Journal of Zoology

ZSL

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Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Community- and species-level responses of reptiles to an avian ecosystem engineer

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Keywords

reptiles; Kalahari; sociable weaver; ecosystem engineer; community ecology; *Philetairus socius*.

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Email: bryanmaritz@gmail.com

Editor: Femke Broekhuis

Associate Editor: Kevin Arbuckle

Received 19 May 2025; revised 25 October 2025; accepted 31 October 2025

doi:10.1111/jzo.70087

Abstract

Ecosystem engineers can alter the distribution and abundance of resources in a landscape, thereby impacting the distribution of other species that use those resources. Although reptiles are known to respond to the ecosystem engineering of birds, case studies are surprisingly rare. Here, we sampled reptile abundance and diversity underneath pairs of trees that do, or do not, contain the thatched colonies of sociable weavers (*Philetairus socius*) in the Kalahari. We conducted our systematic sampling both when the weavers were breeding, and again at the beginning of summer before the onset of breeding. We test the hypotheses that (1) reptile species richness and (2) overall abundance are higher under trees with weaver colonies, and whether differences in those measures vary with season. We additionally explicitly test whether colony trees hosted greater abundances of (3) Kalahari tree skinks (*Trachylepis spilogaster*), and (4) cape thick-toed geckos (*Pachydactylus capensis*)—the two most frequently detected species in our study. We find robust support for all four hypotheses. Trees with colonies had approximately twice the richness of trees without colonies when weavers were breeding but showed no difference in richness outside of the breeding period. Trees with colonies also yielded approximately twice the number of captures (from all reptile species) than did trees without colonies, but this effect was present in both seasons. We found strong support for trees with colonies hosting larger populations of Kalahari tree skinks than noncolony trees in both seasons. We also found strong support for cape thick-toed geckos occurring at higher abundances under colony trees. Taken together, our results indicate that multiple species of reptiles are responding to the presence of sociable weaver colonies in the Kalahari, and that those species effects are summing up to detectable community-wide effects.

Introduction

Through alteration of habitat structure, ecosystem engineers have the capacity to directly influence the distribution and availability of resources to other biota, thereby indirectly altering the distribution and abundance of those organisms (Jones et al., 1994). The effects of ecosystem engineering commonly impact a diversity of vertebrate animals, primarily via soil manipulation (Coggan et al., 2018). These ecosystem changes can lead to substantial impacts on local biodiversity, often by increasing habitat heterogeneity (Wright & Jones, 2006), modifying thermal or moisture regimes (Coggan et al., 2018), and creating refuges or nesting opportunities for other species (Davidson et al., 2008). Although several studies have examined the impacts of ecosystem engineering on reptiles (e.g., Bravo et al., 2009; Davidson et al., 2008; Rymer et al., 2014), most of those cases involve the use of mammalian or avian burrows by reptiles (Coggan et al., 2018). Comparatively few studies have explored the impact of ecosystem engineering on reptiles via other mechanisms such as the construction of nests built from plant material—as is typical of most birds.

Birds that nest colonially can influence the distribution of resources for other animals in several important ways. First, nest structures themselves can be used as refugia from thermal extremes, nesting locations for commensal species, and even provide vantage points for visually oriented, hunting predators (Lowney, Bolopo, et al., 2020; Lowney & Thomson, 2021, 2022). Second, the aggregations of colonial birds can themselves represent a resource hotspot in the landscape, attracting predators that feed on them and/or their eggs and chicks (Natusch et al., 2016). Finally, large aggregations of birds (and commensal animals) can concentrate nutrients around their colonies that influence surrounding vegetation and invertebrate communities (Natusch et al., 2016; Prayag et al., 2020). The strength of these impacts on associated fauna is likely to vary through time (Lowney & Thomson, 2021) such that different species might be attracted to the resources at different times of the year, for different reasons.

One of the few avian ecosystem engineers known to influence the distribution of reptiles through the construction of thatched nests is the sociable weaver (*Philetairus socius*). In southern Africa's Kalahari desert (see Lovegrove, 2021 for a detailed description of the ecosystem), sociable weavers build huge communal colonies that may hold hundreds of chambers (Fig. 1). Sociable weavers use these colonies year-round as night roosts and — when conditions are suitable in summer following sustained rains — for breeding (Maclean, 1973; Mares et al., 2017). Colonies can be maintained for decades making them important, spatially static, features in the arid landscape, with substantial impacts on the local distribution of biodiversity (Lowney & Thomson, 2021, 2022).

Several studies have shown that Kalahari tree skinks (*Trachylepis spilogaster*) are more abundant on trees with sociable weaver colonies than on trees without colonies (Brain, 1969; Cooper Jr & Whiting, 2000; Rymer et al., 2014). Skinks (and probably other species from the local reptile fauna) stand to gain much from associating with colonies. Weaver colonies provide the skinks with opportunities to escape from predators, buffers against thermal extremes, access to food resources, and even early-warning information about approaching predators (Lowney, Flower, & Thomson, 2020; Rymer et al., 2014). Given the (1) myriad advantages that reptiles gain by associating with weaver colonies, and (2) diverse reptile fauna present in the Kalahari (Tolley et al., 2023), it is surprising that other reptile species do not appear to show similar associations with weaver colonies.

Here, we aim to quantify the impact of sociable weaver colonies on the local reptile community. By trapping reptiles underneath trees with and without colonies both prior to and during weaver breeding (because bird breeding activity might change food availability for reptiles), we were able to explore the relative influence of colony presence and bird breeding on the abundance and diversity of reptiles in the landscape. Specifically, we asked whether colony presence and/or bird breeding impacts the overall diversity (species richness) of reptiles at colony and noncolony trees. We also ask whether colony presence impacts the abundance (number of captures of unique individuals) of all reptiles, and the two most frequently detected species in our dataset — Kalahari tree skinks, and cape thick-toed geckos (*Pachydactylus capensis*).

Figure 1 The thatched structure of a sociable weaver (*Philetairus socius*) colony in a shepard's tree (*Boscia albitunca*) at Tswalu Kalahari Reserve showing an installed drift fence and funnel traps below it. Photograph shows EEB inspecting a captured lizard in a bucket while a cape cobra (*Naja nivea*) searches sociable weaver nest chambers overhead. Photo: Bryan Maritz.

Materials and methods

Study site

The study took place at Tswalu Kalahari Reserve (hereafter Tswalu) in the Northern Cape Province, South Africa (27°27′35″ S; 22°45′06″ E). Tswalu is a large, privately owned protected area spanning a diversity of habitats including rocky mountains, sandy plains, and dune fields. The reserve has been described in detail elsewhere (Davis et al., 2010; Tokura et al., 2018). The region is characterized by arid Savanna, with low, variable, annual rainfall (mean annual rainfall between 2017 and 2022 = 377 mm ± SD 143 mm; Scholtz et al., 2025) that occurs predominantly in summer. Air temperatures can exceed 40°C in summer and drop below freezing in winter (Lowney & Thomson, 2021). Hot, dry droughts occur frequently with important negative impacts on reptiles (Scholtz et al., 2025). Tswalu hosts a large population of sociable weavers, including over 250 colonies, which are mostly constructed in camelthorn trees (*Vachellia erioloba*) and shepherd's trees (*Boscia albitrunca*) (Olubodun et al., 2023).

Sampling methods

We adopted a paired-design approach, sampling reptile communities underneath 12 pairs of trees. Each pair included a tree that hosted a sociable weaver colony and a control tree without a sociable weaver colony. Pairs of trees were of the same species, approximately similar in size to each other, and geographically close to each other (mean = 90.58 m; range = 53–231 m) to ensure that trees within a pair were sampling from the same available pool of species and under the same conditions as each other.

Although trees within pairs were selected to be as similar in structure as possible, we recorded several tree covariates to either confirm similarity or to account for systematic differences should these exist. We took two standardized photographs of each tree perpendicular to each other. We scaled these images in ImageJ (Schneider et al., 2012) and calculated tree height (distance between the ground and the top of the canopy), canopy height (distance from the bottom edge of the canopy to the top of the canopy), canopy width (longest distance between the left and right edges of the canopy), and height of the canopy from the ground (distance from the ground to the bottom edge of the canopy) in each image. Each tree was represented by the mean of the measures from the two photographs. We also estimated canopy volume using the equation: canopy volume = $(\pi r^2)/2$, where r = (canopy height + canopy width)/2 (Witkowski et al., 1994). Finally, we recorded the tree species and whether the tree was single or multistemmed.

Under each tree, we trapped reptiles during an 11-day survey in February/March 2022, when the sociable weavers were breeding, and again in September/October 2022, when temperatures were warm, but before the sociable weavers had commenced breeding. A drift fence (length = 6 m; height = 400 mm; buried depth = 100 mm) was installed under each tree and secured in place with metal stakes. Double-ended funnel traps (Fitch, 1987; Maritz et al., 2007; Simmons, 2002) were placed on each side of the drift fence, and a single-ended funnel trap was placed at each end of the fence (Fig. 1). Funnel traps were covered with cut grass to protect them from direct sunshine. Traps were checked twice daily (every morning starting shortly after sunrise; every afternoon culminating just before dark). Every captured reptile was identified to species level, weighed (nearest 0.1 g using a digital balance), measured (snout-vent length and tail length; nearest 1.0 mm using a tape measure or ruler), and temporarily marked with a nontoxic marker pen. We additionally noted whether captured animals had previously been marked. All captured animals were then released into natural vegetation within 3 m of the point of capture.

Data analysis

We tested whether colony trees and control noncolony trees differed systematically in their attributes. There were no systematic differences between colony and noncolony trees in respect of canopy volume (paired t-test: $t_{11} = 1.85$; $P = 0.09$), height above ground (paired t-test: $t_{11} = 0.43$; $P = 0.86$), canopy width (paired t-test: $t_{11} = 1.20$; $P = 0.13$), or whether the tree was single or multistemmed (X^2 test: $X^2_2 = 1.69$; $P = 0.19$). Colony trees did, however, have systematically greater total tree heights (paired t-test: $t_{11} = 3.35$; $P = 0.007$) and canopy heights (paired t-test: $t_{11} = 3.91$; $P = 0.002$) than noncolony trees. However, total tree height and canopy height were strongly positively correlated (Pearson correlation: $r = 0.90$, $P < 0.001$). We accordingly discarded canopy height and included only total tree height as a covariate in our reptile analyses. We additionally tested our data for zero-inflation using a DHARMa zero-inflation test (Hartig, 2024) but found no evidence for problematic zero-inflation in our analyses.

For each tree, in each season, we measured reptile species richness (the number of species detected at that tree during the 11-day survey) and the total number of unique captures (the number of unique individuals of all species captured during the 11-day survey). We additionally analyzed variation in the total number of unique captures of the two most frequently captured species: Kalahari tree skink and cape thick-toed gecko. We performed four separate mixed-effects models (with Poisson distributions due to the count nature of the data), one for each response variable (i.e., species richness, total captures, abundance of tree skinks, abundance of geckos). We initially included colony presence or absence (as a categorical variable), season (as a categorical variable), the interaction between colony and season, and total tree height (as a continuous variable) as fixed effects, as well as tree pair number as a random effect. However, none of the models showed a significant effect of the interaction term (interaction term P-values: 0.31–0.90) and so these were removed and all models were rerun without them. All models were run in R Software V.4.1.1 (R Core Team, 2021) using the glmmTMB package (Brooks et al., 2017). Figures were also produced in R using the packages ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2022), tidyverse (Wickham et al., 2019), and patchwork (Pedersen, 2024). Summarized trap data, and all associated analysis and plotting code are available from the corresponding author on request.

Results

We captured a total of 516 unique individuals from 13 reptile species during the study (six lizard species: *Agama aculeata, Heliobolus lugubris, Lygodactylus bradfieldi, Pachydactylus capensis, Trachylepis punctulata, Trachylepis spilogaster*; six snake species: *Dispholidus typus, Naja nigricincta, Naja nivea, Philothamnus semivariegatus, Psammophis brevirostris, Pseudaspis cana*; one tortoise species: *Stigmochelys pardalis*). Overall, we detected more species ($n = 12$) and individuals ($n = 518$) at colony trees than at noncolony trees (species: $n = 8$; individuals: $n = 149$). Reptile species richness differed significantly ($z = -2.93$, $P < 0.01$) between colony (mean ± SD species richness: 2.67 ± 1.14 species) and noncolony (mean ± SD species richness: 1.33 ± 0.85 species) trees (Fig. 2; Table S1) but was not significantly affected by season ($z = -1.42$, $P = 0.15$) or Total Tree Height ($z = -0.28$, $P = 0.78$). We detected a similar effect of colony on the total number of captured individuals ($z = -8.12$, $P < 0.001$) but also identified a significant effect of season ($z = -8.32$, $P < 0.001$; Fig. 2). Total tree height ($z = 0.24$, $P = 0.81$) did not significantly affect the number of captured individuals. The two most frequently captured species shared similar trends with both species showing significant effects of colony (*T. spilogaster*: $z = -7.28$, $P < 0.001$; *P. capensis*: $z = -3.03$, $P < 0.01$), and both species exhibiting higher abundances at colony trees than noncolony trees (Fig. 3). Season had a significant effect on the number of *T. spilogaster* captured ($z = -7.62$, $P < 0.001$), but not the number of *P. capensis* captured ($z = -1.43$, $P = 0.15$; Fig. 3). Finally, to assess whether our species richness or total number of captures analyses were being leveraged by the strong effects shown by the two most abundant species, we removed these species from the dataset and reran both community-level analyses. We found largely congruent results with significant colony effects still observable for species richness ($z = -2.64$, $P < 0.01$) and total number of captures ($z = -3.63$, $P < 0.01$) in the reduced dataset.

Discussion

We found community- and species-level positive impacts of sociable weaver colonies on the richness and abundance of reptiles, suggesting that the impact of sociable weaver colonies on reptiles is more common than currently appreciated. At the species level, we confirmed that Kalahari tree skink abundance is higher on colony trees than on noncolony trees mirroring the findings of others (Brain, 1969; Cooper Jr & Whiting, 2000; Rymer et al., 2014), but we additionally demonstrate a similar effect for cape thick-toed geckos. Similarly, at the community level, we found evidence for more individual animals and higher species richness under colony trees.

We found evidence that multiple species of reptiles were responding positively to the presence of weaver colonies, and that these accumulated responses were producing an overall community-level species richness effect. The fact that we were able to detect an effect of colony presence on species richness in a reduced dataset that excluded the two most frequently detected species strongly suggests that other species are likely to show similar patterns. Moreover, although a limited sample size precluded a detailed analysis of snake abundances in the study, we found large predatory snakes—combined data from Boomslang (*Dispholidus typus*), Mole snakes (*Pseudaspis cana*), Black spitting cobras (*Naja nigricinta*) and Cape cobras (*N. nivea*)—show similar trends (colony trees: 15 individuals; noncolony trees: 1 individual) across the study suggesting that colony effects might encompass species with very different life histories and ecology.

Figure 2 (a) Mean (±SE) species richness (species.tree^{-1}.survey^{-1}) and (b) mean total captures (individuals.tree^{-1}.survey^{-1}) at trees with (black bars) and without (gray bars) sociable weaver colonies during the weaver breeding and nonbreeding seasons. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{ns}P > 0.05$.

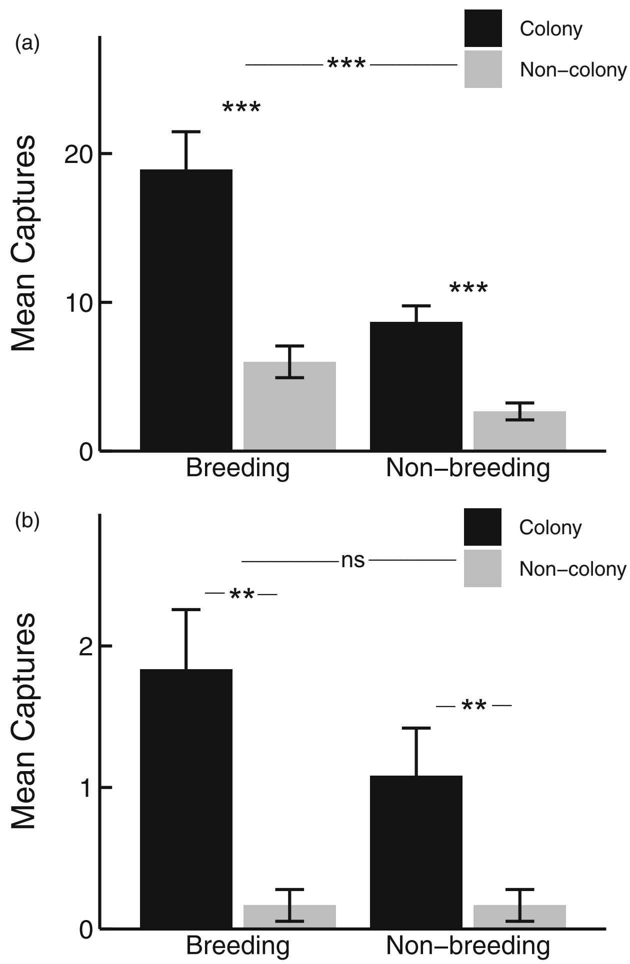

Figure 3 Mean (±SE) number of captures (individuals.tree^{-1}.survey^{-1}) of (a) Kalahari tree skink (*Trachylepis spilogaster*) and (b) cape thick-toed gecko (*Pachydactylus capensis*) at trees with (black bars) and without (gray bars) sociable weaver colonies during the weaver breeding and nonbreeding seasons. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{ns}P > 0.05$.

We found no effect of season on reptile species richness, suggesting that species are not necessarily attracted to colony trees because of increased resources associated with weaver breeding. This result mirrors that of Lowney and Thomson (2021) who examined terrestrial vertebrate diversity (primarily mammalian) and found a strong colony presence effect but no seasonal effect. Our findings suggest that reptiles are predominantly selecting for colony structures and changes to the immediate environment induced by the weavers throughout the year, rather than resources resulting from weaver breeding.

Cape thick-toed geckos are small-bodied (adults up to 67 mm snout-vent length; Branch, 1998) gekkonid lizards that are widespread in southern Africa, including outside of the Kalahari (Tolley et al., 2023). They are typically terrestrial, nocturnal lizards that primarily forage below trees (Pianka & Huey, 1978) although they have been observed inside colony structures (Fig. 4) at night. It is not clear exactly which resources (e.g., thermal, food, or structure) these geckos gain from associating with weaver colonies, and much like Kalahari tree skinks, all three types of advantages offer plausible selective mechanisms. The colony structure likely offers ideal daytime retreats that are largely safe from predators and offers a thermally buffered environment, and colony structures and the ground below them are likely to host increased invertebrate densities (Rymer et al., 2014). However, as colony associates, cape thick-toed geckos differ from Kalahari tree skinks in the costs of associating with colonies. The skinks are diurnal and thus vulnerable to predation by pygmy falcons (*Polihierax semitorquatus*) that are obligate sociable weaver colony commensal species (Covas et al., 2004). These small diurnal raptors consume a diet dominated by lizards (including Kalahari tree skinks). As such, skinks appear to successfully balance the costs of predation risk by falcons with the gains made from associating with weaver colonies (Lowney, Flower, & Thomson, 2020). By contrast, the geckos are nocturnal and individuals experience no predation risk from the falcons. Whether the geckos experience increased risk from other nocturnal predators that also preferentially use weaver colonies remains to be investigated.

An unexpected outcome of our study was a significant effect of season on the abundance of Kalahari tree skinks, with fewer skinks being detected in the nonbreeding season. Given the strong association between skinks and weaver colonies throughout the year (tree skinks were more abundant at colony trees in both seasons), we attribute the seasonal effect to changes in skink behavior. Specifically, we speculate that during the breeding season, skinks move more extensively on the ground and thus are more susceptible to our terrestrial traps. Whether such behavioral changes are indeed the driver of the seasonal effect, or whether such changes are a result of changes in food resource acquisition, social dynamics, or seasonal variation in environmental conditions remains to be tested.

An important limitation of our study is the lack of data examining the impact of colonies on the abundance of invertebrates under trees. Such data might allow us to ascertain whether the mechanism for increased abundance of reptiles under colony trees is simply increased food resources for lizards. Lowney and Thomson (2022) showed that trees with

Figure 4 Cape thick-toed gecko (*Pachydactylus capensis*) foraging at night in a sociable weaver (*Philetairus socius*) colony. Photo: Anthony Lowney.

sociable weaver colonies hosted higher invertebrate abundances —a result that strongly suggests that lizard abundance might be responding to increased food resource availability. This energetic enrichment might scale up through trophic levels, producing increased abundance of small vertebrates for snakes to consume and ultimately driving the overall community effect that we detected. The relative contributions of increased food, and structural and thermal advantages to associating with sociable weaver colonies must be a focus of future research.

Most studies reviewed by Coggan et al. (2018) that explored the impacts of ecosystem engineering on reptiles simply report the use of the engineered habitat by reptiles. The approach of using a paired observational design (as we and selected other studies adopted) thus provides robust support for the effect of ecosystem engineers on reptiles. Unfortunately, such field studies are relatively difficult to implement for many reptile species as they often exhibit low levels of detectability. Even our sampling effort of 2112 funnel trap days only resulted in the detection of 13 of the nearly 30 species of reptiles that occur in the immediate area. In such a context, it is unsurprising that robust measures of reptile detection and abundance are absent from analogous systems, or that robust paired-design studies are comparatively rare.

Reptiles in the Kalahari clearly use the modified habitat resulting from the actions of sociable weavers. The degree to which other reptile communities respond to the construction and utilization of bird nests is unclear. Lowney and Thomson (2022) found evidence that the utilization of sociable weaver colonies by other species increases along an aridity gradient, supporting the stress gradient hypothesis (Bertness & Callaway, 1994). However, Natusch et al. (2016) found a similar pattern of bird nest ecosystem engineering in tropical Australia suggesting it is not necessarily linked to ecosystems with depauperate resources. We predict that the phenomenon is more commonplace than currently appreciated and that the paucity of evidence for reptiles responding to the ecosystem engineering of nesting birds reflects a failure of zoologists to measure such effects, rather than their scarcity.

Acknowledgments

We thank K. Scholtz, R. Mohamed, M. Arendse, R. Maritz, D. Smith, W. Panaino, and T. Beck for support in the field. Research was variously facilitated by Tswalu Kalahari Reserve, the Tswalu Foundation, and Suzuki South Africa. EEB was supported during her degree by a UWC DVCR&I attraction bursary, and the Ada and Bertie Levenstein Foundation. All protocols were approved by the Animal Ethics Research Committee of the University of the Western Cape (Clearance: AR 20/10/2) and the Northern Cape Provincial government (permit: FAUNA 0059/2022).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Generalized linear mixed model results for the species richness, total captures, *Trachylepis spilogaster* and *Pachydactylus capensis*. All models include Colony, Season, and Total Tree Height as fixed effects, Pair as a random effect.