether the presence of breeding pygmy falcons at sociable weaver colonies altered the association of skinks with sociable weaver colonies.

Methods

Study site

Our study site was situated in the sandy plains of Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (27º13"30' S and 22º28' 40' E, altitude 1020–1586 masl). The vegetation is patchily distributed and sparse Shrubby Kalahari Dune Bushveld dominated by the pioneer Kalahari sourgrass (*Schmidtia kalihariensis*). The two dominant tree forms are camel thorn (*Vachellia erioloba*) and shepherd’s tree (*Boscia albitrunca*).

Kalahari tree skinks bask on both tree types (T. Rymer, pers. obs). We sampled skink abundance during May 2002 and December 2012. Abundance is expected to be lower during autumn when reproduction is limited by food resources, as seen in other lygosomine scincids (e.g. striped skinks; Patterson 1991), although perceived abundance may be higher, as skinks potentially bask more frequently for thermoregulation (Huey & Pianka 1977b). Therefore, we analysed the data from each season separately. Sociable weaver nests are near-permanent structures (often decades old, e.g. Spottiswoode 2007, Covas *et al*. 2008) and skinks were observed basking on nests in both seasons (T. Rymer and R. Thomson, pers. obs.) As skinks are preyed on by multiple species (e.g. Cape cobras *Naja nivea*, Maclean 1973) throughout the year, and not just pygmy falcons, we expected predator avoidance behaviour to be consistent between seasons. Furthermore, pygmy falcons show strong site fidelity, with most breeding and then roosting in the same weaver colonies throughout the year (across 2011-2012 seasons: 79% of pygmy falcons remained in the same colony; across 2012-2013 seasons: 76% remained in the same weaver colony; R. Thomson, unpubl. data).

Skink abundance, tree characteristics and weaver nests

In May 2002, we selected 20 trees within each of three categories: 1) camel thorn without sociable weaver nest (CNA); 2.) shepherd's tree without nest (SNA); and 3) camel thorn with nest (CNP). Within the study site a fourth category, shepherd's trees with sociable weaver nests (SNP), were less common and therefore this category was not included in skink counts.

For each of the 20 trees in each of the three categories, we counted the number of individual Kalahari tree skinks. Sampling lasted for approximately 30 minutes/tree and was performed twice per day (08h00 – 16h00) for a total of nine recording days, with a minimum of two hours between observations. Once a tree had been sampled (twice on a day), it was not sampled again. Counting of skinks was conducted from five different positions around the colony tree spending five minutes at each position. The observer started at one position about 15–20 m from the colony tree. After five minutes of active scanning from this position, the observer moved approximately 90 degrees around the tree and again settled for a five minute scan/count. This was continued for a full rotation of the tree. Short breaks of one minute were taken between scans to ensure the observer was rested. For the final five minutes, the observer slowly approached the tree and walked slowly around the base of the tree. These five minutes were useful to clarify any uncertainties about whether some skinks were the same individuals, as not all individuals were visible from all positions. The substrate on which the skinks were seen was also recorded and placed into one of three categories: 1) debris/ground near tree base; 2) tree trunk or branches; and 3) on sociable weaver nest (if present). From the two counts performed at each tree, we used the largest number of skinks observed between both sampling sessions as the estimate of total abundance.

Skink abundance was always highest in the later sampling session. Therefore, we used air temperature (ºC) from the second skink survey only. This allowed us to control for the effect of temperature on sampled skink numbers (Cooper & Whiting 2000a). Temperature was measured 1 m vertically from the tree base, in the shade.

We measured tree structure (height, circumference, maximum canopy length and perpendicular width) from each of the 60 trees sampled for skinks a few days after the skink counts. Tree height was visually estimated and trees were placed into one of three categories: 1) < 2 m; 2) 2-4 m; and 3) > 4 m. We measured circumference using a standard tape measure 1 m from the tree base, or at the base of the first fork if the tree was shorter than 2 m. The maximum canopy length and perpendicular width (both in cm) were measured standing directly beneath the tree, using the tape measure. Canopy cover was determined using the equation: canopy cover = $(\pi r^2)/2$, where r = (maximum length + perpendicular width)/2 (Witkowski *et al*. 1994).

Skink abundance: pygmy falcon presence at weaver nests

In December 2012, we mapped 219 sociable weaver colonies in camel thorn and shepherd’s trees and assessed them for pygmy falcon activity. We determined the size of each sociable weaver nest (in terms of number of chambers) and tree height was measured to the nearest metre using a human about 2 m high as a reference standing at the tree base. Pygmy falcon presence was confirmed at 28 sociable weaver colonies. Thirteen colonies were excluded due to early nest failures and/or logistical issues. For each of the remaining 15 sociable weaver colonies with pygmy falcon nests (all in camel thorn trees), and for 15 matched sociable weaver colonies without pygmy falcon nests (control), we counted the number of individual Kalahari tree skinks. Nest trees were matched by tree species, tree height and the size of the sociable weaver colony as closely as possible. In addition, control trees were selected in close proximity to the matched tree with a pygmy falcon nest in order to account for spatial effects on skink numbers. The distance between paired colonies was (mean ± SE) 720 ± 177 m (range 65–2200 m).

Skink counts were performed for a total of eight recording days in a similar manner to that described above. Counts occurred throughout the day (08h00 – 16h00). A single 30 minute counting period was conducted for each tree. Counts for the matched sociable weaver trees with and without pygmy falcons were conducted on the same day and directly after each other to match air temperature as much as possible. For each matched pair, the tree counted first (either with or without falcons) was alternated to avoid systematic bias in the time of day.

To control for the effect of temperature on sampled skink numbers (Cooper & Whiting 2000a), we placed a temperature data-logger (Tinytag Plus2) in the shade near the base of a neighbouring tree prior to counts at a colony. The logger recorded temperature (˚C) at one minute intervals, but we only used the temperature recorded at the mid-point of the observation period.

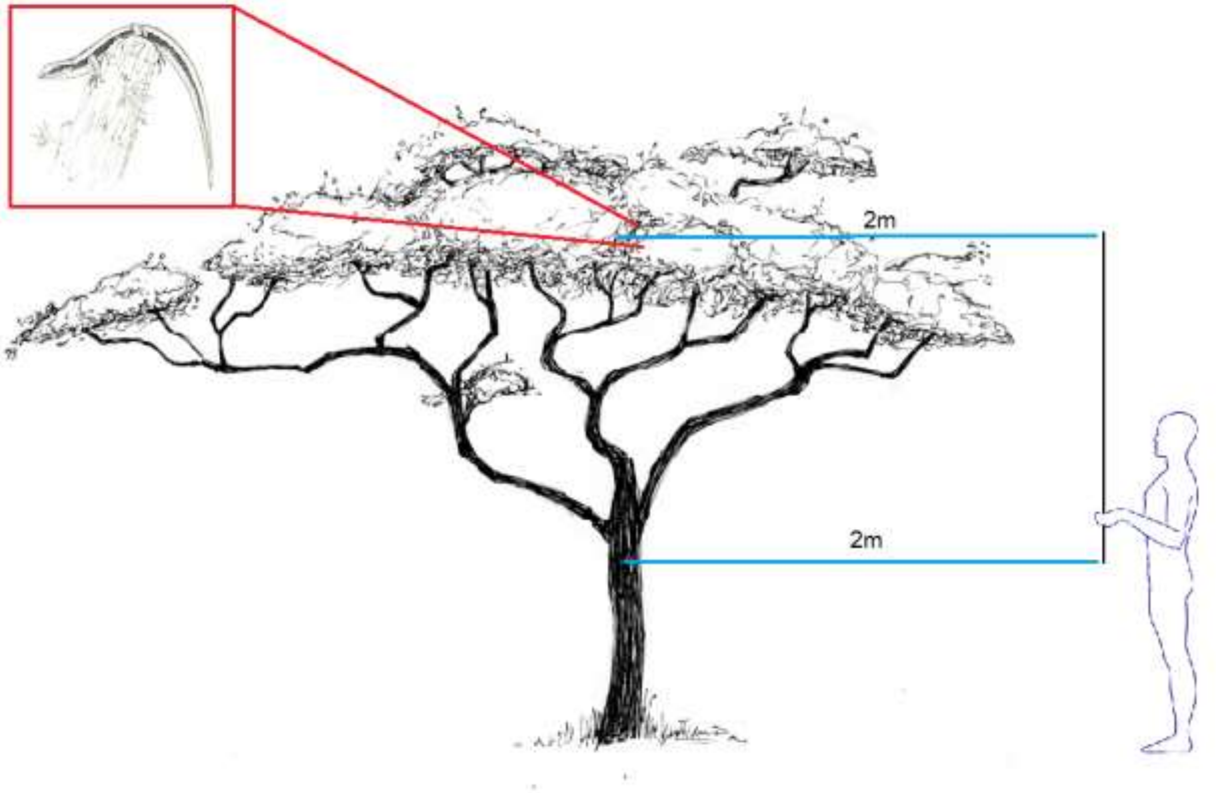
Our sampling design ensured that there were no systematic differences of the potentially confounding variables between colony trees with and without falcons. Tree height (mean ± SE: without falcons 7.1 m ± 0.4; with falcons 7.0 m ± 0.4; one-way ANOVA: df = 1, F = 0.01, p =

0.92), weaver nest size (mean ± SE: without falcons 85.8 chambers ± 11.5; with falcons 73.1 chambers ± 9.1; df = 1, F = 0.27, p = 0.61) and environmental temperature during counts (mean ± SE: without falcons 30.8 ± 0.9 ˚C; with falcons 30.8 ± 0.9 ˚C; df = 1, F = 0.001, p = 0.98) did not differ significantly between nest trees with and without falcons.

Skink escape behaviour

We measured antipredator escape behaviour of skinks during May 2002. A single measurement of flight initiation distance (FID) of a single individual was performed at each of 65 trees. These trees were selected from each of the four category types: 1) CNA (n = 21); 2) SNA (n = 20); 3) CNP (n = 19); and 4) SNP (n= 5). As shepherd's trees with sociable weaver nests (SNP) were rare at the study site, comparison with the other tree categories should be treated cautiously.

We measured FID in the following way. The observer stood 10 m from the tree base (skinks do not react to human observers at this distance; T. Rymer, pers. obs) and randomly located a focal skink using binoculars. We noted the substrate an individual was located on as: 1) debris/ground near tree base; 2) tree trunk or branches; and 3) on sociable weaver nest (if present). The observer then walked at a steady pace (approximately 1.5m/s) toward the tree from the starting position, holding a 3 m collapsible fishing rod vertically upright (Supplementary online material; Fig. A). A marker was dropped on the ground when the



Supplementary online material; Fig. A Measuring anti-predator behaviour using a fishing rod as a vertical extension of the body (see text for details).

skink started to retreat and the observer recorded the distance from the marker to the tree base (cm), or to a point directly below the skink on the ground, as a measure of FID using a standard tape measure. The fishing rod acted as a vertical extension of the body and was necessary because some lizards were less likely to initiate escape without the extra ‘height’ because they were in trees. For example, if the distance measured from the marker to the tree base was 2 m, the assumption was that the closest part of the rod was 2 m from the skink when it decided to flee (Supplementary online material; Fig. A). As the skink began to retreat, we recorded the time taken to reach a refuge (n=60; 92.3% of cases) or until the skink stopped moving (n=5; 7.7%) and we recorded the retreat location as either 1) exposed (if the skink did not run into a refuge); 2) in sociable weaver nest (if present); 3) in a crevice in the tree; or 4) other (e.g. retreating down the tree to a crevice/debris on the ground). We attempted to use only adults. However, in some cases the only individuals visible on trees were juveniles (n=14; 21.2%).

Statistical Analyses

Skink abundance: tree characteristics and weaver nests

Analyses were performed using Statistica 7.1 (Stat-soft Inc, www.statsoft.com). We used a generalised linear model (GLZ) with Poisson distribution and log link function to determine if the total number of skinks (dependent variable) differed by tree category (categorical predictors: CNA, SNA, CNP) and was influenced by particular tree characteristics (continuous predictors: height, circumference, canopy cover). Air temperature was also included as a continuous predictor.

We used chi-square tests to determine whether a) skink number on a particular substrate (tree trunk and branches, debris/ground near tree base) was influenced by tree type (only those trees without nests; CNA and SNA); and b) skink number varied with substrate type regardless of tree type. Thereafter, we used a chi-square test to determine whether skink number varied between substrates on camel thorn trees with nests only.

Skink abundance: pygmy falcon presence at weaver nests

To test if a pygmy falcon nest in a sociable weaver nest had a positive or negative effect on skink numbers, we modelled the number of skinks counted with a GLZ (Proc Genmod in SAS), using a Poisson distribution and log link function. Presence or absence of a falcon nest was entered as a categorical fixed factor and was the main variable of interest. Tree height, sociable weaver nest size (number of chambers) and environmental temperature were entered as continuous predictors. The explanatory variables were entered singly and in combination to test if these predictors could explain variation in skink numbers.

To test if the substrate on which skinks were found differed between nests with and without falcons, we conducted chi-square tests for skink numbers found on each substrate (trunk/branch, debris/ground, weaver nest).

Skink escape behaviour

Analyses were performed using Statistica 7.1 (Stat-soft Inc, www.statsoft.com). Flight initiation distance was normally distributed (Shapiro-Wilks test: W = 0.97, p = 0.12). Therefore, we used a general linear model (GLM) multiple regression to assess flight initiation distance in relation to air temperature, tree type, tree characteristics (circumference, height, canopy cover), initial substrate location and lizard age class (adult and juvenile). Time taken to reach a refuge was not normally distributed (Shapiro-Wilks test: W = 0.83, p < **0.001**), even after transformation (square-root, arcsine and square-root arcsine), therefore we used a GLZ multiple regression model with Poisson distribution and log link function to determine if time taken to reach a refuge was influenced by air temperature, tree type, the various tree characteristics, initial substrate location and lizard age class. We used chi-square tests to determine how many skinks (preference) used a particular escape refuge (retreat location) after the predation risk assessment. We analysed retreat location data (exposed; in sociable weaver nest (if present); in a crevice in the tree) for trees without nests (CNA, SNA) and trees with nests (CNP, SNP) separately. The model level of significance was $\alpha = 0.05$ for all analyses.

Results

Skink abundance: tree characteristics and weaver nests

We observed a total of 127 skinks during the 2002 counts (means ± SE: camel thorn trees with nests (CNP) 3.9 ± 0.54; camel thorn trees without nests (CNA) 1.4 ± 0.21; shepherd's trees without nests (SNA) 1.1 ± 0.22). Tree category was the only significant predictor of the total number of skinks ($\chi^2_2 = 21.89$, $p < 0.001$). Skink abundance on CNP trees was 2.9 times higher than skink abundance on CNA trees (CNA) and 3.7 times higher than skink abundance on SNA trees (SNA; Fig. 2). Skink number was unaffected by tree height ($\chi^2_1 = 0.13$, $p = 0.72$),

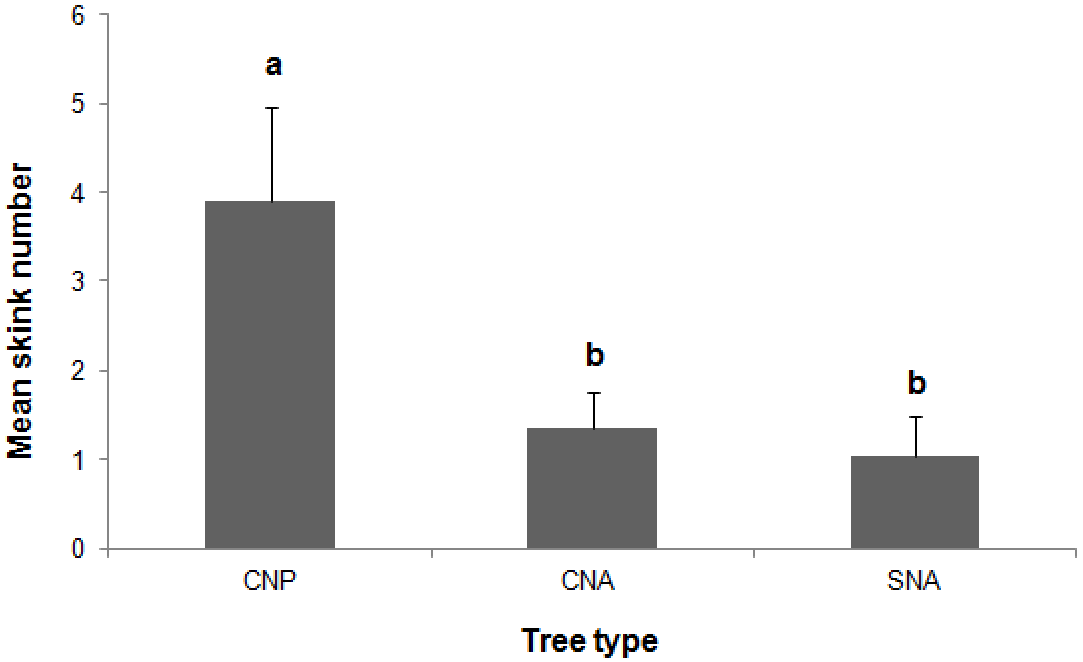


Fig. 2 Mean + 95% confidence interval of skink number on each of three tree types. CNP = camel thorn trees with sociable weaver nests, CNA= camel thorn trees without sociable weaver nests, SNA = shepherd's trees without sociable weaver nests. *Post hoc* comparisons were assessed using beta estimates and predicted means plots (not presented) and bars with different letters indicate significant differences.

circumference ($\chi^2_1 = 0.72$, $p = 0.40$), temperature ($\chi^2_1 = 1.18$, $p = 0.28$) or canopy cover ($\chi^2_1 = 0.40$, $p = 0.53$).

Tree type, in the absence of weaver nests (camel thorn and shepherd's tree), was not a significant predictor of whether skinks were counted on debris/ground near the tree base ($\chi^2_1 = 0.07$, $p = 0.97$) or trees/branches ($\chi^2_1 = 0.57$, $p = 0.68$). When trees without nests were grouped, skinks were 2.2 times more common (total count 33 vs. 15) on tree/branches than on debris/ground near the tree base ($\chi^2_1 = 6.75$; $p = 0.03$). When we compared lizard locations on camel thorn trees with sociable weaver nests present, we found that significantly more skinks were observed on sociable weaver nests than on other substrate types ($\chi^2_2 = 31.00$, $p < 0.001$ Fig. 3).

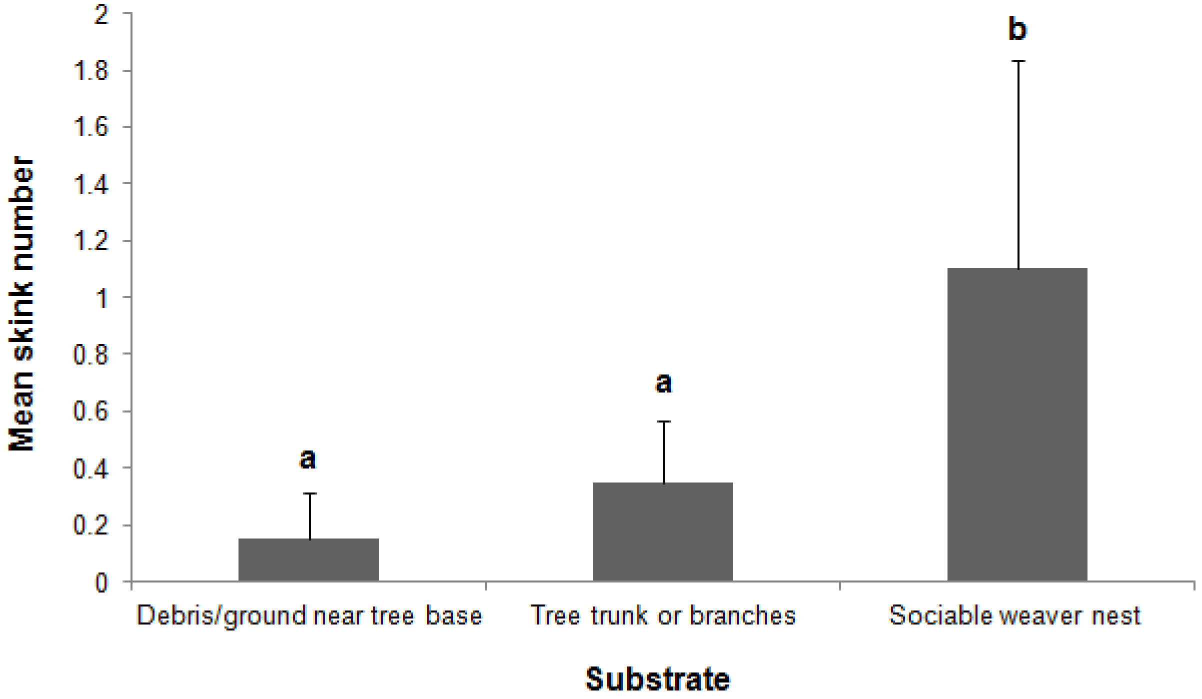


Fig. 3 Mean + 95% confidence interval of skink number observed on three different substrates on camel thorn trees with sociable weaver nests. *Post hoc* comparisons were assessed using beta estimates and predicted means plots (not presented) and bars with different letters indicate significant differences.

Skink abundance: pygmy falcon presence at weaver nests

We observed 45 skinks during the 2012 counts (mean ± SE: with falcons 1.7 ± 0.13; without falcons 1.3 ± 0.35). During our sampling periods, all nests with breeding falcons contained skinks, while three nests without falcons lacked skinks. However, skink numbers were not significantly explained by the presence or absence of pygmy falcons at the sociable weaver nest ($\chi^2_1 = 0.55$, $p = 0.46$, LS means: with falcons = 0.51 [0.12 – 0.90] vs. without falcons = 0.29 [-0.15 – 0.73]). When entered singly into the model with main treatment of falcon presence/absence, none of tree height ($\chi^2_1 = 0.18$, $p = 0.67$), the size of the sociable weaver nest ($\chi^2_1 = 0.94$, $p = 0.33$) or environmental temperature ($\chi^2_1 = 0.01$, $p = 0.93$) explained skink numbers (no significant effects were apparent when multiple terms were entered either). Falcon presence at a nest also did not alter the substrates on which skinks were observed ($\chi^2_2 = 0.6$, $p = 0.74$).

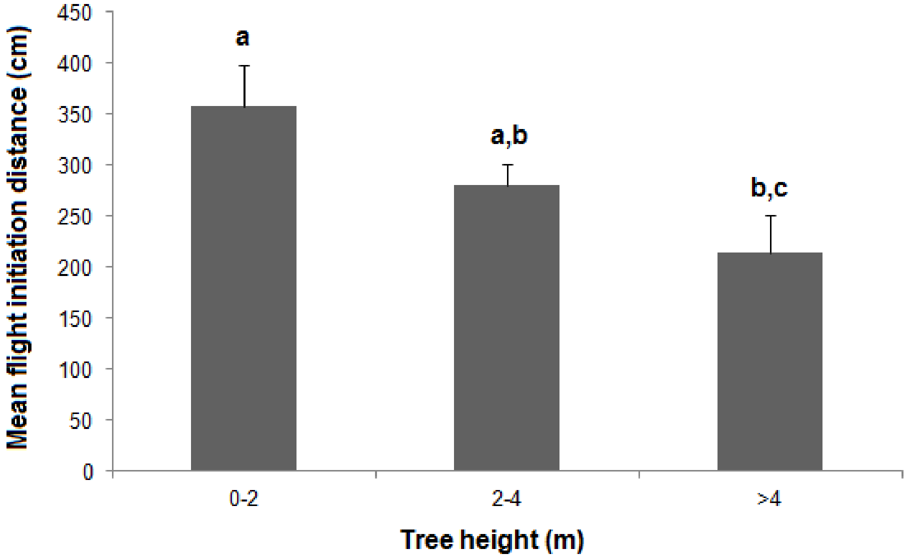


Fig. 4 Mean + 95% confidence interval of flight initiation distance (cm) for lizards on all tree types combined in relation to tree height (m). *Post hoc* comparisons were assessed using beta estimates and predicted means plots (not presented) and bars with different letters indicate significant differences.

Skink escape behaviour

The only variable that influenced flight initiation distance was tree height ($F_{1,57}$ = 4.81, p = 0.03). Skinks initiated flight sooner on small trees (0-2 m) than on large trees (> 4 m; Fig. 4). Skinks on medium-sized trees showed an intermediate response (Fig. 4). Fight initiation distance was unaffected by temperature ($F_{1,57}$ = 0.39, p = 0.56), tree type ($F_{1,57}$ = 3.08, p = 0.08), circumference ($F_{1,57}$ = 1.01, p = 0.32), age ($F_{1,57}$ = 0.00, p = 0.97), canopy cover ($F_{1,57}$ = 0.81, p = 0.37) or initial substrate location ($F_{1,57}$ = 0.81, p = 0.37). Tree type was the only variable influencing the time taken to reach a refuge (χ^2_1 = 3.92, p = 0.05), with skinks on shepherd's trees with nests (SNP) retreating to a refuge significantly faster than skinks on other tree types (Fig. 5). Time taken to reach a refuge was not influenced by temperature (χ^2_1 = 1.24, p = 0.26),

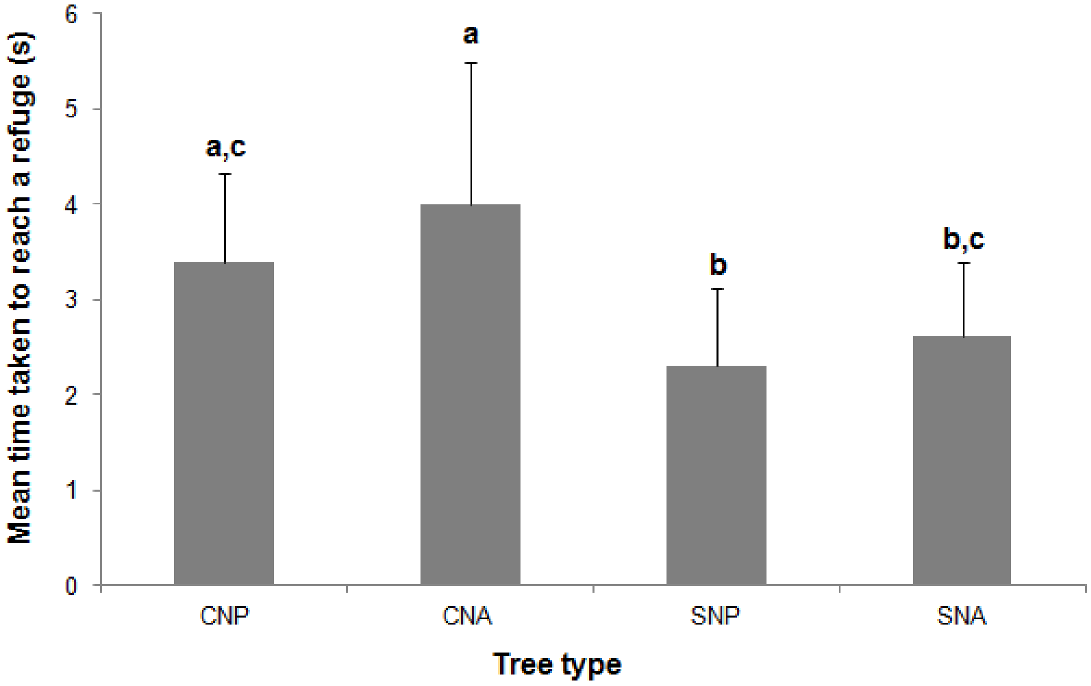


Fig. 5 Mean + 95% confidence interval of time taken to reach a refuge (s) for lizards on all tree types. *Post hoc* comparisons were assessed using beta estimates and predicted means plots (not presented) and bars with different letters indicate significant differences.

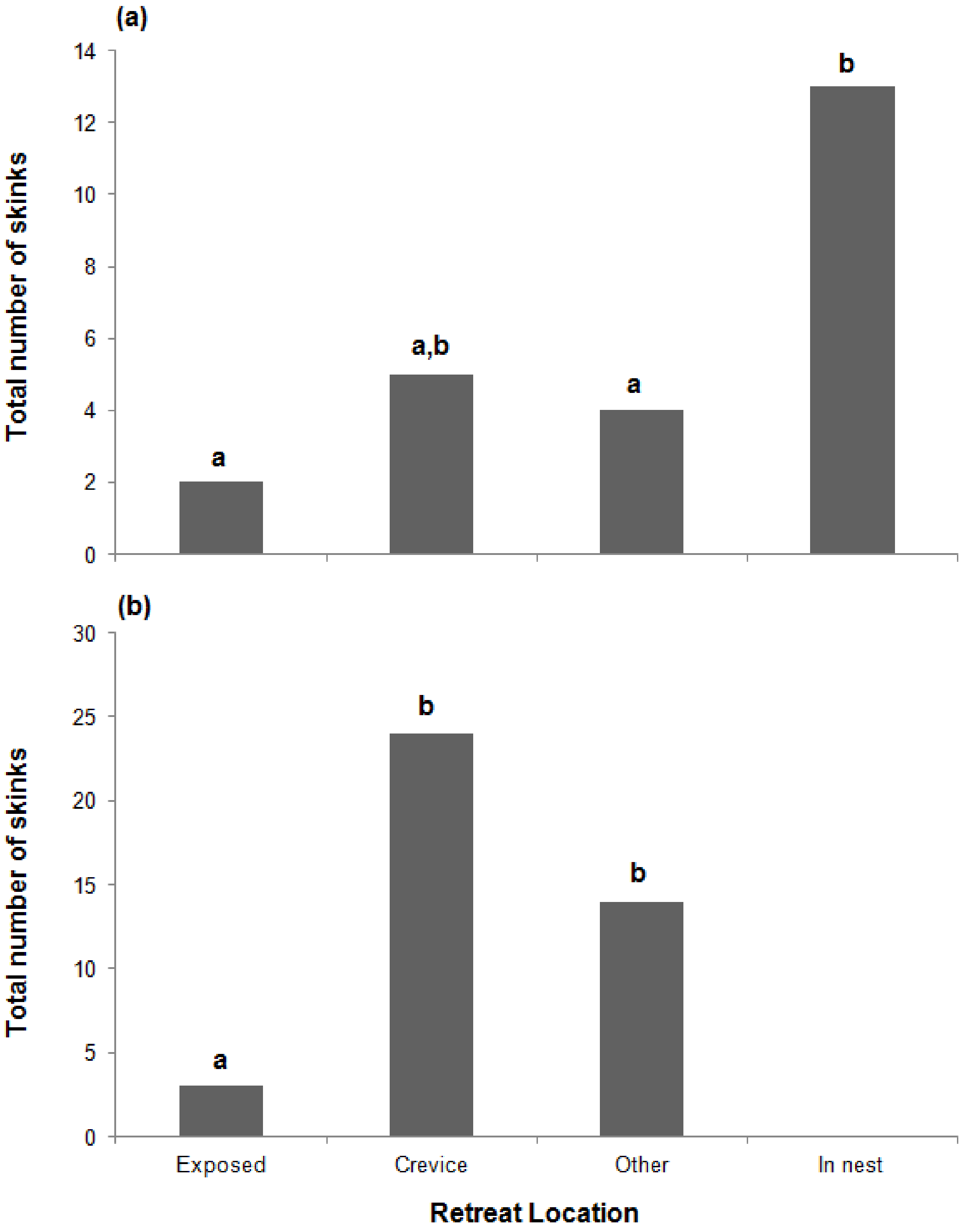


Fig. 6 Total number of skinks using different retreat locations on a) trees with sociable weaver nests; and b) trees without sociable weaver nests. *Post hoc* comparisons were assessed with individual chi-square tests between substrate types.

tree height ($\chi^2_1 = 0.22$, p = 0.64), circumference ($\chi^2_1 = 1.40$, p = 0.24), age ($\chi^2_1 = 0.63$, p = 0.43), canopy cover ($\chi^2_1 = 0.49$, p = 0.48) or initial substrate location ($\chi^2_1 = 1.74$, p = 0.19). Skink retreat location was dependent on whether or not the tree contained a sociable weaver nest. On trees with sociable weaver nests, skinks retreated into sociable weaver nests significantly more often than into other retreat locations ($\chi^2_3 = 11.67$, $p = 0.008$; Fig. 6). On trees with sociable weaver nests, skinks were 3.3 times more likely to retreat into the weaver nest than use ‘other’ retreat locations, were 6.5 times less likely to remain exposed and were 2.6 times less likely to use crevices in trees, although this difference was not significant (Fig. 6a). On trees without sociable weaver nests, skinks were significantly more likely to use crevices as retreat locations than remain exposed ($\chi^2_2 = 16.15$, $p < 0.001$; Fig. 7). In the absence of sociable weaver nests, skinks were 8 times more likely to select crevices in the tree than remain exposed and were 1.7 times less likely to use other retreat locations compared to crevices (Fig. 6b).

Discussion

Our study revealed that Kalahari tree skinks are common residents on camel thorn trees in the Kalahari, which is consistent with Broadley’s (2000) observations. However, we found that the presence of a sociable weaver nest increased the abundance of skinks in trees almost three-fold, indicating a close association between sociable weaver nests and Kalahari tree skinks. Skinks appear to be preferentially selecting trees with an associated sociable weaver nest and it is likely that skinks obtain fitness-related benefits by associating with weaver nests. Even within individual trees, sociable weaver nests also served as a preferred substrate for skinks. This study provides corroborative evidence that sociable weaver nests are used by a wide range of taxa

(Maclean 1973) and supports the notion that, by constructing these large nests, sociable weavers are ecological engineers in this ecosystem.

The strength of the association between Kalahari tree skinks and trees containing sociable weaver nests was highlighted by the persistence of this association on nest trees that ‘permanently’ hosted pygmy falcons. Pygmy falcons are obligatory users of sociable weaver nests for all their roosting and breeding activities (Maclean 1973), and skinks and other small lizards comprise a major part of their diet (Maclean 1970). Yet, despite the presence of actively breeding falcons at weaver nests, we found no evidence that skink abundance was reduced at these sites. In contrast, we observed skinks on all trees with active pygmy falcon nests, while we observed no skinks on three trees without pygmy falcon nests. Sociable weaver nests may also attract and host other potential predators (e.g. Cape cobras; Phelps 2004) and competitive species (e.g. striped skinks; Broadley 2000) that may negatively impact Kalahari tree skinks. However, based on our data, the benefits of sociable weaver nests to Kalahari tree skinks appear substantial and perhaps are quite crucial, outweighing the costs of predation by various nest predators. Nests might even permit increased avoidance of predators and/or may decrease predation risk in other ways, such as through provision of additional refugia. Another possibility may be that pygmy falcon presence provides indirect benefits to skinks, such as protection from other predators or reduced interspecific competition (e.g. Mönkkönen *et al.* 2007).

We found that skinks may benefit from sociable weaver nests through a reduction in predation risk. When trees hosted a sociable weaver nest, skinks were significantly more likely to use the nest as a refuge during a simulated predator attack compared to other refuges. This suggests that Kalahari tree skinks, as for striped skinks (Brain 1969), use weaver nests as a refuge from predation. Trees alone have only a limited number of crevices and nests could provide additional escape refuges. The availability of, and nearest distance to, refuges influences how long an individual remains exposed to a threat (Cooper 1997). Nests provide a close available escape refuge, which could allow Kalahari tree skinks to maximise their time engaged in other activities, such as foraging and basking, while minimising their time required to escape a predation threat.

In the absence of a sociable weaver nest, the type of tree (camel thorn vs. shepherd's tree) did not influence skink abundance. This suggests no specific preference for camel thorn trees in particular, as was the case in southern African tree agamas (*Acanthocercus atricollis atricollis,* Reaney & Whiting 2003). However, tree height played an important role in skink anti-predator behaviour, as skinks on taller trees allowed the 'predator' to approach more closely (i.e. flight initiation distance was longer). Tall trees may be used as vantage points to allow for better detection of approaching predators, as suggested for eastern fence lizards (*Sceloporus undulatus*; Trompeter & Langkilde 2011). Before escaping from a predation threat, an individual should make a decision that optimises the likelihood of escape through an assessment of the fitness effects of the threat and the cost of escaping (Ydenberg & Dill 1986). By using the tree as a vantage point, Kalahari tree skinks could remain exposed for longer periods before retreating into a refuge. This could reduce the energetic costs of unnecessarily escaping to a refuge if a predation threat is unfounded, as suggested for broad-headed skinks (*Eumeces laticeps*, Cooper 1997). In addition, since Kalahari tree skinks are ambush foragers (Cooper & Whiting 2000b), they could also be maximizing the visibility of their surroundings to detect prey (Stamps 1977).

A further benefit to skinks using sociable weaver nests is the thermal advantage these sites provide (van Dijk *et al*. 2013). Surprisingly, we found no effect of ambient temperature on skink abundance, which is usually correlated with lizard activity (Cooper and Whiting 2000a). This may be due to sociable weaver nests acting as a thermal buffer, as suggested by White *et al.* (1975) and Bartholomew *et al.* (1976), and would explain why nests were the preferred substrate, especially in winter. When sociable weaver nests were present, skinks were more likely to perch on nests as opposed to other sites. Interestingly, this is contrary to that reported for the sympatric striped skink, which does not commonly perch on sociable weaver nests (Cooper & Whiting 2000a). Chambers within weaver nests buffer the extremes of environmental temperature and nest chambers remain within a zone of thermal neutrality at both midday in summer (Bartholomew *et al.* 1976) and at night in winter (White *et al.* 1975). In the absence of a nest, however, skinks did not show a preference for any particular substrate on the tree, suggesting that skinks could be exploiting nests to help buffer against environmental extremes, which would be more important for heliotherms than endotherms. While this study did not directly test the potential thermal advantages of these nests to skinks, this benefit seems likely and should be investigated in the future.

Lastly, sociable weaver nests also likely provide significant foraging opportunities for skinks. Nests are home to a wide range of arthropods (R. Thomson, pers. obs) and skinks could reduce movement between prey patches by utilising nests, thereby reducing their exposure to predation. This higher localised prey availability could significantly increase skink fitness and is worth quantifying in the future.

In summary, we show a strong association between Kalahari tree skinks and sociable weaver nests. The benefits to skinks are likely to be manifold and may include refuge from predators, higher localised prey availability and, finally, thermal refuges. While sociable weavers construct large nests primarily for reproduction and roosting, we suggest that this is a form of ecosystem engineering that hosts novel communities that otherwise would not coexist in such close proximity and which derive multiple benefits. Sociable weavers are likely important ecosystem engineers in the extreme environment of the Kalahari Desert where positive interactions should be favoured. Indeed, the thermal benefits provided by sociable weaver nests in a warming climate may become more important and would elevate their already important role to the animal communities they support.

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