

Sociable weaver nests as a resource to local animal communities

Anthony Lowney



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November 2019

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Thesis presented for the degree of Doctor of Philosophy

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Declaration

I hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever.

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Chapter 4. Lowney, A. M., Flower, T. P. & Thomson R. L. Eavesdropping between taxa: skinks use bird presence and alarm calls to manage predation risk and expand realised niche (Manuscript).

Chapter 5. Lowney, A. M. & Thomson R. L. Sleeping with the enemy: African pygmy falcons provide colony defence but inflict apparent direct costs on weaver reproductive output (Manuscript).

I, Anthony Lowney, had the principle responsibility for all data collection, analysis and completion of the manuscripts throughout this thesis. Experimental design for Chapter 4 was designed by Tom Flower, Robert Thomson and myself. All authors in each article contributed to the manuscript preparation.

Abstract

Animal space use in a landscape generally depends on resources. Facilitation by other species may impact resource availability that can positively influence local species diversity and community structure. Species that significantly change resource availability are often termed ecosystem engineers. The challenge here, is not only to document engineers that disproportionately influence ecosystems but also to determine their consequences to communities. I aim to understand the importance of a potential ecological engineer in a desert ecosystem to animal species diversity and community structure. I investigate how the role of this engineer may change with environmental harshness, and further examine specific associations and interactions with the host engineer. Sociable weavers (*Philetairus socius*) are a colonial passerine endemic to the semi-arid and arid Kalahari in the western parts of southern Africa. This species builds massive colonies that appear to form a focal point for the animal community in this system, and some species are known to show strict or strong associations with the colonies. Weaver colonies appear to be a resource to other animals in the environment, with food and nutrients clumped at colonies, and even thermal benefits available to occupants (a potentially crucial resource in arid environments). Nevertheless, the full importance of nest colonies to the surrounding animal community is still unknown.

The main aims of this thesis were to determine the importance of Sociable weaver colonies to the surrounding animal communities and how this importance may change as environment harshness changes. To understand this, I investigate the use of colonies by multiple taxa (mammals, birds, reptiles and invertebrates) across seasonal and spatial aridity gradients. An additional aim is to describe the nature of the interactions between Sociable weavers and their associates. Therefore, determining how multiple species can access the colony resources at the same time and further, understand how these associates may impact the weavers. Here, I consider the interactions between Sociable weavers, Kalahari tree skinks (*Trachylepis spilogaster*), African pygmy falcons (*Polihierax semitorquatus*) and snakes. These species have all been shown to associate with weaver colonies and may impact weavers and each other in different ways.

I show that Sociable weaver colonies create localised biodiversity hot-spots. These strong associations of multiple taxonomic groups which characterises their entire range and suggests a high importance of weaver colonies for the whole surrounding animal community. Although

no variation was observed across a seasonal gradient, colony trees were associated with a greater abundance of animals at sites with lower rainfall, whereas sites with higher rainfall had a more evenly distributed abundance of animals between colony and non-colony trees. Additionally, I set out to describe the nature of the interactions between Sociable weavers and their recognised close associates. Through a series of observational and experimental studies I demonstrate that Kalahari tree skinks can eavesdrop on weaver alarm calls, this likely permits them to manage their predation risk and facilitate their coexistence with a predator, the pygmy falcon, at weaver colonies. The ability to eavesdrop also allows skinks to access riskier foraging habitat, thus, expanding their realised niche. Furthermore, pygmy falcon's defensive behaviour appears to deter predatory snakes from accessing a given colony. However, weaver reproductive output did not improve at falcon hosting colonies, suggesting falcon protection was offset by their predation of weaver chicks. Falcons saw an increase in nest predation when weavers were breeding, due to an increase in snake activity at colonies. When weavers were not breeding, falcons were more likely to fail, because of reasons other than predation (lack of provisioning, abandonment). This all demonstrates that weavers are clear-cut obligate ecosystem engineers, and one that can reduce stress that may allow species to persist in an environment that is predicted to become more harsh, due to global climate change. Furthermore, interactions at colonies demonstrate costs and benefits for weavers and their close associates, suggesting that a complicated ecological web of interactions allow these species to coexist.

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Chapter 1

General introduction



Introduction

Resources are fundamental to sustaining animal populations (Manly et al. 2007). They encompass a wide range of elements that directly contribute to the fitness of an individual (Tilman 1982). Initially, for animals, these elements were categorised as three primary core resources; the elements that make up their bodies, the habitat required to fulfil their life cycles, and the energy needed to undertake any activity (Begon et al. 1986). However, as the field of ecology advances, more resources are identified, including sexual partners (Danchin et al. 2008), and the importance of other species-facilitated resources. For example, species that manipulate the environment and as a result ameliorate conditions or provide accessibility to core resources (Coggan et al. 2018). Additionally, information transfer within and between species is a valuable resource that allows species to locate food and avoid predators (Seppänen et al. 2007). The selection of different resources by different species is fundamental in allowing multiple species to coexist (Rosenzweig 1981). Additionally, numerous species may use the same resource for different reasons (Arsenault and Owen-Smith 2008, Natusch 2017). The need to understand which resources are used by animals is an essential part of conservation biology. This provides us with vital information regarding the ecology of an animal and how it meets its requirements for survival and is, therefore, an ever-expanding topic of behavioural ecology (Manly et al. 2007).

Resources are often concentrated in specific locations within a landscape (Parrish and Edelstein-Keshet 1999). Consequently, this strongly affects the distribution of animals (Dean et al. 1999, McIntyre and Wiens 1999, Hunter et al. 2012), often creating islands of biodiversity (Dean et al. 1999, Natusch et al. 2016) that are particularly prevalent in arid ecosystems (Schlesinger and Cross 1996, Dean et al. 1999, Schade and Hobbie 2005). In arid environments precipitation is unpredictable and resource availability fluctuates between abundant and scarce (Hillel and Tadmor 1962, Rosenzweig 1968). As a result, resource use may change as availability changes, with higher quality resources being preferred during times of plenty, shifting to lower-quality resources when high-quality ones are no longer available (Manly et al. 2007). When consuming lower-quality resources, species are likely to require greater amounts to compensate for the reduction of resource quality (Begon et al. 1986). This, therefore, also affects the distribution of animals and the amount of time an individual may spend interacting with a given resource.

Ecosystem engineers

The availability of resources can also be affected by other species, which in turn can affect local species diversity and community structure (Peek 1986, Bertness and Callaway 1994). This can have adverse effects through competition or predation (Chase et al. 2002), or positive results via facilitation (Bertness and Callaway 1994, reviewed by Soliveres et al. 2015). Species that positively alter the availability of resources are frequently termed ecosystem engineers (Jones et al. 1994, Coggan et al. 2018). Ecosystem engineers can impact resource availability in different ways (Badano and Cavieres 2006). Burrowing species can modify soil properties that directly affect plant community composition and diversity (Bancroft et al. 2005, Natusch et al. 2017), and structural engineers (allogenic engineers, *sensu* Jones et al. 1994) build physical habitats that provide shelter (Berke 2010, Coggan et al. 2018). By altering resources, ecosystem engineers can change the abundance of species that occur within the community (Flecker 1996, Crooks and Khim 1999, Bancroft et al. 2008, Natusch et al. 2016), therefore, changing the evenness of species assemblages. Additionally, animals may now be able to persist in these altered habitats that previously were unsuitable; therefore, ecosystem engineers could increase the realised niche of species and ultimately increase community species richness (Bertness and Callaway 1994, Wright et al. 2002, Castilla et al. 2004, Badano and Cavieres 2006).

The ecosystem engineer concept is not without criticism (Reichman and Seabloom 2002a, 2002b). All species modify their habitat to some degree, with some making minimal changes that have little influence on ecological processes (Reichman and Seabloom 2002b, Coggan et al. 2018). Describing such species as engineers is said to have trivialised this concept (Reichman and Seabloom 2002a, 2002b). However, there are species whose engineering extensively changes habitat, community structure and ecosystem functions (Natusch et al. 2016, Coggan et al. 2018). Therefore, the onus is not to merely identify ‘engineers’ but to describe those that disproportionately affect resource availability and determine an engineer’s importance to communities. By doing so we can understand where engineers have the greatest abiotic and biotic impacts (Reichman and Seabloom 2002b, Crain and Bertness 2006, Soliveres et al. 2015). Recent studies have shifted towards this focus, however, the effects and interactions of ecosystem engineers have primarily been investigated as snapshots in time and across small spatial scales, limiting our understanding of how temporal and spatial context may alter an engineers impact (Coggan et al. 2018).

There has been a taxonomic bias towards mammals when investigating the impacts of land-based ecosystem engineers (Coggan et al. 2018). Our current knowledge is mainly provided by burrowing mammals in arid environments (Reichman and Seabloom 2002a, Davidson et al. 2012, Root-Bernstein et al. 2013), this despite evidence that invertebrates, reptiles and birds actually have more significant ecological impacts as engineers (Romero et al. 2015). By neglecting nonmammalian engineers we lose the opportunity to understand the function of engineers in major biomes or habitat niches that are not heavily influenced by mammalian species. For example, birds in particular have been neglected (Coggan et al. 2018), this is surprising as nest construction can take many shapes and forms (Mainwaring et al. 2015), from subterranean nests that alter vegetation structure and complexity and affect vertebrate fauna, to large communal nests that provide resources for multiple species who use these structures as ecological hotspots (Bancroft et al. 2005, 2008, Natusch et al. 2016). Therefore, to understand the full significance of ecosystem engineers and their ecological functions we need to expand our knowledge across all taxa.

The stress gradient hypothesis

The stress gradient hypothesis (Bertness and Callaway 1994) posits that the importance of facilitative interactions in shaping community structure and function is predicted to increase as environmental harshness increases. Substantial empirical evidence exists to support the hypothesis, demonstrating that associative and positive between-species interactions increase with increased environmental stress, often mediated by identified ecosystem engineers (Wright et al. 2006, Cavieres and Badano 2009, Schöb et al. 2013, He and Bertness 2014, Bulleri et al. 2016). However, the testing of the stress gradient hypothesis has mainly been restricted to plant-plant interactions; with animal ecologists being surprisingly slow to apply this theory to animal communities. Moreover, little has been done to test this hypothesis across spatial gradients. Environmental stress will likely vary across an ecosystem engineer's distribution (Erpenbach et al. 2012, Coggan et al. 2016), and conditions within these environments will also differ between harsher and more benign periods. However, little attention has been paid towards how the impacts of ecosystem engineers change over extended periods (Coggan et al. 2018). Studies across larger spatial scales are challenging to replicate, but they may reveal the importance of engineers to different communities (Coggan et al. 2016). Therefore, observing the impact by engineer's over large-scale ecological gradients may increase our knowledge of how they may mitigate extreme differences between environmental harshness.

Species interactions are likely to be a key feature of communities as they respond to climate change (Harrington et al. 1999, Suttle et al. 2007, Alexander et al. 2015). In arid environments, the frequencies and duration of hot-weather events are predicted to increase as the effects of climate change advance (Meehl and Tebaldi 2004, Akoon et al. 2011). As a result, the species that inhabit these landscapes will experience harsher environments (Erasmus et al. 2002, Isaac 2009). As environments become too severe, changes between species interactions may lead to the disappearance of specific taxa from a given community. Ecosystem engineers link the abiotic and trophic features within communities through their interaction networks (Sanders et al. 2014). For example, the importance of engineered structures that provide thermal refuge is likely to increase as temperatures increase (Coggan et al. 2018), resulting in these structures being used more frequently. Therefore, to determine how communities may change as sites become harsher, it is crucial to understand how engineers affect resources and how this may change as environments become more severe.

Engineers can create niches that allow other species to exist in areas that would otherwise be unsuitable (Bruno et al. 2003). By modifying habitats and altering the availability of resources, engineer may increase local environment carrying capacity and enable range expansions (Kylafis and Loreau 2008, Krakauer et al. 2009). These interactions can form “engineering webs” that, along with recognised trophic interactions, regulate ecosystem functioning (Jones et al. 1994). Additionally, species favoured by the effects of engineering may adapt to novel resources and interactions, resulting in the expansion of the number of niche dimensions available (Schemske et al. 2009). Considering that biotic interactions may increase the rate of adaptation, speciation and coevolution, we would expect greater relevance to these types of interactions (Schemske et al. 2009). Therefore, when engineers modify their physical habitat, they may also modify selection on other species that depend on these physical changes (Laland and Feldman 2003). This may then drive coevolution, strengthen or relieve competition, influence the probability of coexistence, and produce macroevolutionary trends (Krakauer et al. 2009, Laland et al. 2016). As a result, this may allow species to join communities where competitive or predatory members would otherwise preclude their membership.

Associate interactions at engineered resources

Joining a community may expose individuals to increased predation risk (Götmark and Andersson 1984, Groom 1992). Predator and prey species can be positively influenced by the same ecosystem engineer, bringing both species into close proximity (Rymer et al. 2014).

Furthermore, it has been demonstrated that both predator and prey species can coexist within the same engineered habitat, without the predator negatively affecting the prey's association with a given resource (Rymer et al. 2014). How species react to this perceived increase in predation risk is a crucial element in identifying how trophic interactions structure ecosystems (Lima 1998, Abrams 2010). The outcomes of predator-prey interactions can immediately be determined by the prey's behavioural response (Quinn and Cresswell 2004). Furthermore, how species react to the 'fear' of predation can also be used to indirectly assess population dynamics and community structure (Cowlshaw 1997, Owen-Smith and Mills 2006, Creel et al. 2007). For any single species associated closely with a resource, multiple competitors and predators are also close associates. Therefore, a species response to predation may be influenced by other community members (Goodale et al. 2010). Individuals that can use cues or signals from other community members with regards to predator related information will gain immediate and clear benefits (Magrath et al. 2015).

Eavesdropping is common in animal communities (Bradbury and Vehrencamp 1998, Magrath et al. 2015). Individuals that eavesdrop on other species are able to decrease their predation risk and increase foraging efficiency resulting from reduced vigilance (Sullivan 1984, Doligez et al. 2002, McGraw and Bshary 2002, Vitousek et al. 2007, Oommen et al. 2009, Schmidt et al. 2010, Sharpe et al. 2010, Baigrie et al. 2014). However, little is known regarding the importance of eavesdropping for the organisation of community structure, including cross-taxa communities (Goodale et al. 2010), and any benefit may be context-dependent (Oommen et al. 2009). Joining a community may expose individuals to increased risk (Götmark and Andersson 1984, Groom 1992), including from other community members. Eavesdropping could, in principle, offset such costs and facilitate community membership (Oommen et al. 2009). Furthermore, risk-related information from heterospecifics within communities could increase access to higher-risk habitat and therefore expand species' realised niches (Goodale et al. 2010, Ridley et al. 2014, Martinez and Vredenburg 2018). Thus, eavesdropping allows individuals to join diverse taxonomic groups whose predators may otherwise exclude them.

Ecosystem engineers may modify habitats that facilitate the presence of one of its predators (Macleán 1970). Thus, presenting a counter-intuitive scenario where two species that would typically exhibit antagonistic interactions coexist nearby (Rymer et al. 2014). The evolution of such a scenario would suggest a net positive aspect of any interaction. Predators have been shown to provide protection of prey species (reviewed by Quinn and Ueta 2008). This protective association is formed when the predator establishes a protective umbrella around its

nesting site, thereby excluding mutual predators (Bogliani et al. 1999, Sergio and Bogliani 2001, Quinn and Ueta 2008), and therefore providing some protection for the engineer, though these benefits are likely context-dependent depending on biotic and abiotic conditions (Gotmark 1989, Larsen and Grundetjern 1997). For the protective species, there are also potential trade-offs between the costs and benefits of this association (Quinn and Ueta 2008). The protective associate will have access to resources (Young and Titman 1986, Norrdahl et al. 1995). But, for modified habitats that facilitate the presence of a single, or multiple species, then the protective associate may experience increased competition, particularly in harsh landscapes. By adapting to competition and predation, multiple species can use novel behaviours and interactions, allowing them to coexist at the same engineered resource (Schemske et al. 2009).

General aims and study system

I aim to understand the importance of a terrestrial animal ecosystem engineer to animal species diversity and community structure and use this system to test how its impacts may change in response to seasonal and spatial changes in environmental harshness. Our candidate engineer is the Sociable weaver (*Philetairus socius*), a colonial passerine bird endemic to the semi-arid and arid Kalahari in the western parts of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Certain trees species that host Sociable weaver colonies, including camelthorn (*Vachellia erioloba*), have previously been shown to increase biodiversity on a local scale (Dean et al. 1999, Seymour 2006). However, biodiversity may further increase at trees that contain weaver colonies. These massive nest colonies built by weavers can contain hundreds of individual nesting chambers in a single ‘haystack’ and may house hundreds of birds year-round. The nesting chambers provide thermal benefits to occupants (van Dijk et al. 2013, Leighton and Echeverri 2014), a potentially crucial resource in arid environments, while food and nutrient resources may concentrate at nest colonies too (du Toit 2016, Prayag 2016). Weaver colonies may, therefore, be a resource to other animals in the environments. For example, Kalahari tree skinks (*Trachylepis spilogaster*) increase in abundance at trees that host weaver colonies (Rymer et al. 2014), while African pygmy falcons (*Polihierax semitorquatus*), and at least some arthropods are dependent on these structures (Rehn 1965, Maclean 1970, Harvey et al. 2015). Anecdotal data suggest a wide range of other species are associated with these colonies (Maclean 1973b). Nevertheless, the full importance of these nest colonies to the surrounding animal community is still unknown.

I consider the interactions between Sociable weavers and other species that strongly associate with weaver colonies, including Kalahari tree skinks and African pygmy falcons. These skinks are strongly associated with weaver colonies, and appear to gain substantially from weaver colonies, including through refuge, basking, and foraging benefits (Rymer et al. 2014). Pygmy falcons rely on sociable weaver colonies for breeding and roosting year-round, and their diet mainly consists of small lizards (Maclean 1970) including Kalahari tree skinks, whose remains are often found under falcon nests when falcons are breeding (Lowney and Thomson, personal observation). However, trees with colonies inhabited by falcons do not have fewer skinks than colony trees without falcons (Rymer et al. 2014). Sociable weavers also comprise a small proportion of the falcon's diet (Maclean 1970). Therefore, weavers have the potential to provide information to skinks about predators through both their behaviour and vocalisations. Snakes heavily predate on weaver nesting attempts (Covas 2002), yet pygmy falcons may have the potential to act as protective associates and deter predators from weaver colonies. Additionally, pygmy falcons may accrue costs and benefits from this association. In this thesis I aim to describe the nature of the interactions between these species, hoping to determine how all three can coexist at this engineered resource.

Thesis outline

Chapters within this thesis are presented as a series of stand-alone papers formatted to facilitate publication (Chapters 2-5). Therefore, each chapter consists of an abstract, introduction, methods, results and discussion section. As a result, there is a repetition of information with regards to the introduction, methods and discussion in some of these chapters (particularly chapters two and three). Within each chapter, the term “we” is used, due to there being several authors on each potential paper. However, in all cases, I am the principal author and conducted the substantial majority, if not all, of the data collection, and all analyses and writing required to produce each chapter.

Chapter Two quantifies the use of Sociable weaver colonies by mammals and bird species at Tswalu Kalahari across a temporal scale. Surveys were conducted using colony-hosting trees that were paired with non-colony trees. I used camera traps to compare mammal abundance and behaviour at colony and non-colony trees. Point counts were used for comparing bird abundance at colony and non-colony trees and night visits were carried out at colony trees only to determine the number of heterospecifics roosting in a colony at night. Surveys were undertaken across a calendar year to incorporate both harsh and benign seasons.

Chapter Three quantifies the use of weaver colonies across a spatial gradient of harshness; for which, aridity served as a proxy. Here I visited eight sites throughout the weaver's distribution, incorporating a rainfall gradient. Therefore, this data collection not only allowed for a meta-replicated study of chapter one but also to test how vital these colonies are to animal communities as environments change. I investigated the use of weaver colonies across multiple taxa using various techniques specific for each taxon response quantified. Pitfall and pan traps were used to sample invertebrates, species counts for reptiles, point counts and night visits for birds and camera traps for mammals.

In Chapter Four I carried out correlative and experimental studies to determine if Kalahari tree skinks eavesdrop on sociable weavers to expand their realised niche and mitigate any increase in predation threat that associating with weaver colonies may bring. We used skink counts to determine if skinks were more active, and more likely to forage in riskier habitats when weavers were present. Flight initiation distance experiments were used to determine if skinks cued on weavers fleeing for cover as an indication of an approaching predator. Playback experiments were then presented to weavers at colony and non-colony trees to determine if skinks eavesdrop on weaver alarm calls and, if so, whether this behaviour is learned or innate.

Chapter Five sets out to investigate the relationship between Sociable weavers and pygmy falcons. Pygmy falcons are obligate nest associates of sociable weavers, using weaver colonies to breed and roost. Although falcons have been reported to occasionally prey on weavers, they may also have the potential to defend colonies from predators. I conducted observational and experimental tests to understand whether falcons can prevent snakes from entering weaver colonies and, if so, investigated whether this leads to an increase in reproductive output for weavers that share colonies with falcons. Additionally, I monitored falcon breeding attempts and compared the success of falcon nests that overlapped breeding with weavers with falcons that did not.

Chapter 2

Ecosystem engineers across a temporal gradient: Sociable weavers influence the distribution and abundance of Kalahari animal communities.



Photo Liam Charlton

Abstract

Animal distribution in a landscape depends mostly on the availability of resources. This can be facilitated by other species and have positive effects on local species diversity and community structure. Species that significantly change resource availability are often termed ecosystem engineers. Identifying these species is key, but predicting where they have large or small impacts is an even greater challenge. The stress gradient hypothesis predicts that the importance of facilitative interactions that shape community structure and function are anticipated to increase in stressful and harsh environments. To test this hypothesis, we investigate the role of Sociable weavers (*Philetairus socius*) as ecosystem engineers and examine how the association of species to weaver colonies may vary across a temporal gradient. These birds build large colonies that are home to hundreds of weaver individuals but also host a wide range of other species, both avian and non-avian. We investigated the use of weaver colonies on terrestrial and arboreal vertebrates and birds throughout a calendar year, encompassing harsh and benign seasons. We demonstrate that the presence of Sociable weaver colonies creates localised biodiversity hot-spots and that these colonies are important to the local Kalahari animal community. Furthermore, we found overall increased activity due to increased plant productivity, but this was not restricted to weaver colonies, suggesting that the importance of colonies does not vary across seasons. Therefore, the results of this study are not consistent with the stress gradient hypothesis and indicate that this hypothesis may be harder to fit to a temporal gradient than a spatial gradient.

Introduction

The distribution of animals in a landscape depends mostly on the availability of resources (McIntyre and Wiens 1999, Hunter et al. 2012), which can be concentrated in specific locations (Parrish and Edelstein-Keshet 1999). Resource availability can be facilitated by other species, and this can positively affect local species diversity and impact community structure (reviewed by Soliveres et al. 2015). Species that significantly alter the availability of resources in an environment are often termed ecosystem engineers (Jones et al. 1994, Coggan et al. 2018). The concept has received criticism because all species engineer their environments to some degree, and that identifying every species as an ecosystem engineer has trivialised this concept (Reichman and Seabloom 2002a, 2002b). The real value is to identify ‘engineers’ that disproportionately influence resource availability in ecosystems and understand the consequences to communities and where engineers will have the greatest abiotic and biotic

impacts (Crain and Bertness 2006). Despite this gaining increasing attention, the effects and interactions of ecosystem engineers have, overwhelmingly, been investigated as a snapshot in time, limiting our understanding of how temporal contexts may alter impacts (Coggan et al. 2018).

The importance of facilitative interactions in determining community structure and function are expected to increase in stressful and harsh environments (Bertness and Callaway 1994). Termed the stress gradient hypothesis, empirical evidence supports this prediction and shows that there are greater associative and positive between-species impacts as environmental stress increased, often mediated by identified ecosystem engineers (Wright et al. 2006, Cavieres and Badano 2009, Schöb et al. 2013, He and Bertness 2014, Bulleri et al. 2016). Testing of the stress gradient hypothesis has almost exclusively been performed in plant communities; indeed, animal ecologists have been surprisingly slow to apply these ideas to animal communities. Furthermore, little has been done to apply the stress gradient hypothesis to a temporal gradient. In most environments, conditions will fluctuate between harsher and more benign periods, yet how the impacts of ecosystem engineers change over more extended periods has received very little attention (Coggan et al. 2018). Monitoring for longer more extended periods would increase the understanding of how engineers may mitigate the extreme differences between changing seasons and intermediate length studies may be appropriate to understand the importance of engineers that are not the result of an event, such as an engineer being removed or introduced to an area (Coggan et al. 2018). For example, a two-year study Biswas and Wagner (2014) found the presence of non-native garlic mustard (*Alliaria petiolate*) leads to a positive density dependent survival for rosette species during harsher winter periods and that this pattern was reversed during summer.

Ecosystem engineers impact resource availability in various ways (Badano and Cavieres 2006). Structural engineers (allogenic engineers, *sensu* Jones et al. 1994) create physical habitats that provide resources and shelter (Berke 2010). Burrowing species can change soil properties that directly influence the plant community composition and diversity (Whitford and Kay 1999, Bancroft et al. 2005). In doing so, this can alter the abundance of species that already occur within the community (Flecker 1996, Crooks and Khim 1999, Bancroft et al. 2008, Natusch et al. 2016), changing the evenness of species assemblages. Additionally, habitats can also become suitable for species that would not usually be able to persist; therefore, ecosystem engineers could increase the realised niche of species and ultimately increase community species richness (Bertness and Callaway 1994, Wright et al. 2002, Castilla et al. 2004, Badano

and Cavieres 2006). Research into land-based ecosystem engineers has revealed a considerable taxonomic bias towards mammals and invertebrates, with very few studies showing birds to be engineers (Coggan et al. 2018). This is surprising as nest construction can take many shapes and forms; with large communal nests providing resources for species that gravitate towards these structures, and nests burrowed underground that alter vegetation structural complexity and vertebrate fauna (Bancroft et al. 2005, 2008, Mainwaring et al. 2015, Natusch et al. 2016).

We aim to understand the importance of a terrestrial animal ecosystem engineer to animal species diversity and community structure and use this system to test how its impacts may change in response to seasonal changes in environmental harshness. Our candidate engineer is the Sociable weaver (*Philetairus socius*; henceforth weavers), a colonial passerine endemic to the semi-arid and arid Kalahari in the western parts of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Certain trees species that host weaver colonies, including camelthorn (*Vachellia erioloba*), have previously been shown to increase biodiversity on a local scale (Dean et al. 1999, Seymour 2006). However, biodiversity may further increase at trees that contain weaver colonies. These massive nest colonies built by weavers can contain hundreds of individual nesting chambers in a single 'haystack' and may house hundreds of birds year-round. The nesting chambers provide thermal benefits to occupants (van Dijk et al. 2013, Leighton and Echeverri 2014), a potentially crucial resource in arid environments, while food and nutrient resources may concentrate at nest colonies too (Prayag, du Toit, Cramer and Thomson, unpublished). Weaver colonies may, therefore, be a resource to other animals in the environment. For example, Kalahari tree skinks (*Trachylepis spilogaster*) increase in abundance at trees that host weaver colonies (Rymer et al. 2014), while African pygmy falcons (*Polihierax semitorquatus*), and at least some arthropods are dependent on these structures (Rehn 1965, Maclean 1970, Harvey et al. 2015). Anecdotal data suggests a wide range of other species associated with these colonies (Maclean 1973b). Nevertheless, the full importance of these nest colonies to the surrounding animal community is still unknown.

Plant productivity signifies the basal component of most ecosystems (Loreau et al. 2001). In arid environments where precipitation is unpredictable, vegetation cover can fluctuate between scarce and plentiful (Hillel and Tadmor 1962, Rosenzweig 1968), and in turn, determines the availability of resources to other species further up the food web (Polis 1991). The Kalahari is characterised by hot summers with rare but generally quite violent rainstorms and cold and dry winters, resulting in substantial seasonal variation; with some seasons being considered harsh, while other seasons are benign. These extremes present different conditions to animal

communities and the impact (or value to the ecosystem) of any engineer may change depending on these environmental contexts. In ecology, biotic interactions and their outcomes are often context-dependent (Loreau et al. 2001, Leung et al. 2012, Mellard et al. 2019). Therefore, to understand the impact of weaver colonies to the surrounding Kalahari community, we not only need to quantify how the presence of a colony influences the associations of the local animal community but also how this may change through seasons.

Here we investigated the use of weaver colonies by the Kalahari animal community. We monitored animals at, and interactions with, colonies using camera traps, point counts and night visits by an observer over a calendar year to determine if the use of the weaver colonies changes as seasonal harshness changes. Our response included multiple animal taxa; large vertebrates and birds which we compared between trees containing a colony and control, non-colony trees.

Materials and Methods

Study site

We collected data at Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (27°13'30"S and 22°28'40"E). Tswalu has a hot and arid climate with temperatures that exceed 40°C in summer and drop below zero during winter (van Rooyen and van Rooyen 2017), it has highly variable rainfall (mean 361.4 mm \pm SD 169.2mm) that mainly falls between December and March (Tokura et al. 2018). Tswalu Kalahari contains an almost full range of natural indigenous fauna of the Kalahari, including 75 mammal species (Tokura et al. 2018) and nearly 200 bird species (South African Bird Projects; <http://sabap2.adu.org.za/>). Our study area consisted of 130 km² within the 100,000-ha reserve and contained over 250 weaver colonies, mostly in the two dominant tree species; camelthorn and Shephard's tree (*Boscia albitrunca*).

Survey Methods

We carried out surveys to compare colony use by multiple-taxa. These include the abundance and behaviour of terrestrial and arboreal vertebrates, the abundance of avian species and the abundance of heterospecific birds roosting in colonies at night. Unless otherwise stated, surveys were carried out between 1st January and 31st December 2016. Firstly, we selected 52 trees randomly that contained weaver colonies to survey. However, after the study had started, this was reduced to 43 trees, due to logistical reasons. We focussed on weaver colonies found in camelthorn and Shephard's trees. Weaver colonies vary dramatically in size. Chamber number is a good indicator of colony size (Leighton and Echeverri 2014), and in our study area,

weaver nests contained an average of 50 chambers (± 43 SD, range 1 – 244). We wanted to exclude the smallest colonies that were only recently built and would likely have lower ecosystem impacts; therefore, we only included trees containing weaver colonies with more than twenty nesting chambers. Selected colony trees were then paired with a non-colony tree of the same species and with a similar size/structure. Paired trees were less than 200 m apart (92.44 mean ± 9.03 SE; all means are presented with standard error unless otherwise stated), to account for any spatial differences.

We recorded the main characteristics of each tree (both colony and non-colony trees) in the survey. We measured tree height (and colony height above ground) by taking photographs with a reference ladder placed at the tree and using the ImageJ software package (Schindelin et al. 2012). Trunk diameter was measured as the diameter at breast height (DBH) with a standard tape measure. Alternatively, if the trunk split before this point, it was measured at the base of this split. Canopy cover was calculated by measuring the maximum length and perpendicular width, and applying these to the equation: canopy cover = $(\pi r^2)/2$, where $r = (\text{maximum length} + \text{perpendicular width})/2$ (Witkowski et al. 1994). We used a principal component analysis to reduce confounding effects that the tree characteristics may have on our subsequent analysis (Pearson correlation matrix: canopy cover v tree height $|r| = 0.55$; canopy cover v DBH $|r| = 0.24$; tree height v DBH $|r| = 0.22$). Response variables loaded heavily on principal component 1 (98.4%; Appendix 1); therefore, this was the only component used in our analyses.

Four sampling methods were used to quantify the abundance and diversity of fauna present at each tree with (“colony tree”) or without (“non-colony tree”) a weaver colony. Different sampling methods targeted broad animal taxa groups.

Abundance and behaviour of terrestrial vertebrates: We used camera traps to survey the terrestrial vertebrates using the 43 colony trees and the 43 paired control trees, with two tree pairs (i.e. four trees) being surveyed at a given time. Each tree was surveyed twice during the study. Camera traps (Cuddelback C) were equipped with a black flash, 8 GB memory card and deployed on metal stakes 60 cm above the ground and placed so that they had a clear view of the area under the tree and the surrounding vegetation. Camera traps were set to be motion-triggered and to take three consecutive photographs and a twenty-second video; a minimum period of one minute would elapse before the camera could be triggered again. If a camera trap failed or was interfered with by animals, we would take the time of the last photograph from the failed/interfered camera and use this as the cut-off point with its paired camera (resulting

in under 7-day survey periods). We calculated the number of days that paired cameras were operational and used this as an offset within our statistical models.

We used images and videos from camera traps to determine if weaver colonies create localised biodiversity hotspots. We extracted the following data: the number of camera trap events – a single event was defined as the moment an individual enters the area visible under the tree until it leaves. If multiple individuals entered the area, the event would be defined as the moment the first individual entered until the last individual left. If numerous species were captured, then a separate event was allocated to each species. For each event, we recorded the species identity, the number of individuals and the behaviour carried out by the individual(s). Behaviours were categorised as either foraging, using the colonies for shade, displays of territoriality (scent marking, chasing, fighting), and passing by. All individuals that we categorised as ‘passing by’ were subsequently removed from all analysis, because these individuals were deemed not to be interacting with the tree and/or colony. We also calculated the amount of time each event lasted (minutes), using the timestamps on each photo to determine when an event began and finished.

Abundance of arboreal vertebrates: We used the same protocol and extracted the same variables as described for terrestrial vertebrates. However, this survey was undertaken between March and December 2016, and used 39 colony and 39 paired non-colony trees, these were a subset of the original colony and non-colony trees used for the terrestrial mammal sampling. Terrestrial and arboreal camera traps for a given tree were deployed at the same time and ran concurrently. For colony trees, camera traps (Ltl Acorn 6210MC) were deployed so that they viewed along the top of the colony; when this was not possible they were placed so that they focused along the supporting branch towards the colony. For paired non-colony control trees, cameras were deployed so that they focused along the thickest branch of the tree. When an individual was captured by both arboreal and terrestrial cameras, then only the data from the arboreal camera was used. It was difficult to determine why many of the animals visited colony and non-colony trees; therefore, it was not possible to extract behavioural information from these events.

Abundance of avian species: We compared avian abundance around colony and non-colony trees, by carrying out point counts once a month for five months between September 2017 and January 2018. A subset of 25 colony trees were randomly selected and paired with different control trees, from those used earlier. This was to reduce the likelihood of counting the same

individual twice. Control trees were a minimum of 250 meters apart (355 ± 13.3) and were matched for tree species and size. We recorded all birds seen or heard within 25 m of the tree. Point counts at paired trees were carried out directly after each other, and the order was rotated between each visit. The first point count started at sunrise, and the final point count on a given day started within three hours of the first count. The survey period ran for four consecutive days every four weeks.

Abundance of roosting birds: We undertook night surveys at 46 different colonies to investigate which bird species that use weaver colony chambers for roosting. Surveys were conducted every four weeks when no moon was visible to avoid birds flushing from colonies. We visited each colony thirteen times during this study. Starting a minimum of 30 minutes after sunset, we visited colonies for about five mins in the dark and scanned chamber entrances using a head torch. Birds occupying the chambers were generally visible and could be identified easily. Multiple colonies were visited on a given night; however, we found that as the temperature decreased, birds moved to the back of the chambers and detection rates dropped. Consequently, surveys were only carried out for one hour on a given night before temperatures dropped, taking four consecutive nights to visit each of the 46 colonies. Therefore, ensuring that we recorded all individuals using colonies at that time.

To determine if the number of heterospecific individuals observed roosting in weaver colonies changed throughout the year, we needed to control the abundance of these species within the local community. Therefore, we carried out point counts at 29 of the 46 colony trees. We only used 29 colony trees for point counts as several trees we visited at night were clumped together, and were too close to be able to carry out independent point counts. We undertook point counts at colony trees the morning after we visited for a night survey and surveyed for birds at 0 m, 200 m and 400 m along a transect away from the focal colony tree. No point counts were conducted within 400 m of another colony tree. Each point count lasted five minutes, with the observer recording all birds that were seen or heard within 100 m. The surveys started at sunrise, and the final survey finished three hours after sunrise. The order of the survey changed between each visit. Point counts were undertaken from each colony thirteen times during this study. The total counts of each species, for each of the thirteen surveys, was later used as an offset in our statistical models that investigated heterospecific birds roosting in colonies.

Colony use across a temporal gradient: We compared the importance of colonies to the animal community across a year-long temporal gradient, using temperature and normalised difference

vegetation index (NDVI) as measures of a seasonal changing environmental stress. Temperature tolerance is considered an essential constraint for animals, with those living in hot, arid environments facing temperatures that can induce lethal hyperthermia (Cunningham et al. 2013). NDVI is a measure of greenness that allows for analysis of terrestrial vegetation conditions (Solano et al. 2010) and is calculated from reflectance in the near-infrared and red portions of the electromagnetic spectrum (Hurlbert and Haskell 2003). This can provide a reasonable estimate of net primary productivity (Lo Seen Chong et al. 1993, Goward et al. 1994), and can be assumed to correlate positively with food availability within the environment (Hurlbert and Haskell 2003). Vegetation in arid climates responds strongly to rainstorm events; however, these events are unpredictable (Noy-Meir 1973, Reynolds et al. 2004). Consequently, periods of plant production are also variable, and the timing of such events can vary between years (Hillel and Tadmor 1962, Rosenzweig 1968). Calculating NDVI allows for a reliable understanding of when the environment is more or less productive and therefore, can serve as a proxy for harshness.

Daily minimum and maximum temperature data were supplied by the South African Weather Service (SAWS). We calculated the average daily temperature using the following formula:

$$\text{Average temperature} = \frac{\text{Maximum temperature} + \text{Minimum temperature}}{2}$$

NDVI values were acquired from MODIS NDVI time series of eight-day composites from the satellite Terra (MOD09A1 V6) from December 2015 to January 2017. We calculated NDVI values for every day, using ArcGIS 10.4, for the same grid-square (resolution 500 m) in the centre of our study site. To calculate values for each of the days between the eight-day composite, we used the following formula:

$$\text{Day}^n = \text{Day 1} + \left(n * \frac{\text{Day 8} - \text{Day 1}}{8} \right)$$

Statistical Analysis: We analysed data using the R statistical package 3.4.0 (R Core Team 2017), carrying out linear mixed models (LMMs) and generalised linear mixed models (GLMMs) to compare the animal abundance related response variables between colony trees and paired non-colony trees. These were carried out using the glmmTMB package due to its ability to handle zero-inflated models (Brooks et al. 2019).

Where count data were over-dispersed models were fitted with either a quasi-Poisson or negative binomial distributions (Hara and Kotze 2010). On the one occasion when a binomial distribution, still could not account for overdispersion, we log-transformed this data, therefore making it continuous and, thus, fitted with a gaussian distribution (Ives 2015). Zero-inflation was also applied when needed. We used the `emmeans` and `emtrends` functions from the `emmeans` package (Lenth 2018) to undertake post-hoc analyses to check for significant differences between factor levels, concerning environmental stress (NDVI, Temperature; see Appendix 5 for further model details).

We used ‘tree’ as the sampling unit for each response variable, unless otherwise stated; summarising data so that each of the response variables was calculated per tree. We used colony presence (present/absent, our primary variable of interest), tree species (camelthorn/Shephard’s tree), characteristics (PCA1 loading score), NDVI and temperature as explanatory variables in each of these models. Different tree species effects biodiversity differently (Dean et al. 1999), and how colonies effect this may also differ, therefore we fitted an interaction between tree species and colony presence. To determine if colony presence or absence differently influences the ‘events’ at trees of the local animal community depending on the environmental variables, we fitted interactions between NDVI and colony presence, and temperature and colony presence. Tree characteristics, NDVI and temperature variables were always scaled within each model. Each colony tree and its corresponding control tree was given a unique pair ID, these were both used as random effects in the models, with pair ID being nested within site ID. For analyses where interactions were fitted, we explored interactions where p values were less than 0.1 using post-hoc tests. Those that had a value greater than 0.1, or where post-hoc tests revealed no significant differences were subsequently removed from the models. All explanatory variables and random effects mentioned above were used when testing all models, unless otherwise stated.

For terrestrial and arboreal vertebrates, we used the number of camera trap events, event duration, species richness and Shannon-Weiner diversity index (hereafter, Shannon diversity) as response variables. We used a ‘day’ as the sampling unit by summarising the data, so the total number of camera trap events, and the number of individuals of a species were all calculated for a given day at a given tree. However, it was not possible to calculate the Shannon diversity index using this sampling unit due to certain days having minimal or no events. Therefore, we calculated the Shannon diversity index only once for each tree (`vegan` package, Oksanen et al. 2017), using all the data combined for a given tree. Therefore, we omitted the

random factor tree ID from this, and all subsequent diversity analyses. In addition, to reduce any bias created by rare observations, we removed species that had been recorded less than five times across all sampled units before calculating species diversity. Whereas, to analyse the event duration, we used each ‘event’ captured as the sampling unit.

To identify the mechanisms behind each event, we analysed the different behaviours carried out at colony and non-colony trees. We used the camera trap ‘event’ as the sampling unit and used a binomial GLMM to calculate the probability of whether animals used the trees for shade or exhibited foraging or territorial behaviour. We then compared the amount of time (minutes) that each behaviour lasted at colony and non-colony trees. Here, we subset the data so that shade, foraging and territorial behaviour could be used as sampling units and compared independently. We analysed event duration using GLMMs with negative binomial distribution.

When comparing the number of birds observed at colony and non-colony trees, we used the total number of individuals, species richness and Shannon diversity as response variables. We removed Sociable weaver observations from all analysis. We investigated the changes in the abundance of roosting birds, using the number of individuals of each bird species and the total number of heterospecific species (non-sociable weaver) roosting in colonies as response variables (Appendix 5). Colony size (number of chambers), colony height, proximity index (see description below), NDVI and temperature were used as explanatory variables. We used the number of conspecifics observed during the point counts carried out during the morning following roosting assessment as an offset variable in the model (Appendix 5). Tree ID was used as a random term, and we fitted either quasi-Poisson distributions or Poisson distributions to account for overdispersion of specific response variables (Appendix 5). Shannon diversity was also tested using a linear model calculated for each tree, using the total counts.

As colony presence explains response variables (see Results), we subset the data to include only colony trees, and GLMMs used to determine if colony characteristics further influence any of the response variables mentioned above. We used colony size, height and proximity index to other colonies as explanatory variables and used Tree ID as a random effect (Appendix 5). The proximity index was calculated for each colony tree by setting a buffer of 400 m around the colony tree. For each colony, within this buffer, we squared the total numbers of chambers and divided this by the squared distance from the focal colony. We did this for each colony within the buffer and then added these values together.

Results

Abundance of terrestrial vertebrates and behaviour: We collected data for 1106 camera trap days (mean days per tree = 7.18 ± 0.07), observed 35 unique species (mean species per tree per day = 0.5 ± 0.02) and captured 696 events (Appendix 3; mean events per tree, per day = 0.6 ± 0.03). The mean duration of events equalled 4.87 minutes (± 0.52 ; range 1-152 minutes). Cheetahs (*Acinonyx jubatus*), Chacma baboons (*Papio ursinus*), impalas (*Aepyceros melampus*), Cape porcupines (*Hystrix africaeaustralis*) and black-backed jackals (*Canis mesomelas*) were recorded in a greater number of events at colony trees than at non-colony trees (Appendix 3). Cheetahs, giraffes, greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), and baboons, spent longer at colony trees (Appendix 4). Cheetahs used the colonies solely for territorial purposes, while jackals and porcupines foraged below the colony structure (Appendix 3). Kudu spent longer using colonies for shade and giraffes spent twice as long browsing on colony trees than non-colony trees (Appendix 4).

The number of daily animal events was explained by an interaction between colony presence/absence and tree species (Appendix 2.1a). Post-hoc tests revealed that there were 50% more events at camelthorn trees with weaver colonies than those without (Figure 1, $t = 3.02$, $p = <0.05$). No difference was observed in event duration between Shephard's trees with colonies compared to those without (Figure 1, $t = -0.218$, $p = 0.99$). No differences were observed between camelthorns with weaver colonies and Shephard's trees with colonies ($t = 2.57$, $p = 0.10$) and Shephard's trees without colonies (Figure 1, $t = 2.06$, $p = 0.17$). In addition, NDVI significantly explained variation in the number of animal events. Increasing NDVI was associated with increasing animal events, showing a 4½ times increase in mean daily animal events across the range of NDVI measured (NDVI range = 0.16 – 0.39). Temperature, tree characteristics, tree species and the interactions between colony presence and tree species, colony presence and NDVI, and colony presence and temperature did not explain animal events (Appendix 2.1a).

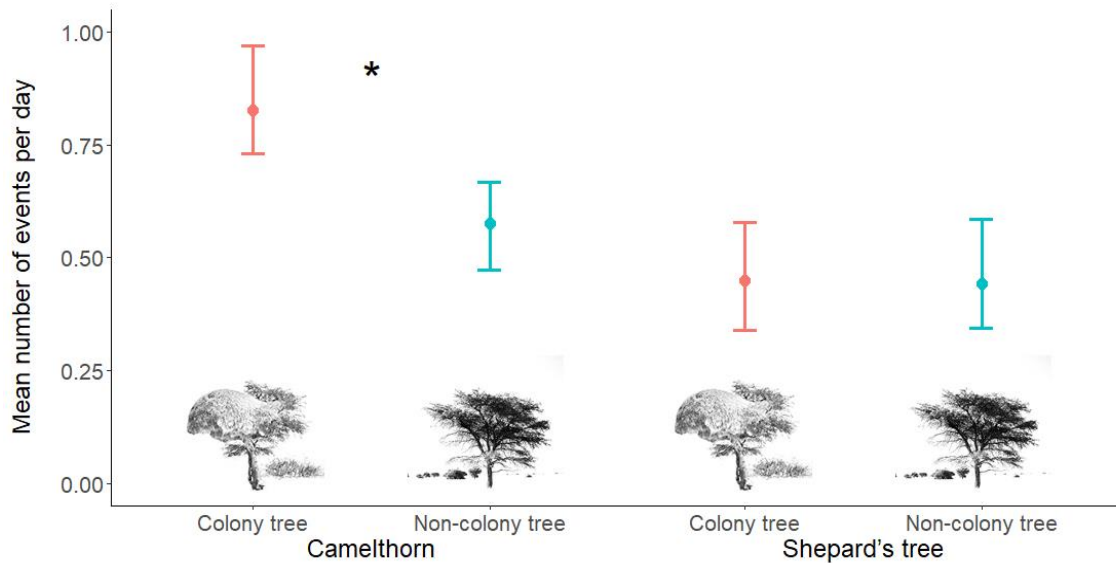


Figure 1. The mean number of camera trap events (raw values \pm 95% CI) at both camelthorn and Shepard's trees with and without weaver colonies. An interaction ($p=0.09$) was observed between trees species and colony presence (* denotes $p < 0.05$).

Animal event duration was explained by tree species and NDVI (Appendix 2.1b; Figure 2). Animal events at camelthorns lasted 1.5 times longer than at Shepard's trees and reduced by 113% as NDVI increased across the range (0.16-0.39). Colony presence, temperature, tree characteristics or the interactions between colony presence and tree species, colony presence and NDVI, and colony presence and temperature did not explain significant variation, therefore all interactions were removed from the final model (Appendix 2.1b).

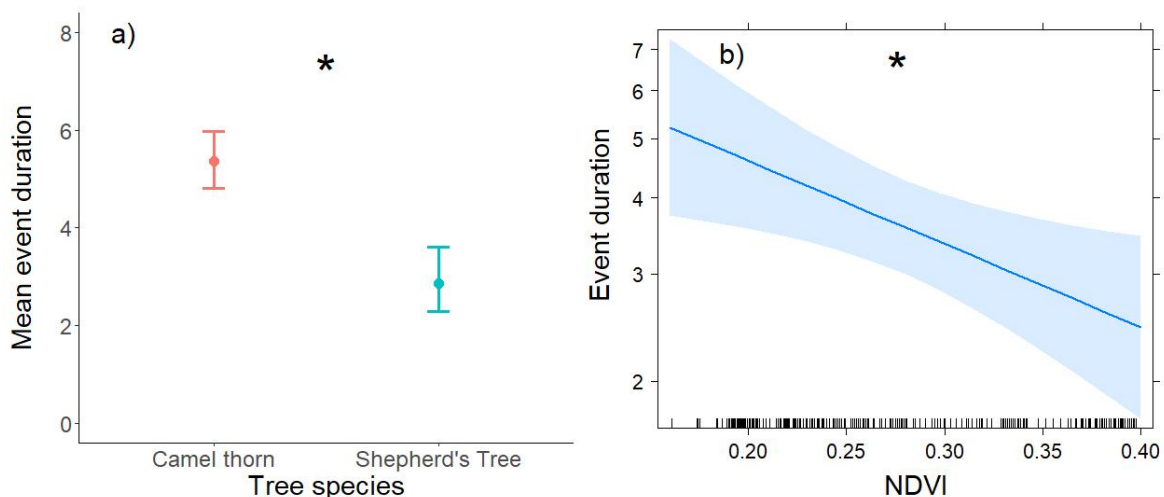


Figure 2. The event duration at camelthorns and Shepard's trees. (a) Mean events (raw values \pm 95% CI) at camelthorn trees than Shepard's trees, (b) Relationship between NDVI scores and event duration (model produced values \pm 95% CI; Y axes in log scale; * denotes $p < 0.05$).

Species richness was significantly explained by colony presence. Daily species richness was 37% higher at colony trees than non-colony trees (mean 0.63 ± 0.037 vs 0.46 ± 0.033). This result is supported by species accumulation curves that show increased steepness in the accumulation of new species, before smoothing out sooner for colony compared to non-colony trees (Figure 3). Furthermore, both species accumulation curves plateau, suggesting that sampling of species was near complete, with a low probability of adding unique species (Figure 3). NDVI also significantly explained variation in species richness at trees (Appendix 2.1c); with richness increasing three-fold (0.25 to 0.97 species per day) as NDVI increased across the range of NDVI values (range = 0.16 – 0.39). Temperature, tree characteristics, tree species and the interactions between colony presence and tree species, colony presence and NDVI, and colony presence and temperature did not explain species richness (Appendix 2.1c).

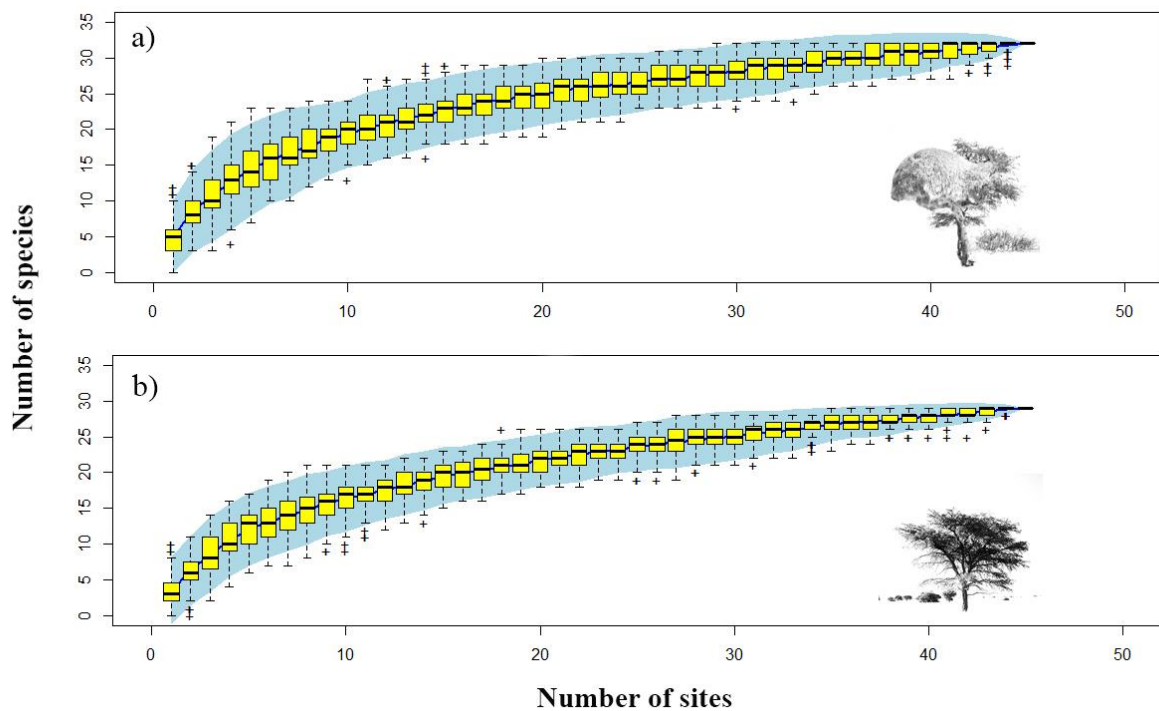


Figure 3. Species accumulation curves of terrestrial vertebrates at (a) colony and (b) non-colony trees.

Colony presence/absence explained significant variation in Shannon diversity (Appendix 2.1d); with diversity being 20% higher at colony trees (Figure 4). The interaction between colony presence and tree species did not explain any variation observed (Appendix 2.1d).

To determine if any of the weaver colony characteristics influenced any of the response variables tested above, we subset the data and concentrated only on data collected at colony

trees. The proximity of the colony in regards to other colonies significantly increased species richness. However, this was driven by a single colony and was subsequently removed from this analysis. Additionally, colony height explained significant variation duration, with animals staying up to 20 times longer under colonies higher from the ground (height range 160 cm to 460 cm; Figure 5). Colony size did not correlate with any of these response variables (Appendix 2.2).

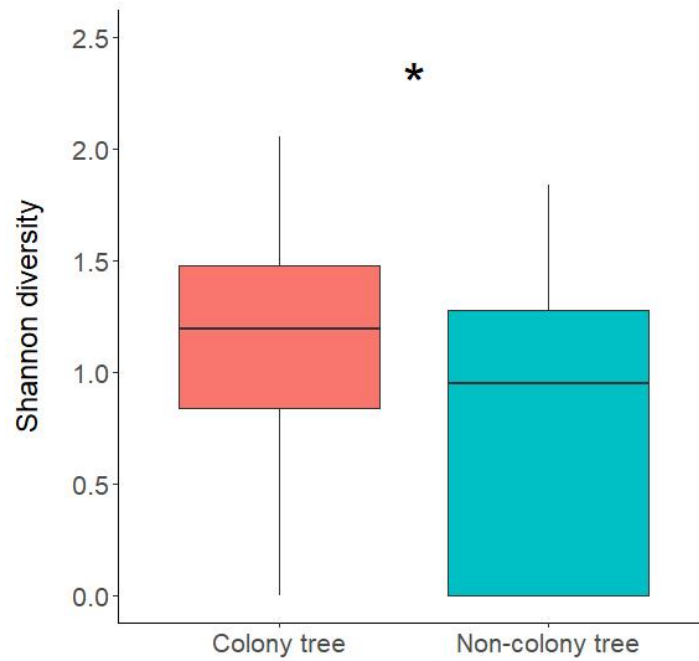


Figure 4. Boxplot indicating Shannon diversity of terrestrial vertebrates at colony and non-colony trees (* $p < 0.05$). The solid line indicates the median, the boxes the 1st and 3rd quartiles, the whiskers indicate the 95% CIs.

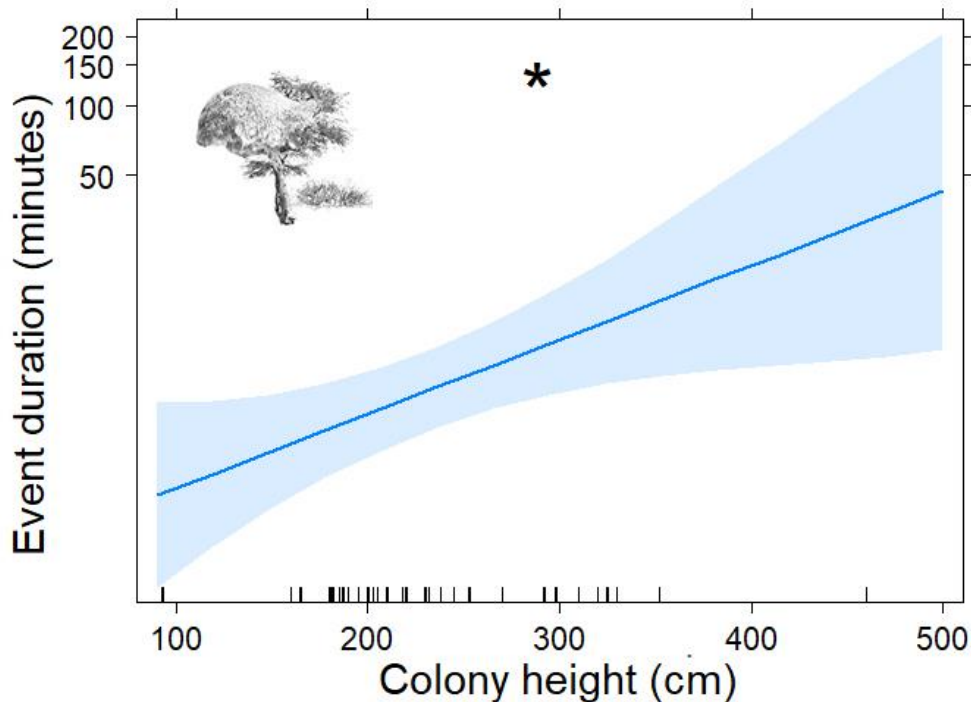


Figure 5. The duration of animal events at colony trees compared with colony height (model produced values \pm 95% CI; Y axes in log scale; * denotes $p < 0.05$).

Of the 696 events, 587 were of animals foraging, 69 of animals using trees for shade and 40 of animals exhibiting territorial behaviours. The mean foraging event duration lasted 3.31 minutes (\pm 0.27), shade 16.7 minutes (\pm 3.78) and territory 7.18 minutes (\pm 3.90). The probability of animals foraging was significantly explained by temperature (Appendix 2.3a); reducing by 26% across the temperature range (4-40°C). As NDVI and temperature increased, foraging duration reduced by 44% and 55% respectively (Appendix 2.3b). Differences in foraging events were explained by the interaction between colony presence and temperature (Appendix 2.3a), while differences in foraging duration were explained by the interaction between colony presence and NDVI (Appendix 2.3b). However, post-hoc tests failed to reveal any differences between colony and non-colony trees, therefore these interactions were subsequently removed from the analysis. Colony presence, tree characteristics, tree species and the interactions between colony presence and tree species, colony presence and tree species did not explain foraging activity (Appendix 2.3).

The probability of animals using trees for shade was significantly explained by NDVI, and a strong trend was explained by temperature (Appendix 2.3c). Animals were 15 times less likely to seek shade as NDVI increased, and 13 times more likely as temperature increased, across

each of the respective ranges. The duration of time animals spent in the shade of colony and non-colony trees was significantly explained by the interaction between colony and non-colony trees. Post-hoc analyses revealed significant differences between the duration of time animals used colony and non-colony trees for shade as temperature increased ($t = 3.30, p = 0.0016$). At colony trees the length of event duration increased as temperature increased (estimate \pm CI = 0.094 ± 0.04 ; Figure 6), with the reverse being observed at non-colony trees (estimate \pm CI = -0.11 ± 0.05 ; Figure 6). Tree characteristics, NDVI, and the interactions between colony presences and tree species, and colony presence and NDVI failed to explain significant variation.

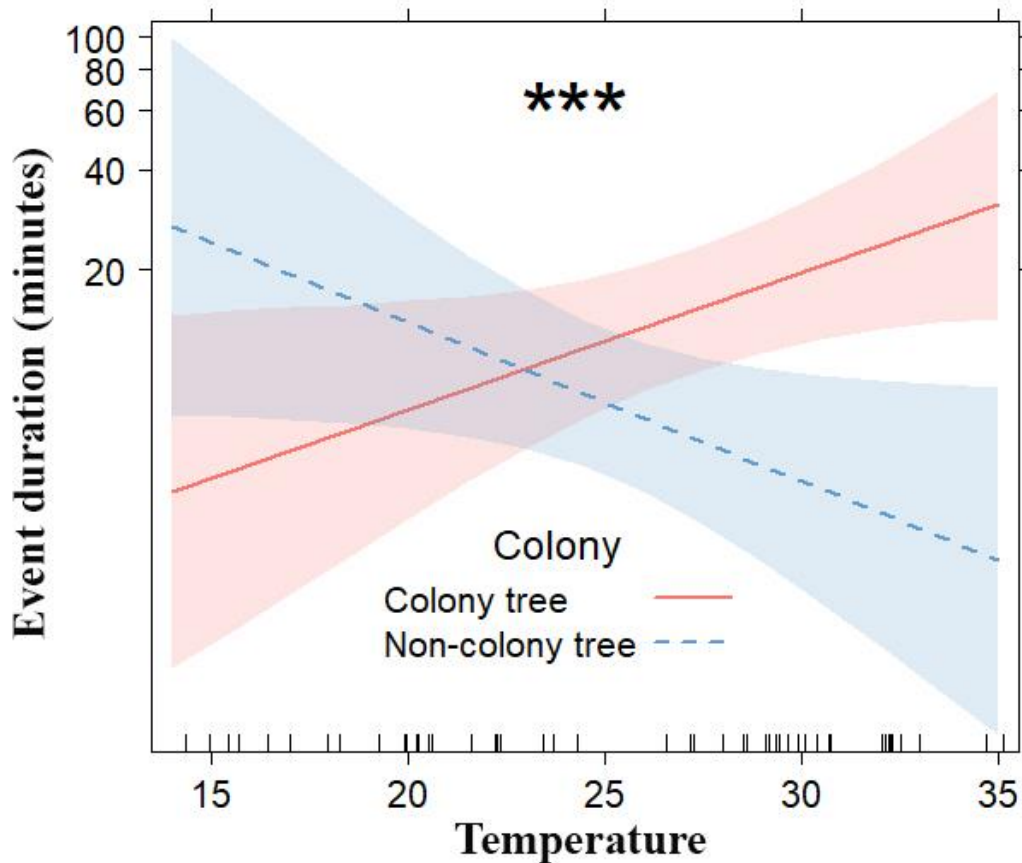


Figure 6. The duration of animals using trees for shade (model produced values \pm 95% CI; Y axes in log scale; *** denotes $p < 0.001$).

The probability of animals exhibiting territorial behaviour was significantly explained by colony presence (Appendix 2.3e; Figure 7). Territorial behaviour was 60% more likely at

colony trees than non-colony trees. Tree species, tree characteristics, NDVI, temperature and the interactions between colony presence and tree species, and colony presence and NDVI failed to explain significant variation (Appendix 2.3e). Neither of the explanatory terms explained significant variation in regards to the territorial event duration (Appendix 2.3f).

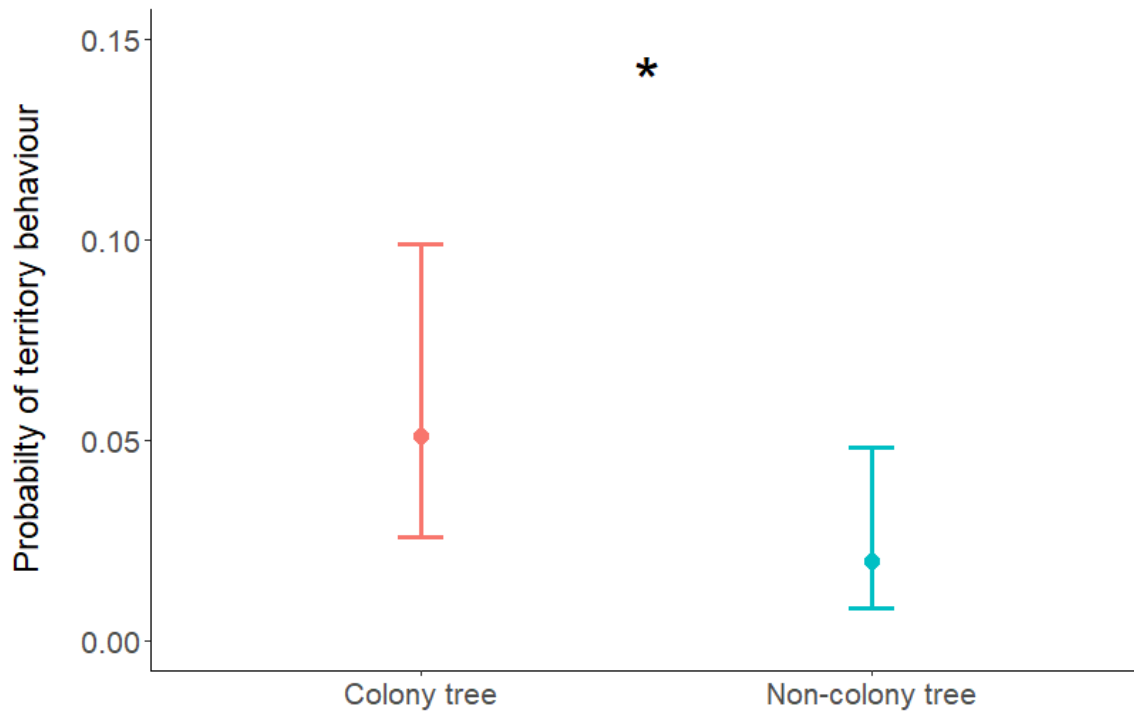


Figure 7. The probability of animals exhibiting territorial behaviour at colony and non-colony trees (model produced values \pm 95% CI; * denotes $p < 0.05$).

Abundance of arboreal vertebrates: We collected a total of 713 camera traps days (mean per tree = 7.9 ± 0.3) for arboreal vertebrates, observing 12 unique species (mean species per tree per day = 0.14 ± 0.01) and capturing 198 events (Appendix 3; mean events per tree, per day = 0.28 ± 0.03). Mean event duration equalled 4.04 minutes (± 0.71 , range 1 – 66 minutes). Woodland dormouse (*Graphiurus murinus*), black-tailed tree rats, large-spotted genets (*Genetta tigrine*), slender mongooses (*Galerella sanguinea*), and African wildcats (*Felis libyca*), were observed foraging on top of weaver colonies. Genets were also seen recorded scent marking, while mongooses were recorded using the colonies during winter nights (Appendix 3).

Colony presence/absence and NDVI explained significant variation in the number of animal events (Figure 8; Appendix 2.4a). Our model revealed that there were 34 times as many animal events at colony trees than non-colony trees and that the number of events dropped by 40 times across the NDVI range (0.16-0.39; Figure 8; Appendix 2.4a). Temperature, tree characteristics, tree species did not explain animal events (Appendix 2.4a). Furthermore, due to the lack of individuals observed at non-colony trees, it was not possible to view the interaction results with any confidence; therefore, we omitted these from arboreal vertebrate analysis. No differences were observed with regards to arboreal event duration (Appendix 2.4b).

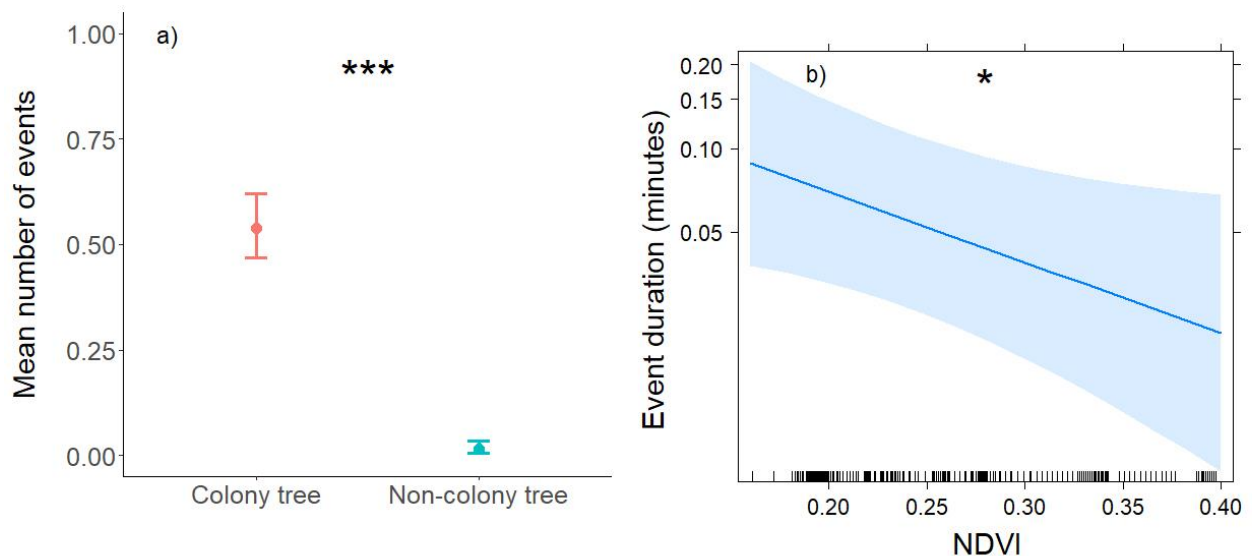


Figure 8. The responses for (a) the number of arboreal camera trap events between colony and non-colony trees (mean raw values \pm 95% CI), (b) and the event duration compared with NDVI (model values \pm 95% CI; Y axes in log scale; ** = $p < 0.01$; *** $p < 0.001$).

Colony presence significantly increased species richness (Appendix 2.4c); with species richness per day being 35 times higher at colony than non-colony trees (mean 0.28 ± 0.03 vs 0.008 ± 0.005), this is supported by species accumulation curves (Figure 9). NDVI, temperature, tree characteristics, tree species and the interactions between colony presence and tree species, colony presence and NDVI, and colony presence and temperature did not explain arboreal animal events (Appendix 2.4c). Due to the low frequency of species recorded, reliable

diversity indices could not be calculated. Additionally, Colony size, explained significant variation in event duration, with animals spending more than 7.5 times longer on top of larger colonies (range 12 to 117; Figure 10). Colony height and proximity index did not influence any of the response variables (Appendix 2.5).

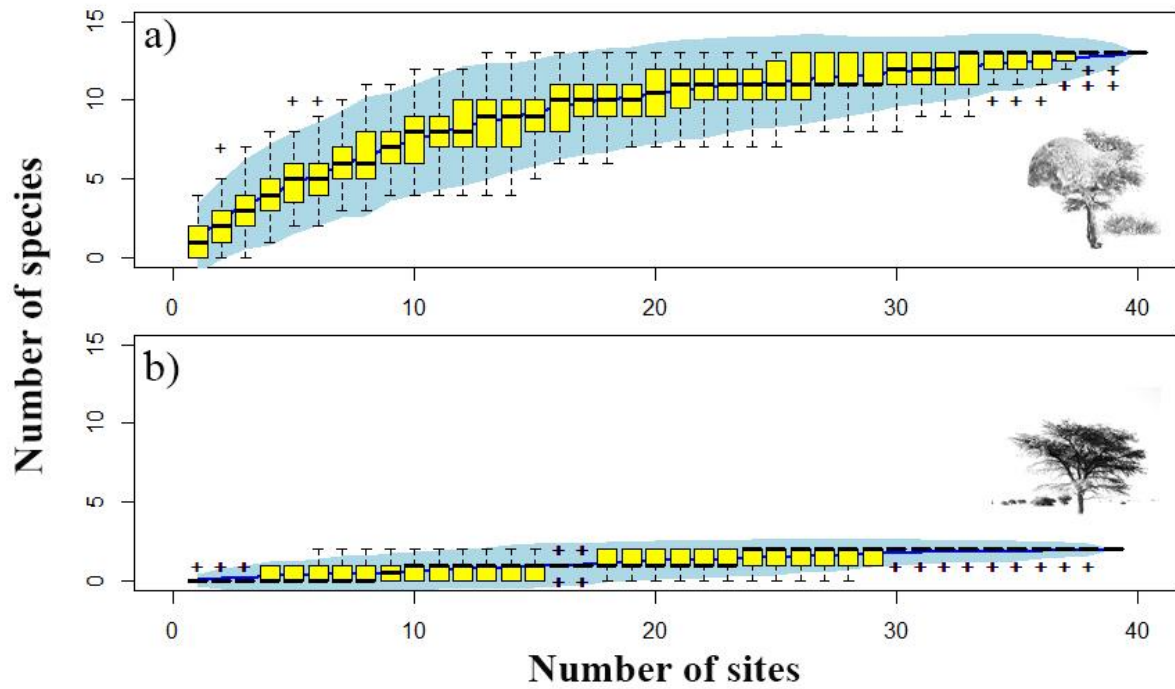


Figure 9. Species accumulation curves of arboreal vertebrates at (a) colony and (b) non-colony trees.

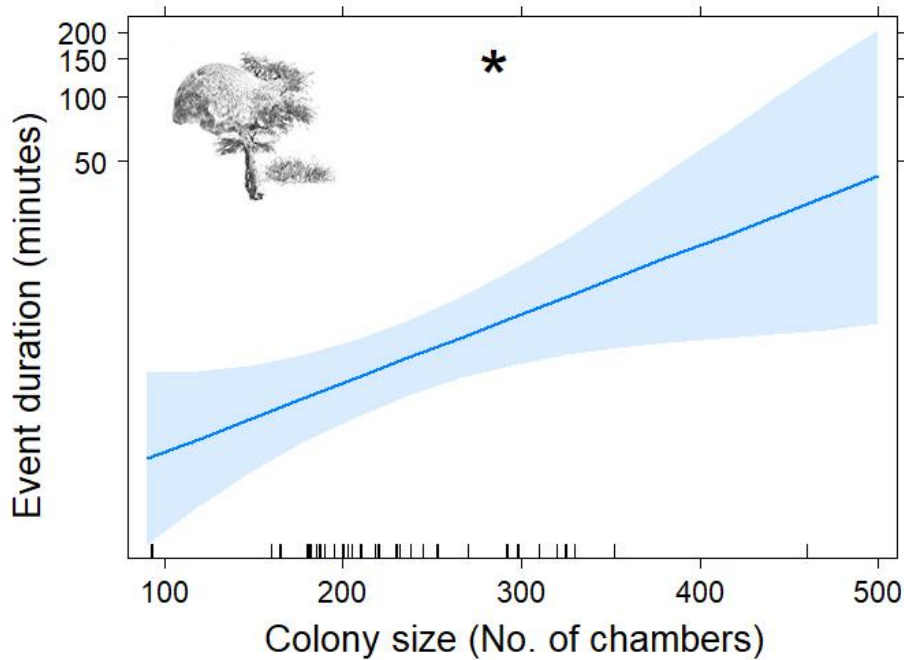


Figure 10. The duration of arboreal animal events at colony trees compared with colony size (model produced values \pm 95% CI; Y axes in log scale; * denotes $p < 0.05$).

Abundance of avian species: A total of 125 point counts were carried out at both colony and non-colony trees. Forty unique species (mean 0.97 species/count \pm 0.08) and 433 individuals (mean 1.8 individuals /count \pm 0.35) were observed.

Colony presence did not explain the numbers of individuals or species richness (Appendix 2.6). Whereas, increasing temperature was associated with a significant reduction in both the number of individuals and species richness (Appendix 2.6). The number of individuals more than halved (2.37 to 1.05) and species richness reduced by 35% (1.3 species per count to 0.74) across the temperature range (14.6 – 28.12°C). Tree characteristics, tree species, NDVI, temperature and the interactions failed to explain any of the variation (Appendix 2.6).

Differences in Shannon diversity were significantly explained by the interaction between colony presence and tree species (Appendix 2.6). However, post-hoc tests failed to reveal any differences between colony and non-colony trees, regardless of species, therefore this interaction was subsequently removed from the analysis. Additionally, colony size, colony height and proximity index did not influence any of the response variables (Appendix 2.7).

Night use of colony chambers: Of the 46 nest colonies sampled at night to document the abundance of heterospecific roosting bird species, 39 (87%) were occupied by other avian species at least once. Four species were recorded (mean 0.6 species per colony, per visit \pm 0.02), African pygmy falcons, Acacia pied barbets (*Tricholaema leucomelas*), ashy tits (*Melaniparus cinerascens*) and scaly-feathered finches (*Sporopipes squamifrons*). A mean of 1.26 ± 0.09 individuals was observed per tree per visit.

The proximity of the colony in regards to other colonies significantly increased species richness. However, this was driven by a single colony, which we subsequently removed from our analysis. Additionally, colony size or height did not correlate with the number of heterospecifics or species richness. (Appendix 2.8). However, colony size significantly explained species diversity variation with the Shannon diversity index more than doubling in larger colonies (Figure 11, Appendix 2.8; range 16 to 117).

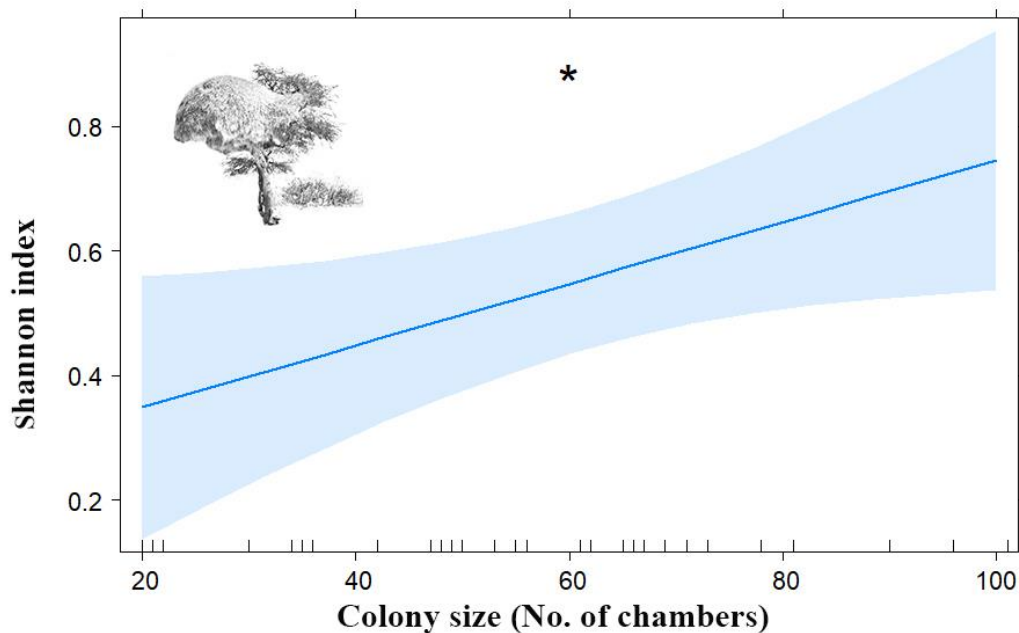


Figure 11. Shannon diversity comparisons with colony size, with outliers, removed model values \pm 95% CI; * denotes $p < 0.05$).

Discussion

Our results show that the presence of a Sociable weaver colony in a tree creates localised biodiversity hot-spots. Across the taxa that we measured, we found that individuals visited trees more often when they contained a weaver colony and that the amount of time spent at colony and non-colony trees depended on the reason of visit. Overwhelmingly, we demonstrate the

importance of weaver colonies to the Kalahari animal community. Weavers are a clear-cut case of an obligate ecosystem engineer, defined by Coggan et al. (2018); as their colonies appear to act as focal points of activity in the broader landscape and create habitat, increase habitat heterogeneity and likely influence community structure. The physical influences are defining elements of their habitat, and seemingly provide resources utilised by birds and small arboreal mammals; even large mammals congregate at these colonies. The resources provided by these colonies change as abiotic factors change; however, the colony influence on structure and diversity of animal communities is maintained throughout our temporal gradient.

Weaver colonies create islands of biodiversity in the Kalahari landscape. High animal activity and diversity likely feedback into creating localised patches of nutrient-rich soils in this otherwise oligotrophic landscape (Prayag, du Toit, Cramer & Thomson unpublished), reinforcing the existing island of fertility created by large trees in the Kalahari (Dean et al. 1999). Small and large mammals visited camelthorn trees with colonies more frequently than camelthorns without colonies. However, no differences were observed for terrestrial mammals at Shephard's trees, whether or not they contained a colony. Animals also stayed longer at camelthorns than at Shephard's trees, independent of colony presence. Canopy structure between the two tree species are different and may explain why animals prefer camelthorn trees. Shephard's trees often have low overhanging canopies, making it difficult for larger animals to access the resources below. Whereas, the camelthorns trees have an umbrella-type structure meaning it is easier to access resources underneath the canopy (Dean et al. 1999, Dudley 1999, Seymour 2006). Our results also show the importance of colonies for avian species; 87% of colonies hosted heterospecific roosting birds, and across the landscape, avian diversity appears to increase around trees hosting colonies. Weaver colonies may, therefore, appear to be important to Kalahari animal community structure, and accounting for the spatial dispersion of colonies in the landscape is likely necessary when investigating aspects of this community and indeed even for management of game populations.

Overall, animal activity and diversity changed across the environmental gradients we tested; however, the impact of weaver colonies did not differ. NDVI led to an increased number of animal events, species richness and diversity, but a reduction in event duration. Furthermore, the overall effects of NDVI did not differ between colony and non-colony trees, suggesting that these individuals were becoming more active as landscape productivity increased, and more resources became available. Additionally, as NDVI increased the amount of time animals spent foraging reduced, likely due to an increase in the quality of vegetation available within

the environment (Begon et al. 1986). Conversely, as temperature increased, foraging, along with overall activities, reduced as more animals spent longer using the colonies for shade (Figure 10). Animal exhibiting territorial behaviours (scent marking, chasing, fighting) were primarily carried out at colony trees, and this may be attributed to species, including cheetahs, using prominent landmarks to scent-mark within their territory (Caro 1994, Lowney and Charlton 2017). However, territorial behaviours did not vary depending on NDVI or Temperature.

Arboreal activity reduced as NDVI increased. This coupled with the lack of observations at non-colony trees suggests that colonies become increasingly important to arboreal mammals as landscape productivity reduces, and this would fit the stress gradient hypotheses. However, the lack of observations at non-colony trees does mean that this could not be tested in this study but should be the focus of future research.

Increasing temperature reduced bird abundance at colony and non-colony trees. Nevertheless, variation due to NDVI and temperature did not differ between colony and non-colony trees, suggesting that the importance of these colonies to the surrounding avian community varies very little across a temporal gradient. Other studies have shown that the effects of birds as ecosystem engineers varies across a temporal gradient (Natusch et al. 2016). However, these studies focused on migratory species, whose influence on local communities is strongly influenced by the presence/absence of the engineer in question (Bancroft et al. 2008, Natusch et al. 2016), whereas weavers are non-migratory, and the colony as a structure to other species is maintained year-round. Overall, the lack of variation in species abundance and diversity across the temporal scale, maybe due to our investigation of the avian community as a whole, and not at the species level. However, the reasons for animals using colony trees differed (Appendix 3), suggesting that the resources are context-dependent. Therefore, we recommend that further research investigates change at the species level and in functional groupings.

We further the scientific knowledge in this field by demonstrating the positive effects of a small structural (allogenic) engineer on a community assemblage that contains mega-fauna in excess of 200 kgs. Other studies have shown that allogenic engineers improve biodiversity, but the extent of our responses in native species from small birds and mammals to antelope and predators is noteworthy. We found that weaver colonies had the most significant impact on arboreal vertebrates. On average allogenic species increase species richness by 25% (Romero et al. 2015), but here we reveal an increase of 37%. Colony structures provide refuge for

arboreal rodents, but also create a platform that larger mammals, including leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), use as resting places or vantage points (Lowney and Charlton 2017). The fact that 87% of the colonies studied were used by roosting heterospecific birds shows the importance of these colonies to other bird species. Birds that roost within the colony chambers receive thermal benefits during the high summer and cold winter temperatures (van Dijk et al. 2013, Leighton and Echeverri 2014). Additionally, by roosting with hundreds of other heterospecifics, these individuals may gain a reduction in predation, via a dilution effect (Eiserer 1984, Beauchamp 1999). However, understanding the full benefits to the species within this community needs further examination.

Weaver colonies provide habitat for a wide range of species, some of which would otherwise not exist within this environment. For example, African pygmy falcons do not build their own nest and rely solely on Sociable weaver chambers for roosting and breeding (Maclean 1970). Furthermore, two groups not included in this study, arthropods and herptiles, are expected to benefit most from terrestrial engineers (meta-analysis by Romero et al. 2015), and this is supported by studies that have shown increased abundance of invertebrates and reptiles at weaver colonies (Rehn 1965, Covas 2002, Rymer et al. 2014, Harvey et al. 2015, Chapter 3). Many of these studies were species-specific and, along with this study, were carried across small spatial scales. Therefore, we suggest investigating the effects of these colonies across the entire weaver distribution as we predict that these structures provide resources for species not present in this community, and the importance of this resource will vary.

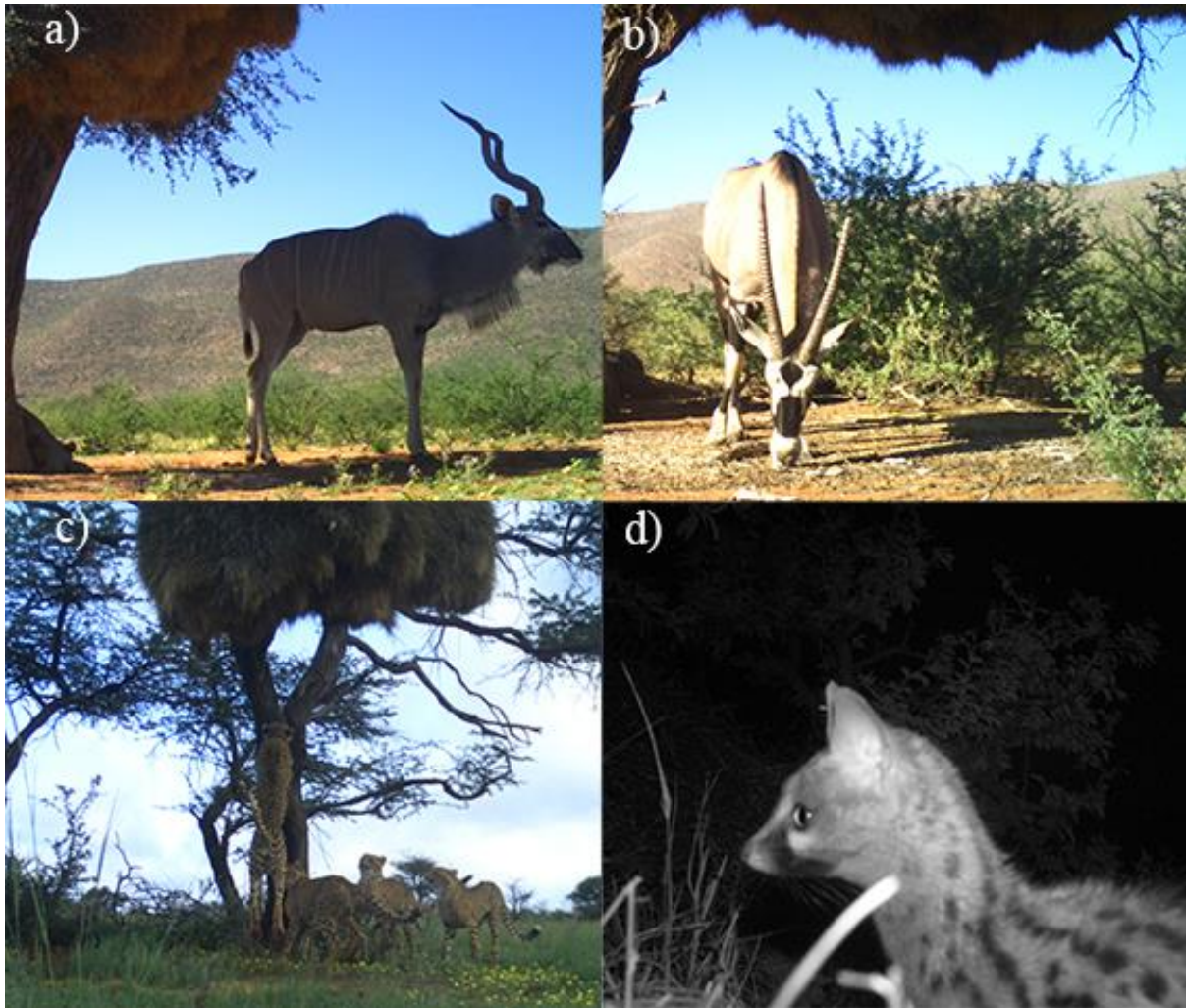


Figure 12. Sociable weaver colonies being utilised by members of the local animal community. (a) Greater kudu (*Tragelaphus strepsiceros*) using the shade cast by the colony, (b) gemsbok (*Oryx gazelle*) foraging on sprouting vegetation below a colony, (c) four cheetahs climbing up to the top of a colony (d) and small-spotted genet (*Genetta genetta*) foraging on top of a colony.

Colony characteristics influenced mammal event duration and roosting bird diversity. Terrestrial mammals spent longer at colonies that were higher above the ground, possibly due to higher structures casting larger shadows, whereas arboreal mammals spent longer on larger colonies, as these would create larger platforms to rest and use as vantage points. Larger colonies also have a greater diversity of avian species roosting in the chambers, and this is understandable as these colonies have more chambers for more species to use, i.e. can provide more of the chamber ‘resource’. However, this argument does not explain the lack of variation between the number of roosting heterospecifics at colonies of differing sizes. The lack of other effects may be due, in part, to our selection criteria of choosing colonies with more than twenty chambers. Once colonies have reached this size the biodiversity effects may already be quite

significant, and already plateauing off. Furthermore, colonies are conspicuous within a landscape and last for more than 100 years (Friedmann 1930). Therefore, once a colony is established, it would be an easy resource to locate. We are unsure of how fast a colony grows and at what size a colony starts to influence the local community. But we expect this will vary between the associated species. We suggest that future studies lower the chamber threshold to understand how large a colony needs to be before it starts to influence the local animal community. Studies may also wish to monitor the expansion of new colonies and monitor the change in effects as colonies age, expand and collapse.

In summary, our findings add to the growing literature that ecosystem engineering is a significant biological interaction (Hastings et al. 2007, Romero et al. 2015, Coggan et al. 2018). We demonstrate the importance of Sociable weavers as a structural engineer and the significance of their colonies in structuring the surrounding animal community. Despite different species using colonies to mitigate environmental stress, many species observed using these structures would most likely occur within the same landscape without colonies. However, whether their densities and reproductive success would be similar in areas without weaver colonies needs to be tested. Despite showing the importance of weaver colonies at the community level we did not find any change over a temporal scale. This may be due to the length of our study, as longer studies covering multiple years may be more likely to find changes over time, if such changes exist. We were, however, able to show that different species use these structures for various reasons, for example: the greater kudu will use the colonies for shade, whereas Cape porcupines and Black-backed jackals will forage directly underneath a colony (Appendix 3); meaning changes may occur at the species level, and this needs to be further tested. Furthermore, when compared to non-colony trees we show that the number of visits to colony trees by arboreal species increases exponentially. It appears that Sociable Weaver colonies are not only characteristic of the Kalahari, but have huge ecological importance to local animal communities and that by mitigating environmental stress, may be increasingly important as human driven climate change advances.

Appendix 1. Loading scores from the Principle Component Analysis (PCA), comparing tree characteristics measured; tree height, canopy cover and circumference at chest height.

Principle Component	Percent variation
Loading score 1	93.7%
Loading score 2	6.3%
Loading score 3	0.0%

Appendix 2.1. Results from the generalised linear mixed models investigating the terrestrial vertebrate abundance variables to colony presence, NDVI, temperature, tree species and tree characteristics at 43 colony trees and 43 paired non-colony trees. Interactions with *p* values greater than 0.10 were removed from the final models. All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	± SE	χ^2	<i>P</i>
a) Animal events n=1106	Colony (yes/no)			9.01	< 0.01
	Tree species			5.13	<0.05
	Tree characteristics	0.01	0.07	0.01	0.90
	NDVI	0.43	0.07	40.56	< 0.001
	Temperature	0.10	0.07	2.04	0.15
	Colony present*Tree species	0.48	0.28	2.87	0.09
Interactions removed					
	Colony present*NDVI	-0.07	0.12	0.33	0.57
	Colony present*temperature	-0.18	0.13	2.05	0.15
b) Event duration n= 696	Colony (yes/no)			2.60	0.11
	Tree species			4.14	< 0.05
	Tree characteristics	0.05	0.09	0.31	0.58
	NDVI	-0.23	0.09	6.58	< 0.05
	Temperature	0.01	0.08	0.01	0.91
Interactions removed					
	Colony present*Tree species	0.31	0.41	0.58	0.44

	Colony present*NDVI	-0.14	0.19	0.59	0.44
	Colony present*temperature	-0.21	0.13	2.42	0.12
c) Species richness	Colony (yes/no)			7.48	<0.01
	Tree species			1.94	0.16
n=1106	Tree characteristics	0.01	0.06	0.02	0.88
	NDVI	0.39	0.07	35.82	<0.001
	Temperature	0.08	0.07	1.60	0.21
Interactions removed					
	Colony present*Tree Species	0.41	0.26	2.56	0.11
	Colony present*NDVI	-0.11	0.11	0.85	0.35
	Colony present*temperature	0.17	0.12	2.01	0.15
d) Shannon diversity	Colony (yes/no)			4.38	<0.05
	Tree species			0.54	0.46
n= 86	Tree characteristics	0.05	0.49	1.07	0.30
Interaction removed					
	Colony present*Tree Species	-0.03	0.21	0.02	0.89

Appendix 2.2. Results from the generalised linear mixed models investigating the effects on terrestrial vertebrate abundance variables, at colony trees only, to colony size, height and proximity index (camera trap days n = 533 at 43 colony trees; species diversity n = 43). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Events	Colony Size	0.04	0.09	0.21	0.65
n=533	Colony Height	-0.13	0.10	2.1	0.15
	Proximity Index	0.11	0.07	2.3	0.14
b) Event duration	Colony Size	-0.28	0.18	2.47	0.11
n=533	Colony Height	0.46	0.18	6.28	<0.05
	Proximity Index	-0.12	0.23	0.26	0.61

c) Species richness n=533	Colony Size	0.05	0.09	0.35	0.55
	Colony Height	-0.17	0.10	2.93	0.08
	Proximity Index	0.11	0.09	1.54	0.21
d) Shannon diversity n=43	Colony Size	-0.06	0.09	0.48	0.49
	Colony Height	-0.134	0.09	2.2	0.146
	Proximity Index	0.014	0.09	0.03	0.87

Appendix 2.3. Results from the generalised linear mixed models investigating the terrestrial vertebrate behaviour variables to colony presence, NDVI, temperature, tree species and tree characteristics at 43 colony trees and 43 paired non-colony trees (sample sizes, within table). Interactions with p values greater than 0.10 were removed from the final models. The significant interaction between colony presence and temperature, resulting from the foraging probability analysis (a), and colony presence and NDVI (b) were also removed, due to post-hoc tests demonstrating differences to be none significant (250 point counts at 50 trees). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Foraging probability n=696	Colony (yes/no)			1.58	0.21
	Tree species			2.52	0.11
	Tree characteristics	0.01	0.15	0.01	0.94
	NDVI	0.31	0.20	2.48	0.12
	Temperature	-0.37	0.18	4.20	<0.05
Interactions removed					
	Colony present*NDVI	4.27	0.28	2.28	0.13
	Colony present*Tree Species	-0.16	0.72	0.05	0.83
	Colony present*temperature	0.60	0.33	3.45	0.06
b) Foraging duration n=587	Colony (yes/no)			0.61	0.44
	Tree species			1.27	0.26
	Tree characteristics	0.02	0.09	0.07	0.80
	NDVI	-0.18	0.09	4.31	<0.05

	Temperature	-0.18	0.81	4.80	<0.05
Interaction removed					
	Colony present*Tree Species	-0.11	0.38	0.08	0.77
	Colony present*NDVI	-0.29	0.17	2.81	0.09
	Colony present*temperature	0.09	0.16	0.29	0.59
c) Shade probability	Colony (yes/no)			0.21	0.65
	Tree species			1.67	0.20
n=696	Tree characteristics	-0.12	0.17	0.48	0.50
	NDVI	-0.80	0.28	8.18	<0.01
	Temperature	0.43	0.23	3.52	0.06
Interactions removed					
	Colony present*Tree species	0.76	0.98	0.60	0.44
	Colony present*NDVI	-0.35	0.50	0.49	0.48
	Colony present*temperature	-0.37	0.40	0.85	0.36
d) Shade duration	Colony (yes/no)			4.45	<0.05
n=69	Tree species			0.01	0.92
	Tree characteristics	-0.05	0.21	0.06	0.80
	NDVI	-0.42	0.25	2.69	0.10
	Temperature	0.58	0.27	4.45	<0.05
	Colony present*temperature	-1.26	0.38	10.91	0.0009
Interactions removed					
	Colony present*Tree species	-0.22	1.22	0.03	0.86
	Colony present*NDVI	0.89	0.48	1.57	0.21
e) Territory probability	Colony (yes/no)			5.16	<0.05
	Tree species			1.33	0.25
n=696	Tree characteristics	0.11	0.25	0.21	0.65
	NDVI	0.31	0.31	1.06	0.30
	Temperature	0.14	0.28	0.24	0.62
Interactions removed					

	Colony present*Tree Species	0.01	1.31	0.001	0.99
	Colony present*NDVI	-1.03	0.64	2.54	0.11
	Colony present*Temperature	-0.63	0.49	1.62	0.20
f) Territory duration	Colony (yes/no)			1.20	0.27
	Tree species			0.53	0.46
n=40	Tree characteristics	-0.92	1.25	0.04	0.85
	NDVI	-0.39	0.45	0.73	0.39
	Temperature	0.82	0.51	2.61	0.11
Interaction removed					
	Colony present*Tree Species	-1.57	2.53	0.38	0.54
	Colony present*NDVI	1.49	1.40	1.12	0.12
	Colony present*temperature	1.13	1.0	1.25	0.26

Appendix 2.4. Results from the generalised linear mixed models investigating arboreal vertebrate abundance in response to colony presence, NDVI, temperature, tree species and tree characteristics (camera trap days n=716; species diversity n=78). Interactions with *p* values greater than 0.10 were removed from the final models. All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Animal events	Colony (yes/no)			37.09	<0.001
	Tree species			0.09	0.76
n=716	Tree characteristics	0.15	0.50	0.06	0.81
	NDVI	-0.34	0.16	4.34	<0.05
	Temperature	-0.10	0.18	0.34	0.56
b) Event duration	Colony present			0.006	0.94
	Tree species			0.93	0.33
n=716	Tree characteristics	-0.13	0.15	0.76	0.38
	NDVI	-0.06	0.15	0.22	0.64
	Temperature	0.07	0.16	0.16	0.69

c) Species richness n=716	Colony (yes/no)			32.62	<0.001
	Tree species			0.13	0.71
	Tree characteristics	0.02	0.13	0.02	0.90
	NDVI	-0.34	0.18	3.44	0.06
	Temperature	-0.20	0.18	1.27	0.26
d) Species diversity n=43	Colony (yes/no)	0.28	0.05	18.95	<0.001
	Tree species	-0.02	0.07	0.12	0.73
	Tree characteristics	0.01	0.03	0.12	0.73
Interaction removed					
	Colony present*Tree Species	0.008	0.09	0.009	0.92

Appendix 2.5. Results from the generalised linear mixed models investigating the effects of colonies on arboreal vertebrate abundance, at colony trees only to, variables to colony size, height and proximity index (camera trap days n=358 days; species diversity n= at 39). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Animal Events n=358	Colony Size	0.204	0.248	0.68	0.41
	Colony Height	-0.003	0.256	0.0001	0.99
	Proximity Index	0.06	0.24	0.07	0.8
b) Event duration n=358	Colony Size	0.75	0.36	4.3	<0.05
	Colony Height	-0.26	0.29	0.79	0.37
	Proximity Index	-0.39	0.30	1.62	0.20
c) Species richness n=358	Colony Size	0.18	0.19	0.97	0.33
	Colony Height	-0.08	0.19	0.18	0.67
	Proximity Index	0.08	0.18	0.19	0.66
d) Species Diversity n=39	Colony Size	-0.10	0.06	2.43	-0.12
	Colony Height	-0.06	0.06	1.11	0.29
	Proximity Index	0.02	0.06	0.16	0.68

Appendix 2.6. Results from the generalised linear mixed models investigating bird count data at trees with and without colonies, NDVI, temperature, tree species and tree characteristics (point counts $n = 250$; diversity $n = 50$). Interactions with p values greater than 0.10 were removed from the final models. The significant interaction between colony presence and tree species, resulting from the species diversity analysis (c), was also removed, due to post-hoc tests demonstrating differences to be none significant (250 point counts at 50 trees). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Number of individuals	Colony (yes/no)			1.08	0.30
	Tree species			0.79	0.38
	Tree characteristics	-0.03	0.11	0.06	0.80
	NDVI	0.05	0.09	0.26	0.62
	Temperature	0.26	0.09	8.52	<0.01
Interaction Removed					
	Colony present * Tree species	-0.11	0.43	0.06	0.79
	Colony present*NDVI	-0.10	1.8	0.38	0.54
	Colony present*temperature	0.24	1.8	1.79	0.18
b) Species richness	Colony (yes/no)			0.52	0.47
	Tree species			0.46	0.50
	Tree characteristics	0.02	0.03	0.37	0.54
	NDVI	0.04	0.03	1.61	0.20
	Temperature	-0.10	0.03	11.78	<0.001
Interaction Removed					
	Colony present * Tree species	0.28	0.39	0.50	0.48
	Colony present*NDVI	0.07	0.18	0.13	0.72
	Colony present*temperature	9.29	0.17	0.03	0.87
c) Species diversity	Colony(yes/no)			0.18	0.67
	Tree species			0.63	0.43
	Tree characteristics	-0.06	0.06	1.01	0.31
Interaction Removed					
	Colony present * Tree species	0.58	0.25	5.62	<0.02

Appendix 2.7. Results from the generalised linear mixed models investigating the effects on avian abundance variables, at colony trees only, to colony size, height and proximity index (n =125; species diversity n = 50). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Total individuals n=125	Colony Size	0.17	0.13	5.14	0.18
	Colony Height	-0.02	0.11	1.73	0.86
	Proximity Index	0.11	0.09	1.56	0.21
b) Species richness n=125	Colony Size	0.11	0.10	1.44	0.23
	Colony Height	-0.05	0.11	0.20	0.65
	Proximity Index	-.03	0.11	0.06	0.80
c) Shannon diversity n=25	Colony Size	0.08	0.09	0.74	0.40
	Colony Height	-0.106	0.09	1.43	0.23
	Proximity Index	0.84	0.09	0.97	0.32

Appendix 2.8. Results from the generalised linear mixed models investigating roosting birds at colony trees only, NDVI, temperature, tree species and tree characteristics (Night visits n = 598; species diversity n = 46). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 5.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Heterospecific abundance n=598	Colony size	0.004	0.004	0.92	0.34
	Colony height	0.209	0.165	1.61	0.20
	Proximity index	-0.354	0.195	3.28	0.07
	NDVI	0.037	0.065	0.33	0.57
	Temperature	0.078	0.067	1.36	0.24
b) Species richness n=598	Colony size	0.197	0.134	2.18	0.14
	Colony height	0.113	0.135	0.70	0.40
	Proximity index	-0.318	0.170	3.52	0.06
	NDVI	0.033	0.06	0.25	0.62
	Temperature	0.067	0.068	0.98	0.32
c) Species diversity n=46	Colony size	0.14	0.06	5.10	<0.05
	Colony height	-0.01	0.06	0.01	0.91
	Proximity index	-0.03	0.06	0.34	0.56

Appendix 3. The number of animal events for the most abundant vertebrates captured by camera traps at colony and non-colony trees

Terrestrial species		Total		Foraging		Shade		Territory	
		Colony Present		Colony Present		Colony Present		Colony Present	
		Yes	No	Yes	No	Yes	No	Yes	No
Gemsbok	<i>Oryx gazella</i>	76	74	70	69	2	3	4	2
Greater Kudu	<i>Tragelaphus strepsiceros</i>	58	58	28	31	30	26		1
Blue Wildebeest	<i>Connochaetes taurinus</i>	35	27	31	25	2	1	2	1
Springbok	<i>Antidorcas marsupialis</i>	27	31	26	27	1	4		
Eland	<i>Taurotragus oryx</i>	23	18	20	17		1	3	
Warthog	<i>Phacochoerus africanus</i>	23	12	22	12			1	
Cape Porcupine	<i>Hystrix africaeaustralis</i>	20	8	20	8				
Common Duiker	<i>Sylvicapra grimmia</i>	19	16	12	16			7	
Black-backed Jackal	<i>Canis mesomelas</i>	17	2	16	2			1	
Impala	<i>Aepyceros melampus</i>	16	9	14	4	2	4		1
Giraffe	<i>Giraffa camelopardalis</i>	14	13	14	13				
Cheetah	<i>Acinonyx jubatus</i>	13	2	0	0			13	2
Chacma Baboon	<i>Papio ursinus</i>	11	2	10	2	1			
Mountain Zebra	<i>Equus zebra</i>	7	10	6	10	1			
Aardvark	<i>Orycteropus afer</i>	6	2	6	2				

Arboreal species						
Woodland Dormouse	<i>Graphiurus murinus</i>	68		68		
Large-spotted Genet	<i>Genetta tigrina</i>	37		33		4 0
Slender Mongoose	<i>Galerella sanguinea</i>	37		30		7 0
Black-tailed Tree Rat	<i>Thallomys nigricauda</i>	24	3	24	3	
African Wildcat	<i>Felis libyca</i>	9		9		
Chacma Baboon	<i>Papio ursinus</i>	2	2	2	2	
Leopard	<i>Panthera pardus</i>	2	0			2 0

Appendix 4. The length of event duration (mean minutes) for those animals that spent the most amount of time at colony and non-colony trees.

Terrestrial species		Total		Foraging		Shade		Territory	
		Colony Present		Colony Present		Colony Present		Colony Present	
		Yes	No	Yes	No	Yes	No	Yes	No
Leopard	<i>Panthera pardus</i>	40	0	0	0	79	0	0	0
Cheetah	<i>Acinonyx jubatus</i>	18.38	1.0	0	0	0	0	18.38	1.0
Giraffe	<i>Giraffa camelopardalis</i>	14.5	7.79	14.5	7.79	0	0	0	0
Impala	<i>Aepyceros melampus</i>	9.37	9.33	11.21	7.5	1.0	13.25	0	0
Greater Kudu	<i>Tragelaphus strepsiceros</i>	14.56	4.6	2.8	3.09	25.19	6.46	0	5.0
Springbok	<i>Antidorcas marsupialis</i>	6.93	1.0	7.15	4.54	1.0	7.25	0	0
Chacma Baboon	<i>Papio ursinus</i>	5.0	1.5	5.4	2.0	1.0	0	0	0
Hartebeest	<i>Alcelaphus buselaphus</i>	7.25	2.2	7.25	2.5	0	1.0	0	0
Mountain zebra	<i>Equus zebra</i>	5.29	2.6	5.33	2.6	5.0	0	0	0
Blue Wildebeest	<i>Connochaetes taurinus</i>	2.75	3.03	2.88	2.93	1.5	8.0	2	0
Eland	<i>Taurotragus oryx</i>	1.67	4.25	1.76	3.11	0	1.0	1.0	28.0
Common Duiker	<i>Sylvicapra grimmia</i>	3.4	1.44	3.54	1.41	0	0	3.14	0
Gemsbok	<i>Oryx gazella</i>	2.2	2.74	1.75	2.76	20.00	0	1.0	1.0
Steenbok	<i>Raphicerus campestris</i>	2.67	1.0	2.67	1.0	0	0	0	0
Warthog	<i>Phacochoerus africanus</i>	2.4	1.4	2.46	1.5	0	0	1.0	0
Arboreal species									

Slender Mongoose	<i>Galerella sanguinea</i>	9.16	0	9.4	0	0	0	8.12	0
Chacma Baboon	<i>Papio ursinus</i>	11	2.5	11	2.5	0	0	0	0
African Wildcat	<i>Felis libyca</i>	5	0	5	0	0	0	0	0
Black-tailed tree-rat	<i>Thallomys nigricauda</i>	3.54	2.33	3.54	2.33	0	0	0	0
Large-spotted Genet	<i>Genetta tigrina</i>	0	2.06	0	2.12	0	0	0	0
Woodland Dormouse	<i>Graphiurus murinus</i>	0	1.8	0	1.8	0	0	0	0
Leopard	<i>Panthera pardus</i>	0	0	0	0	1.0	0	0	0

Appendix 5. Complete list of models used, including response, explanatory and random effects. Distribution, transformations, zero inflations and overdispersion parameters are also shown. All carried models were carried out in the glmmTMB package using the glmmTMB function (Brooks et al. 2019).

Response variables	Model	Distribution	Explanatory variables	Random effects	Transformation	Zero inflation	Overdispersion parameter
<u>Abundance and behaviour of terrestrial vertebrates</u>							
Camera trap events	GLMM	Quasi-Poisson	Colony (present/absent) Tree species Tree characteristics NDVI Temperature Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID		No	0.415
Event duration (minutes)	GLMM	Quasi-Poisson	Colony (present/absent) Tree species Tree characteristics NDVI Temperature	Pair ID / Tree ID		No	0.903

			Colony present * Tree species Colony present * NDVI Colony present * Temperature				
Species richness	GLMM	Quasi-Poisson	Colony (present/absent) Tree species Tree characteristics NDVI Temperature Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID		No	0.061
Shannon Diversity	LM	Gaussian	Colony (present/absent) Tree species Tree characteristics Colony present * Tree species		sqrt	No	0.098
Probability of animals foraging	GLLM	Binomial	Colony (present/absent) Tree characteristics NDVI Temperature	Pair ID / Tree ID Tree species			

			Sample duration (offset)			
			Colony present * Tree species			
			Colony present * NDVI			
			Colony present * Temperature			
Foraging duration	GLLM	Negative binomial	Colony (present/absent)	Pair ID / Tree ID	No	1.29
			Tree characteristics	Tree species		
			NDVI			
			Temperature			
			Sample duration (offset)			
			Colony present * Tree species			
			Colony present * NDVI			
			Colony present * Temperature			
Probability of animals using trees for shade	GLLM	Binomial	Colony (present/absent)	Pair ID / Tree ID		
			Tree characteristics	Tree species		
			NDVI			
			Temperature			
			Sample duration (offset)			
			Colony present * Tree species			
			Colony present * NDVI			
			Colony present * Temperature			

Shade duration	GLLM	Negative binomial	Colony (present/absent) Tree characteristics NDVI Temperature Sample duration (offset) Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID Tree species	No	0.63
Probability of animals displaying territorial behaviour	GLLM	Binomial	Colony (present/absent) Tree characteristics NDVI Temperature Sample duration (offset) Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID Tree species		
Territory duration	GLLM	Negative binomial	Colony (present/absent) Tree characteristics NDVI	Pair ID/Tree ID Tree species	No	2.69

Temperature
 Sample duration (offset)
 Colony present * Tree species
 Colony present * NDVI
 Colony present * Temperature

Effects of colony characteristics on terrestrial
 vertebrates

Camera trap events	GLMM	Quasi-Poisson	Colony size Colony height Proximity index Sample duration (offset)	Tree ID		No	0.555
Colony duration	GLMM	Negative binomial	Colony size Colony height Proximity index Sample duration (offset)	Tree ID	log10 +1	No	0.184
Species richness	GLMM	Quasi-Poisson	Colony size Colony height Proximity index	Tree ID		No	0.111

Sample duration (offset)

Abundance of arboreal vertebrates

Camera trap events	GLMM	Poisson	Colony (present/absent) Tree species Tree characteristics NDVI Temperature	Pair ID/Tree ID	Yes	
Event duration (minutes)	GLMM	Negative binomial	Colony (present/absent) Tree species Tree characteristics NDVI Temperature	Pair ID / Tree ID	No	1.01
Species richness	GLMM	Poisson	Colony (present/absent) Tree species Tree characteristics NDVI Temperature	Pair ID / Tree ID	Yes	

Shannon-Wiener index	LM	Gaussian	Colony (present/absent)		log1 + 1	No	0.322
			Tree species				
			Tree characteristics				
			Colony present*Tree species				

Effects of colony characteristics on arboreal vertebrates

Camera trap events	GLMM	Quasi-Poisson	Colony size	Tree ID		Yes	0.153
			Colony height				
			Proximity index				
			Sample duration (offset)				

Event duration (minutes)	GLMM	Negative binomial	Colony size	Tree ID			0.78
			Colony height				
			Proximity index				
			Sample duration (offset)				

Species richness	GLMM	Poisson	Colony size	Tree ID		Yes	
			Colony height				
			Proximity index				
			Sample duration (offset)				

Comparison of bird count data at trees with and without colonies

Total number of birds	GLMM	Negative binomial	Colony (present/absent) Tree species Tree Characteristics NDVI Temperature Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID		No	1.11
Species Richness	LMM	Gaussian	Colony (present/absent) Tree species Tree Characteristics NDVI Temperature Colony present * Tree species Colony present * NDVI Colony present * Temperature	Pair ID / Tree ID	Log + 1	No	
Shannon diversity index	LM	Gaussian	Colony (present/absent) Tree species		sqrt	No	

Tree characteristics
 Colony * Tree species

Effects of colony characteristics on bird point count data

Total number of birds	GLLM	Quasi-Poisson	Colony size Colony height Proximity index	Tree ID	No	1.11
Species Richness	GLLM	Poisson	Colony size Colony height Proximity index	Tree ID	No	
Species Diversity	LM	Gaussian	Colony size Colony height Proximity index		sqrt	No
Colony influence on the abundance of roosting birds						
Heterospecific abundance	GLLM	Quasi-Poisson	Colony size Nest Height Proximity index	Tree ID	No	1.25

			NDVI		
			Temperature		
			Point counts (offset)		
Species richness	GLLM	Poisson	Colony size	Tree ID	No
			Nest Height		
			Proximity index		
			NDVI		
			Temperature		
			Point counts (offset)		
Shannon diversity index	LM	Gaussian	Colony size	sqrt	No
			Nest height		
			Proximity index		

Chapter 3

Ecosystem engineering across a spatial aridity gradient: Sociable Weaver colonies as a key facilitator of animal associations with increasing environmental harshness.



Abstract

Animal spatial distribution in a landscape depends mainly on resource availability. Resource availability is often facilitated by other species and can positively influence local species diversity and community structure. Species that significantly change resource availability are often termed ecosystem engineers. Identifying these species is important, but predicting where they have large or small impacts is a key challenge that will enhance the usefulness of the ecosystem engineering concept. The stress gradient hypothesis predicts that the importance of facilitative interactions that shape community structure and function are anticipated to increase in stressful and harsh environments. To test this hypothesis, we investigate the role of Sociable weavers (*Philetairus socius*) as ecosystem engineers and investigate how this impact varies across a spatial gradient of harshness, for which aridity served as a proxy. These birds build large colonies that are home to hundreds of weaver individuals but also host a wide range of other species, both avian and non-avian. How vital these colonies are to these species and how this importance may change as environment changes are unknown. We investigated the use of weaver colonies on multiple taxa (mammals, birds, reptiles and invertebrates) at multiple sites. We demonstrate that the presence of Sociable weaver colonies creates localised biodiversity hot-spots and that the importance of weaver colonies to the surrounding animal community characterises their entire range. Furthermore, colony trees were associated with a greater abundance of animals at sites with lower rainfall, whereas sites with higher rainfall had a more evenly distributed abundance of animals between colony and non-colony trees. Therefore, results from our study were consistent with the stress gradient hypothesis and demonstrate that this hypothesis can be extended to animal communities and that these engineers help mitigate some of the extreme differences between environments differing in harshness.

Introduction

Animal spatial distribution in a landscape depends on resource availability (McIntyre and Wiens 1999, Hunter et al. 2012), which can be concentrated in certain locations (Parrish and Edelstein-Keshet 1999). Resource availability is often facilitated by other species, and this can positively influence local species diversity and impact community structure (reviewed by Soliveres et al. 2015). Species that significantly change resource availability in an environment are frequently termed ecosystem engineers (Jones et al. 1994). This concept is not without criticism because all species engineer their environments to some degree and describing all species as engineers are said to have trivialising this concept (Reichman and Seabloom 2002a,

2002b). Therefore, the real value is not to only document engineers that disproportionately influence ecosystems, but also to determine their consequences to communities. Importantly, ecosystem effects may be context-dependent, therefore where these ‘engineers’ will have the greatest abiotic and biotic impacts is critical to understand (Crain and Bertness 2006, reviewed by Coggan et al. 2018). However, the impacts and interactions of ecosystem engineers have been mainly carried out across small spatial scales, limiting our understanding of how spatial context may alter impacts.

Ecosystem engineers can impact resource availability in multiple ways (Badano and Cavieres 2006). For example, species that affect soil properties can directly influence plant community composition and diversity by altering species abundance and changing the evenness of species assemblages (Flecker 1996, Crooks and Khim 1999, Whitford and Kay 1999). Additionally, ecosystem engineers could provide resources or a refuge that alters habitats to become suitable for species that would not usually be able to persist; increasing the realised niche of species and ultimately increasing community species richness (Bertness and Callaway 1994, Wright et al. 2002, Castilla et al. 2004, Badano and Cavieres 2006). Structural engineers (allogenic engineers, *sensu* Jones et al. 1994) create physical habitat that provides resources and shelter (Berke 2010). The impacts of structural engineers are among the most studied engineering interactions. However, research into land-based ecosystem engineers has revealed a considerable taxonomic bias towards mammals and invertebrates. Few studies show birds to be engineers (Coggan et al. 2018), which is surprising as bird nests have been shown to create ecological hot-spots, and nest construction can take many shapes and sizes (Bancroft et al. 2005, Mainwaring et al. 2015, Natusch et al. 2016).

The significance of facilitative interactions in shaping community structure and function are anticipated to increase as environmental harshness increases; the stress gradient hypothesis (Bertness and Callaway 1994). Substantial empirical evidence supports this prediction and demonstrates that there are greater associative and positive between-species impacts under higher environmental stress, often mediated by identified ecosystem engineers (Wright et al. 2006, Cavieres and Badano 2009, Schöb et al. 2013, He and Bertness 2014, Bulleri et al. 2016). Testing of the stress gradient hypothesis has almost exclusively been carried out on plant communities; indeed, animal ecologists have been surprisingly slow to apply these ideas to animal communities. Moreover, studies across broader spatial scales are challenging to replicate but may demonstrate the importance of engineers to different communities. Environmental stress will likely vary significantly across an engineer’s distribution (Erpenbach

et al. 2012, Coggan et al. 2016). Therefore, monitoring an engineer's impact over large-scale ecological gradients would enable a greater understanding of how they may mitigate the extreme differences between environments differing in harshness.

Species interactions are likely a key factor as communities respond to climate change (Harrington et al. 1999, Suttle et al. 2007, Alexander et al. 2015). In arid environments, in particular, climate change will predominantly cause increasing frequencies and duration of hot-weather events (Meehl and Tebaldi 2004, Akoon et al. 2011), conditions that will make these environments harsher to the majority of species (Erasmus et al. 2002, Isaac 2009). Altered species interactions due to an environment becoming too harsh may lead to a loss of certain species from a given community, long before species-specific temperature thresholds are reached. Ecosystem engineers join the abiotic and trophic aspects of communities via their interaction networks (Sanders et al. 2014). For example, engineered structures that would typically provide thermal refuges may be crucial under increasing higher temperatures (Coogan et al. 2018), resulting in increased use of these structures. Using an aridity gradient as a 'space for time' proxy allows comparison of species interactions with ecosystem engineers as environmental stress increases. The 'space for time' approach may allow more accurate predictions of how animal community structure and species interactions may change as benign sites become harsher, and how engineers could mitigate stress. Therefore, understanding how interactions with engineers may change will help determine what may happen to species communities in sites that are not already identified as being harsh.

We aim to understand the importance of a terrestrial animal ecosystem engineer to animal species diversity and community structure and use the system to test how its impacts may change in response to environmental harshness. Our candidate engineer is the Sociable weaver (*Philetairus socius*; hereafter, weaver), a colonial passerine endemic to the semi-arid and arid Kalahari in the western parts of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Weavers build massive colonies that can contain hundreds of nesting chambers and house hundreds of individual weavers (Maclean 1973a). Camelthorn trees (*Vachellia erioloba*), often host weaver colonies (Maclean 1973c). These trees have already been shown to increase biodiversity on a local scale (Dean et al. 1999, Seymour 2006). However, impacts on community biodiversity may further increase if these trees contain weaver colonies. Weaver colony structures provide additional resources, including thermal benefits to occupants (Batholomew et al. 1975, White et al. 1975, van Dijk et al. 2013), a potentially crucial resource in arid environments, while food and nutrient resources may concentrate at nest colonies too

(du Toit 2016, Prayag 2016). Weaver colonies may, therefore, be a resource to other animals in the environment (Chapter 2). For example, Kalahari tree skinks (*Trachylepis spilogaster*) increase in abundance at trees that host weaver colonies (Rymer et al. 2014), while African pygmy falcons (*Polihierax semitorquatus*) and at least some arthropods are entirely dependent on these structures (Rehn 1965, Maclean 1970, Harvey et al. 2015). A wide range of vertebrate taxa also associate with these colonies (Chapter 2, Maclean 1973b, Lowney and Charlton 2017). Nevertheless, the full importance of these nest colonies to the surrounding animal community is still unknown.

Water availability is key to environmental productivity and is often used as an indicator of environmental stress (Barchuk and Díaz 2005, Coggan et al. 2016). Up to 40% of the Earth's surface is classified as arid (Salem 1989), and rainfall can vary considerably within dry environments (Sharon 1972). The stress experienced by animal communities can change significantly across these arid environments. The climate within the weaver's distribution (Figure 1) is characterised by hot summers with rare, but heavy rainstorms and cold and dry winters. Precipitation is unpredictable, and as a result, the vegetation in arid environments respond strongly to storm events (Noy-Meir 1973, Reynolds et al. 2004). This unpredictability often results in fluctuations between little or plentiful vegetation cover (Hillel and Tadmor 1962, Rosenzweig 1968), which in turn, determines the availability of resources to other species further up the food web (Polis 1991). These extremes provide radically different conditions to animal communities, and the impact of any engineer may change depending on these environmental contexts.

To determine the impact of weaver colonies, we quantified how the presence of a weaver colony influenced the composition of the local community at trees with and without colonies. We use multiple sites, and in doing so, can undertake a meta-replicated study of weavers as ecosystem engineers. Our previous study used only one site (Chapter 2), but by comparing across multiple sites we can test the generality of our previous results. The eight sites selected for this study differed in aridity and represented a 'harshness gradient' that allowed us to test the predictions of the stress gradient hypothesis. The principles behind this hypothesis suggest that positive interactions should be more frequent in communities under high physical stress, but when the physical environment is relatively benign then facilitation should be rare (Bertness & Callaway 1994). Support for this hypothesis would be that more stressful sites have an increased probability of animals interacting with trees with colonies, than trees without. We monitored the number of animals that visited and interacted with colonies, using camera

traps, observations, and insect traps. Our response included multiple animal taxa; large vertebrates, reptiles, birds and invertebrates, which we compared between trees hosting weaver colonies and tree without weaver colonies.

Materials and Methods

Study site

We visited eight different field sites between March and May 2018 (Figure 1). Sites were visited one after the other, with the first five sites in South Africa and the final three in Namibia. We chose sites to incorporate a rainfall gradient, and we visited these in the following order: Dedebeben ('Tswalu Kalahari' 27°17'13.12"S , 22°29'4.45"E, mean rainfall per year 361 mm, study area approx. 32 km²), Kimberly ('Benfontein Nature Reserve' 28°49'27.26"S, 24°49'13.89"E, 430 mm, study area approx. 20 km²), Marydale (29°21'8.38"S, 22°15'49.86"E, 132 mm, study area approx. 6.5 km²), Askham ('Murray Ranch' 26°59'7.56"S, 20°51'52.25"E, 93 mm, study area approx. 15 km²), Rietkloof ('Uitkoms guest farm' 28°32'38.47"S, 22°27'42.71"E, 241 mm, study area approx. 27 km²), Keetmanshoop ('Quiver tree forest' 26°28'53.19"S, 18°14'36.53"E 138 mm, study area approx. 15 km²), Aus (26°33'39.02"S, 16°29'2.48"E, 84 mm, study area approx. 29 km²) and Sesriem ('Desert homestead' 24°39'40.07"S, 15°56'28.41"E, 62 mm, study area approx. 15 km²; Figure 1). There was a minimum nearest neighbour distance of 91km between each site (mean nearest neighbour distance 161 km \pm 53.9 SD, range 91 km - 237 km).

We mapped all weaver colonies, at each site, during the first 24 hours on site. From mapped colonies, we randomly selected colonies, focusing only on those found in camelthorn trees, as these trees are frequently used by weavers throughout their distribution. We paired each selected colony tree with a tree of the same species and similar in structure that did not contain a weaver colony. To account for spatial effects within sites, paired trees were less than 200m apart (mean 90 m \pm 51.5 SD). Initially, 16 colony trees and 16 control trees were selected at each site, with eight used for large vertebrate sampling and eight used to sample other taxa, this was planned to reduce disturbance at each tree; however, after the first site (Tswalu Kalahari), it became clear that some sites would not contain enough colonies to follow this protocol. Therefore, we performed all sampling at the same eight colony trees and their eight paired control trees per site. When sampling bird taxa, we used different control trees to those mentioned above. This was to reduce the likelihood of the same bird being counted at colony and non-colony control trees. Therefore, we used paired control trees that were a minimum of

200 meters away from the colony trees (249 mean \pm 59.37 SD), still matching for tree species and size.

We recorded the main characteristics of each tree used for sampling. We measured tree height by taking photographs with a reference ladder placed at the tree and using Image J software (Schindelin et al. 2012). Trunk diameter was measured as the diameter at breast height (DBH) with a standard tape measure; if the trunk split before this point, the diameter was measured immediately below this split. We calculated canopy cover, by measuring the maximum length and perpendicular width of the canopy, and applying these to the equation: canopy cover = $(\pi r^2)/2$, where $r = (\text{maximum length} + \text{perpendicular width})/2$ (Witkowski *et al.* 1994). We used a principal component analysis to reduce confounding effects that the tree characteristics may have on our subsequent analysis (Pearson correlation matrix: canopy cover v tree height $|r| = 0.44$; canopy cover v DBH $|r| = 0.27$; tree height v DBH $|r| = 0.30$). Response variables loaded heavily on principal component 1 (95.8%; Appendix 1); therefore, this was the only component used in our analyses. Response variables loaded heavily on principal component 1 (95.8% of the variance explained; Appendix 1); this was the only component used in our analyses.

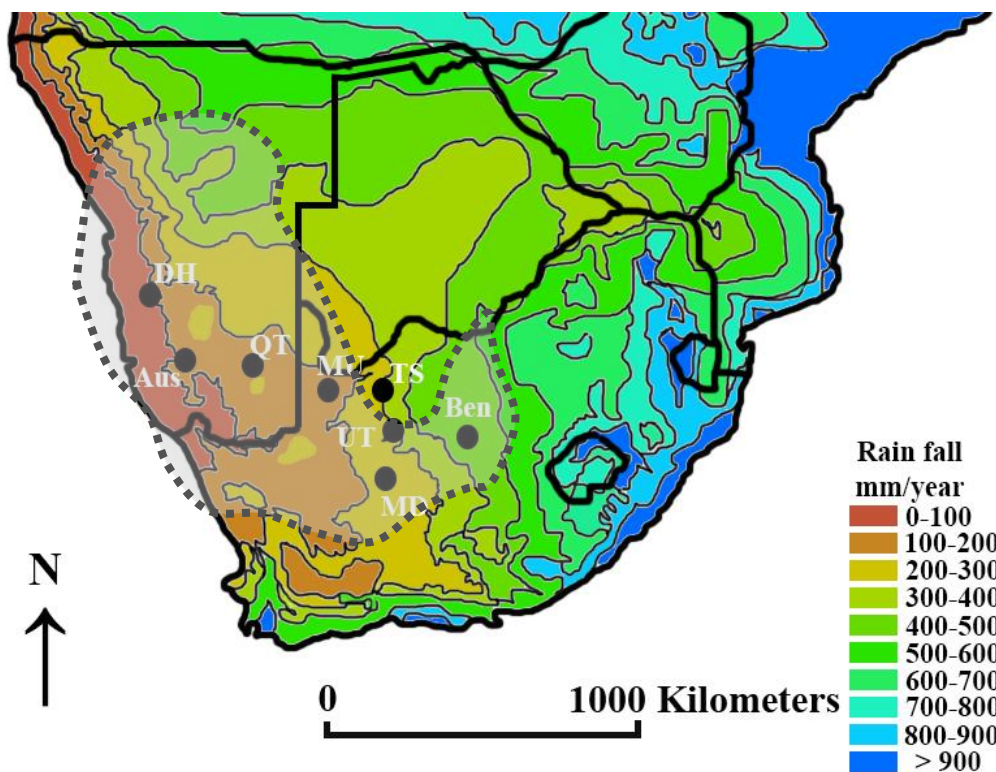


Figure 1. Eight field sites were selected across a range of annual rainfall. These sites were Desert homestead (DH), Aus (Aus), Quiver tree forest (QT), Murray ranch (MU), Tswalu Kalahari (TS), Uitkoms guest farm (UT), Marydale (MD), and Benfontein (Ben). Dotted lines represent the weaver distribution.

Sampling of animals

We used five taxa-specific sampling methods to quantify the abundance and diversity of fauna present at each colony (n = 8) and non-colony (n = 8) tree within each site.

Abundance of mammals: we used camera traps to sample mammals using the eight colony and eight paired control trees. We surveyed paired trees concurrently for five consecutive days. Camera traps (Bushnell, Cuddleback, Little Acorn, Natureview and Scoutguard) were equipped with a black flash and 8gb memory card. We deployed two cameras at each tree. The first was used to sample terrestrial species and was attached to a metal stake set 60 cm above the ground and placed so that they had a clear view of the area under the tree and the surrounding vegetation. The second was deployed to monitor arboreal vertebrates and was attached to the tree so that it had a clear view along the top of the weaver colony. When this was not possible, they were placed so that they focused along the supporting branch towards the colony. For paired non-colony control trees, the arboreal tree cameras were deployed so that they focused along the thickest branch of that tree. Cameras at paired trees were always of the same make and model with identical sensitivity settings. Camera traps were set to be motion-triggered and to take three consecutive photographs and a ten-second video; a minimum period of one minute would elapse before the camera could be triggered again.

We extracted the following data from the camera traps: the number of camera trap events – a single event was defined as the moment an animal triggered the camera until it leaves. If multiple individuals of the same species entered the area, this would be defined as a single event that started the moment the first individual entered until the last individual left. If multiple species were captured simultaneously, then a separate event was allocated to each species. For each event captured, the species, number of individuals, and behaviour performed were recorded. Behaviour was classified as either foraging, displays of territoriality (fighting, chasing, scent marking), using the colony for shade, and passing by. All individuals that were categorised as ‘passing by’ were subsequently removed from all analyses, because these individuals were deemed not to be interacting with the tree and/or colony. We also calculated the amount the time each event lasted by using the timestamps on each photo. If an individual

was captured by both arboreal and terrestrial cameras, then only the data from the arboreal camera was used.

Abundance of reptiles: We followed Rymer and colleague's (2014) protocol, to sample reptile abundance. We carried out counts from four locations around a colony tree, each lasting four minutes, using spotting scopes (Kowa TSN-881 and Kowa 20-60x eyepiece). The observer was located at least 50 meters from the tree, and after each 4-minute count, the observer moved to the next location, approximately 90 degrees around the tree. Once a full rotation of the tree had been carried out, a further four minutes were used for the observer to walk towards and around the tree slowly; this helped identify individuals on the floor, as these individuals were difficult to see from a distance of 50 metres and to clarify any uncertainties about whether some individuals may have been counted twice. Counts were carried out by two different observers, one counting reptiles at the colony tree, while the other counting reptiles at the paired non-colony tree. Counts at colony and paired trees were undertaken at the same time, with observers rotating between colony and non-colony tree between each tree count.

Abundance of avian species: To determine avian abundance we undertook point counts at each tree between sunrise and within 3 hours from sunrise. All point counts were carried out by a single observer (AL). Once the observer arrived at the sample tree, one minute was waited to allow for any disturbance to subside before starting the point count. A single point count, each lasted four minutes, was carried out at each tree. All bird species seen or heard within 25 m of the tree were noted. The order of point counts was rotated between paired trees; therefore, colony and non-colony trees received their counts first an equal number of times.

Abundance of invertebrates: We used two complementary sampling techniques to sample invertebrate abundance. Pitfall traps to sample terrestrial invertebrates and pan traps to sample aerial insects. These were deployed at trees and left undisturbed for three consecutive nights. Pitfall traps consisted of 50 ml falcon tubes (30-mm diameter), filled with ~ 20 ml of a 1:1 solution of water and propylene glycol, and buried so that the lip of the tube was flush with the soil surface. Six pitfall traps were placed under each tree at 2 m intervals in a transect running outward and starting at the base of the trunk and directly under the colony. Pan trapping consisted of yellow plastic trays (40 cm length, 30.5 cm width, and 8 cm deep) that were half-filled with a 1:1 solution of water and propylene glycol. Colour preference of invertebrates can bias sampling, and when undertaking comparative biodiversity studies high reflectance colour trays (white or yellow) should be used (Vrdoljak and Samways 2012). A single trap was placed

on the ground under each tree. At colony trees, traps were placed as near to the colony as possible, without being directly underneath as these traps would quickly fill with faecal matter. When setting traps at colony trees, distance and direction from the base of tree were recorded and used to place a trap in same location at paired non-colony trees.

We stored insects in 99% ethanol until later identification. All individuals were initially identified to morphospecies then to family level and where possible to genus or species. Morphospecies are commonly used in ecological studies and can be used as surrogates for formal species (Vrdoljak and Samways 2012).

Night use of colony chambers: We carried out night visits to investigate heterospecific birds that use the colony chambers at night. We started surveys thirty minutes after sunset and visited colonies for about five minutes in the dark, scanning chambers using a head torch. Animals occupying the chambers were generally visible and were easily identified. All selected colonies at a given site were visited once and on the same night.

To determine if the proportion of animal community observed roosting in colonies changed between sites, we needed to control the abundance of these species within the local community. We used the point count data, mentioned above, to estimate the avian species pool for each site. The point count data only used the species observed within 25 metres of a given tree; however, to gain a better understanding of the species pool we included all birds observed within 100 m. This was later used as an offset in our statistical models that investigated heterospecific birds roosting in colonies.

Measures of environmental harshness: We used normalised difference vegetation index (NDVI) and rainfall as measures of aridity and environmental stress in each site. NDVI is a measure of greenness that allows for analysis of terrestrial vegetation conditions (Solano et al. 2010). NDVI is calculated from the reflectance in the near-infrared and red portions of the electromagnetic spectrum (Hurlbert and Haskell 2003) and provides a reasonable estimate of net primary productivity (Lo Seen Chong et al. 1993, Goward et al. 1994), and is assumed to correlate positively with food availability within the environment (Hurlbert and Haskell 2003). Vegetation in arid environments responds strongly to rainstorm events; however, these events are unpredictable (Noy-Meir 1973, Reynolds et al. 2004). Consequently, periods of plant production are also unpredictable and the timing of such events can vary between years (Hillel and Tadmor 1962, Rosenzweig 1968). Calculating NDVI allows for a reliable understanding of when the environment is more or less productive and therefore can serve as a proxy for

harshness. NDVI values were acquired from MODIS NDVI time series of eight-day composites from the satellite Terra (MOD09A1 V6). Satellite images had a 500m resolution and were downloaded for each site for the dates we visited. We calculated NDVI values, once for each set of paired trees using the GPS location of the colony tree in ArcGIS 10.4.

Due to vegetation responding strongly in response to rain events, NDVI values will be higher at a site if it has received recent rainfall. Therefore, to gain a deeper understanding of the long-term harshness of each site we also used the total rainfall for the 24 months before our visit. Rainfall for all South African sites was provided by the South African Weather Services, while rainfall for Keetmanshoop was provided by Namibian Meteorological Service. Rainfall data for Aus and Sesriem's Desert homestead were provided by Klein-Aus Vista and NamibRand Nature Reserve, respectively.

Statistical analyses: We analysed data using the R statistical package 3.4.0 (R Core Team 2017), carrying out linear mixed models (LMMs) and generalised linear mixed models (GLMMs) to compare response variables between colony trees and paired non-colony trees, using the glmmTMB package (Brooks et al. 2019) due to its ability to handle zero-inflated models. We used the function `emtrends` from `emmeans` (Lenth 2018) to calculate the trend of colony use in relation to environmental stress (Rain, NDVI). Poisson distributions were used to analyse count data. When count data were overdispersed, models were fitted with either a quasi-Poisson or negative binomial distributions (Hara and Kotze 2010). Zero-inflation was also applied when needed. On occasions when binomial distributions, still could not account for overdispersion, then count data was log-transformed and fitted with a gaussian distribution (Ives 2015). All other models used gaussian distributions, with response variables transformed when needed. For analyses where interactions were fitted, we explored interactions where p values were less than 0.1 using post-hoc tests. Those that had a value greater than 0.1, or where post-hoc tests revealed no significant differences were subsequently removed from the models. All explanatory variables and random effects mentioned above were used when testing all models, unless otherwise stated. For each response variable, the full model terms and structure, the error distribution used, and any data transformation performed are detailed in Appendix 4.

For mammals, we used the number of camera trap events, event duration, species richness and Shannon-Weiner diversity index (hereafter, Shannon diversity) as response variables. For the abundance of avian species, invertebrates, and night use of chambers, we used the number of individuals, species richness and Shannon diversity index as response variables. Whereas, for

reptile abundance, we used the number of individuals only. Terrestrial and aerial invertebrates were analysed separately. Shannon diversity was calculated using the vegan package (Oksanen et al. 2017).

For each of the response variables, apart from event duration, we used ‘tree’ as the sampling unit; summarising the data so that each of the response variables was calculated per tree. For event duration, we used each ‘event’ captured as the sampling unit. As explanatory variables in each of these models, we used colony presence (present/absent, our primary variable of interest), tree characteristics (PCA loading score) and one of rainfall or NDVI. A strong correlation (Pearson $|r| = 0.83$) was shown to exist between rainfall and NDVI, and therefore we tested both separately but report only the results of rainfall, although results for NDVI was qualitatively the same. We fitted the interaction between rainfall and colony presence to determine if the influence of rainfall (aridity) on taxa response variables is different when weaver colony was present or absent. Interactions with p values greater than 0.05 were removed from the final models. Tree characteristics and rainfall variables were always scaled within each model. Each colony tree and its corresponding control tree was given a unique pair ID, and each site was also given a unique ID. These were both used as random effects in the models, with pair ID being nested within site ID. All explanatory variables and random effects mentioned above were used when testing all models, except those testing the night use of colony chambers. For reptile response models we included time of observation as an additional explanatory term because reptiles show peak activity levels early and late in the day (Huey and Prianka 1977). Time was recorded in the 24-hour format and was converted to decimal (e.g. 12:30 became 12.5) before being used in the models.

Results

Abundance of mammals

We observed 41 unique species over a total of 1280 camera trap days at 128 trees across the eight sites. On average we recorded 2.02 ± 0.17 SE (all means are presented with standard error) species per tree for the five-day sampling period. A total of 303 events were captured (mean events per tree = 2.37 ± 0.21), and event durations averaged 34.38 minutes ± 8.68 per tree (Appendix 3).

Our models investigating mammal associations found that colony presence explained significant variation in the number of events, event duration and species diversity, but not species richness (Appendix 2.1). On average colony trees showed a 70% increase in animal

events (colony tree: $2.98 \text{ events/day} \pm 0.45$; non-colony tree: 1.75 ± 0.3 ; Appendix 2.1a; Figure 2a). In addition, event durations lasted 11 times longer (colony tree $51.8 \text{ mins} \pm 13.6$; non-colony tree: $4.62 \text{ mins} \pm 1.3$; Appendix 2.1b; Figure 2b) and species diversity doubled (colony tree: 0.49 ± 0.26 ; non-colony tree: 0.11 ± 0.08 ; Appendix 2.1d; Figure 2d) at colony trees compared to non-colony trees. Our models also revealed that rainfall explained significant variation in the number of events, species richness and species diversity between sites (Appendix 2.1). Increasing rainfall was associated with increasing numbers of animal events, with four times as many events across the range of rainfall (Appendix 2.1a; Figure 3a), increasing species richness (two times higher; Appendix 2.1c; Figure 3b), and increasing species diversity (three times higher; Appendix 2.1d; Figure 3c) across the range of rainfall (22mm – 732mm across a 24 month period). The interaction between colony presence and rainfall did not explain the variation and was removed from the final models (Appendix 2.1).

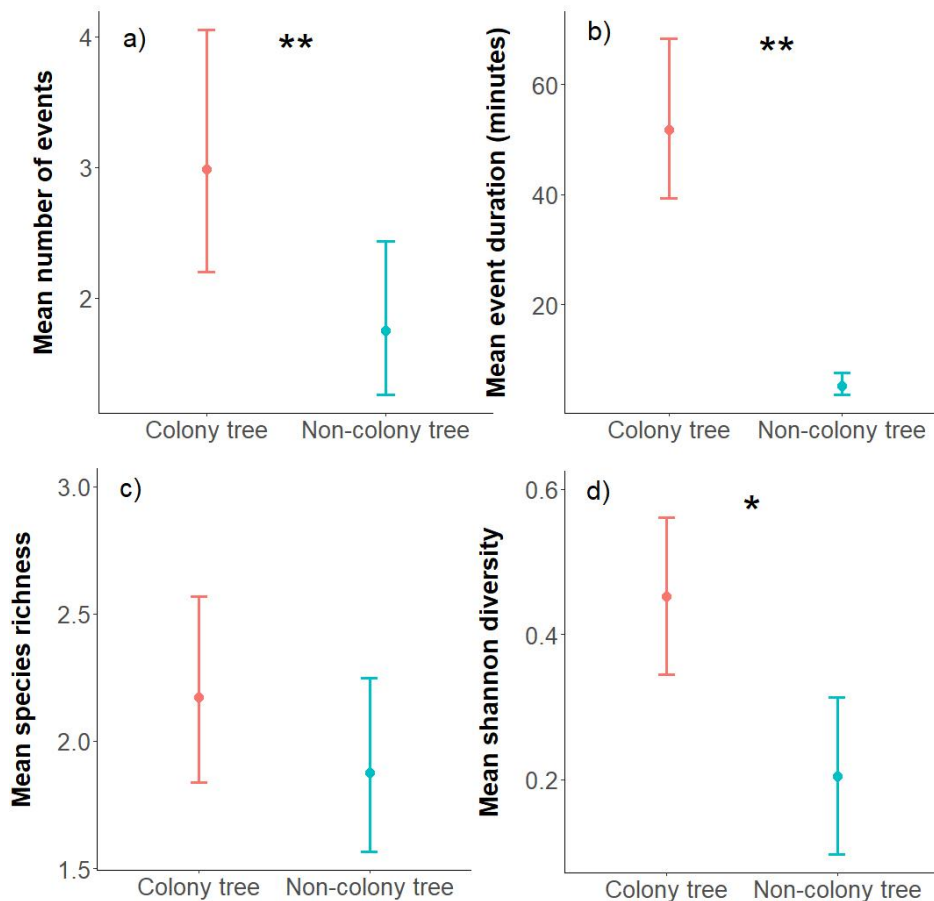


Figure 2. The mean responses (using raw data \pm 95% CI) for the (a) number of camera trap events, (b) event duration, (c) species richness and (d) Shannon diversity (** denotes $p < 0.01$; * denotes $p < 0.05$) of mammals encountered at Camelthorn trees with (colony) and without (non-colony) weaver nests.

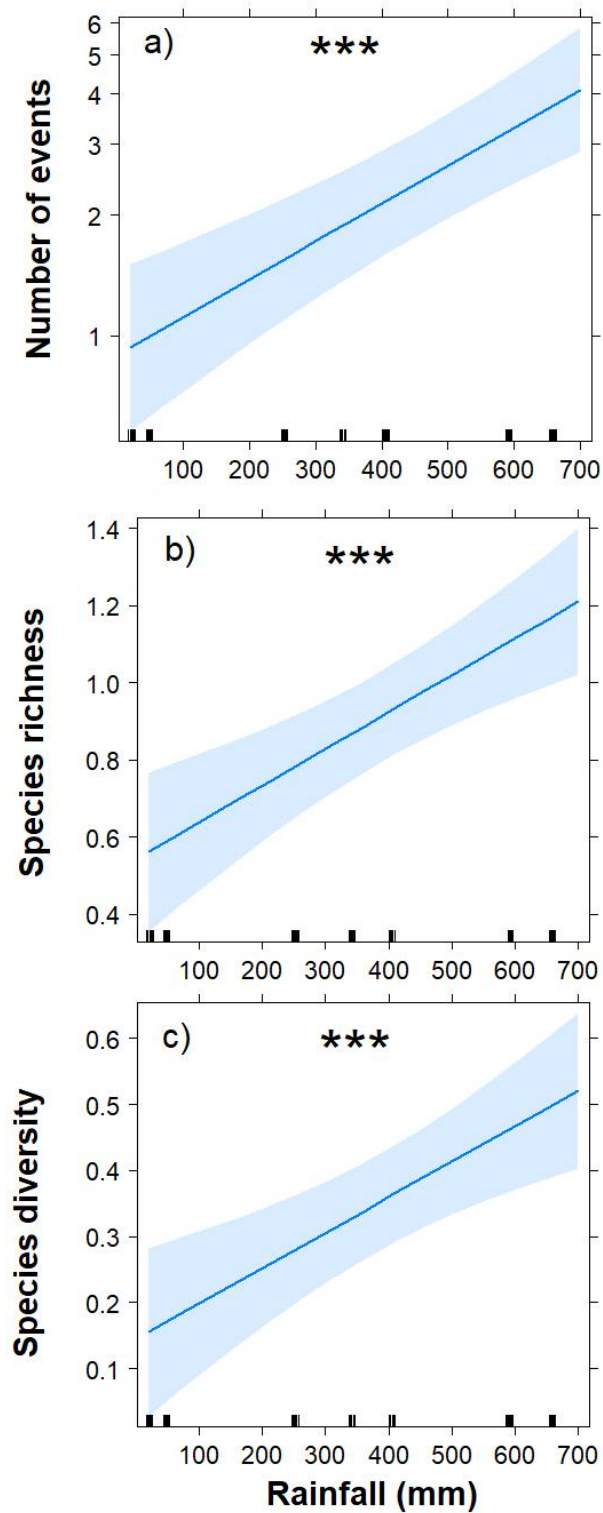


Figure 3. Relationship between total rainfall of the last 24 months and measures of mammal responses (model values \pm 95%CI), (a) the number of events (Y axes in log scale), (b) the mean number of species and (c) Shannon diversity (***) indicates $p = 0.001$) at combined colony and non-colony camelthorn trees across the eight sampled sites.

Abundance of reptiles

In total, 80 (mean 0.63 ± 0.89) reptiles consisting of two species, the Kalahari (*Trachylepis spilogaster*) and Karasburg tree skinks (*Trachylepis sparsa*), were observed at 128 sampled trees. Our models revealed that the interaction between colony presence and rainfall explained variation in the number of individuals and species richness at a given tree (Appendix 2.2). However, post-hoc analyses revealed the relationship to be non-significant ($t = 1.75$; $p = 0.08$). Weaver colony presence explained significant variation in the number of individuals observed. On average colony trees almost had one reptile per tree (0.87 individuals ± 0.14) while only every second non-colony tree hosted a reptile (0.47 ± 0.10 , Appendix 2.2; Figure 4). Rainfall, tree characteristics, and the time of day did not explain variation, with the interaction being subsequently removed from the final model (Appendix 2.2).

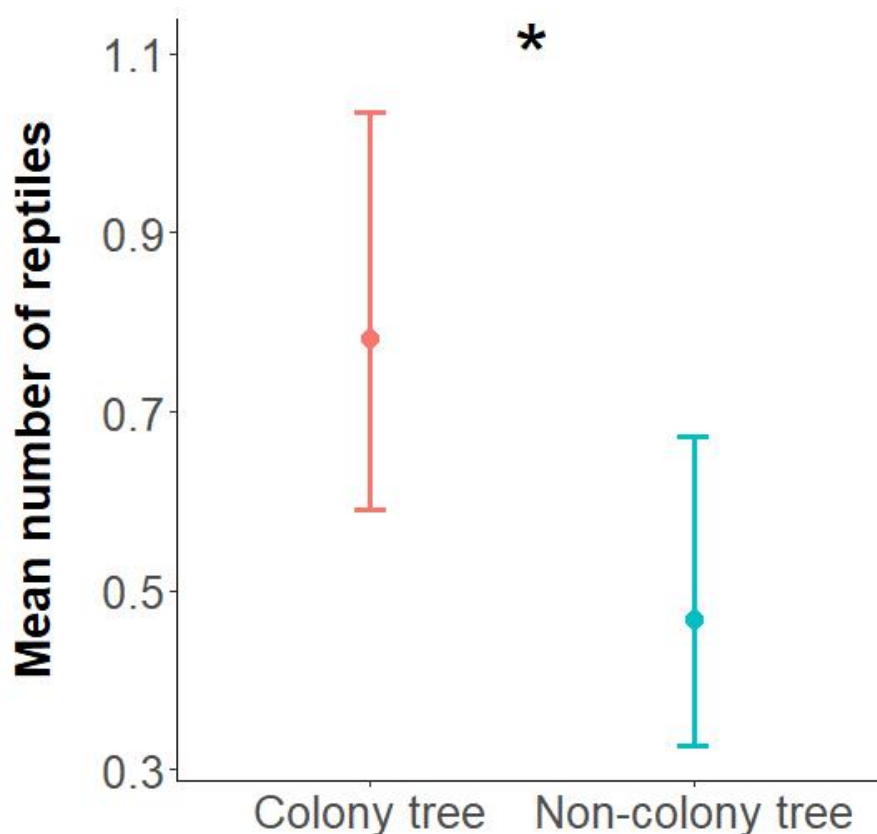


Figure 4. The mean number of reptile individuals (raw data \pm 95% CI) counted at colony and non-colony trees (* indicates $p < 0.05$).

Avian abundance

A total of 118 (mean 1.08 ± 0.15) bird individuals of 33 species (0.8 species per tree count ± 0.19) were recorded at 124 trees. Our models revealed that the interaction between colony presence and rainfall explained significant variation in the number of individuals and species richness at a given tree (Appendix 2.3, Figure 5). Post-hoc analyses revealed a significant positive relationship with increasing rainfall at non-colony trees, for the number of birds observed (estimate \pm CI = 0.0012 ± 0.005 ; Figure 5a), and species richness (estimate \pm CI = 0.0009 ± 0.005 Figure 5b). Whereas, no association was observed at colony trees (estimate \pm CI = -0.0013 ± 0.0021 ; Figure 5a; species richness: estimate \pm CI = -0.0014 ± 0.0019 Figure 5b). Relative to the control tree, colony presence increased the number of individuals and species richness only at low rainfall sites, whereas there was no difference at high rainfall sites (Figure 5). Differences in Shannon diversity were significantly explained by the interaction between colony presence and rainfall (Appendix 2.3). However, post-hoc tests failed to reveal any differences between colony and non-colony trees, therefore this interaction was subsequently removed from the analysis (Appendix 2.3c).

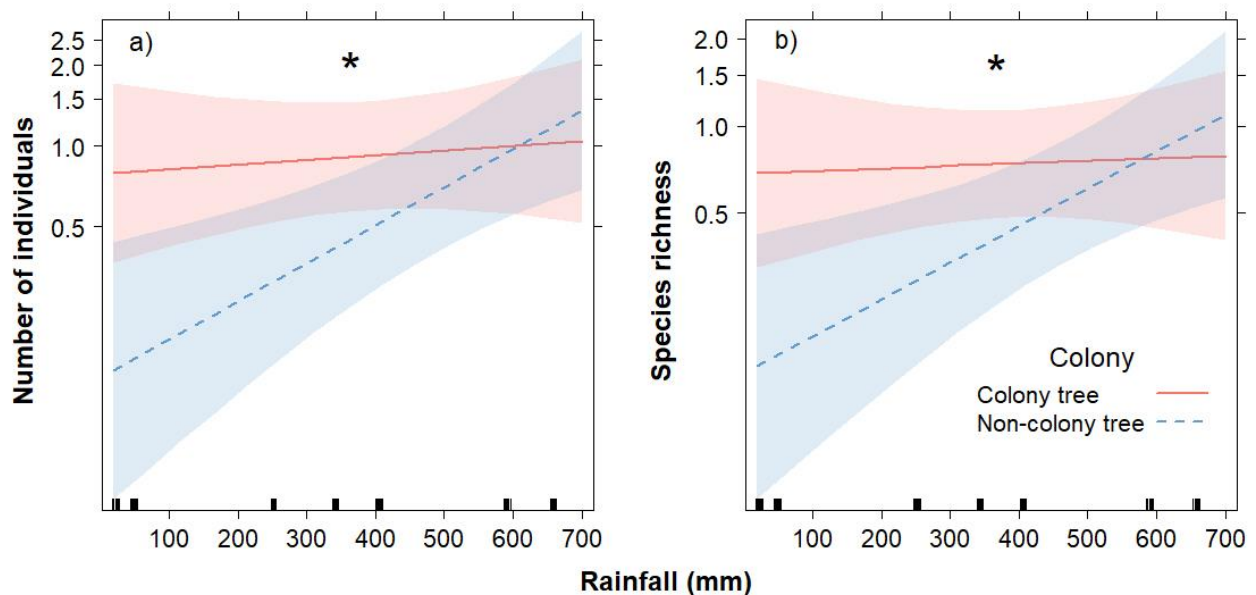


Figure 5. The relationship of rainfall on the avian abundance (model values \pm 95% CI, Y axes in log scale) in terms of (a) number of individuals and (b) species richness at colony and non-colony trees showing the colony presence by rainfall interaction in the data. The lines represent the model predicted values with 95% confidence intervals (* indicates $p < 0.05$).

Invertebrate abundance

Terrestrial invertebrates: A total of 5966 (mean 9.32 per trap \pm 0.46) invertebrates were captured in pitfall traps. Colony presence explained significant variation in the number of individuals at a given tree, with 61% more individuals being sampled under colony trees (Appendix 2.4a; Figure 6a). Neither rainfall, tree characteristics or interactions between colony presence and rainfall explained the variation observed (Appendix 2.4a). Variation in species richness and diversity of terrestrial invertebrates was explained by the interaction between colony presence and rainfall (Appendix 2.4b). Post-hoc analyses revealed a significant positive relationship with an increase in rainfall at non-colony trees, for species richness (estimate \pm CI = 0.0003 \pm 0.001; Figure 6b), and Shannon diversity index (estimate \pm CI = 0.0001 \pm 0.001; Figure 6c). Whereas, no association was observed at colony trees (estimate \pm CI = 0.0001 \pm 0.0008; Figure 6b; Shannon diversity index: trend \pm CI = 0.002 \pm 0.006; Figure 6c). Relative to the control tree, colony presence increased the number of individuals and species richness only at low rainfall sites, whereas there was no difference at high rainfall sites.

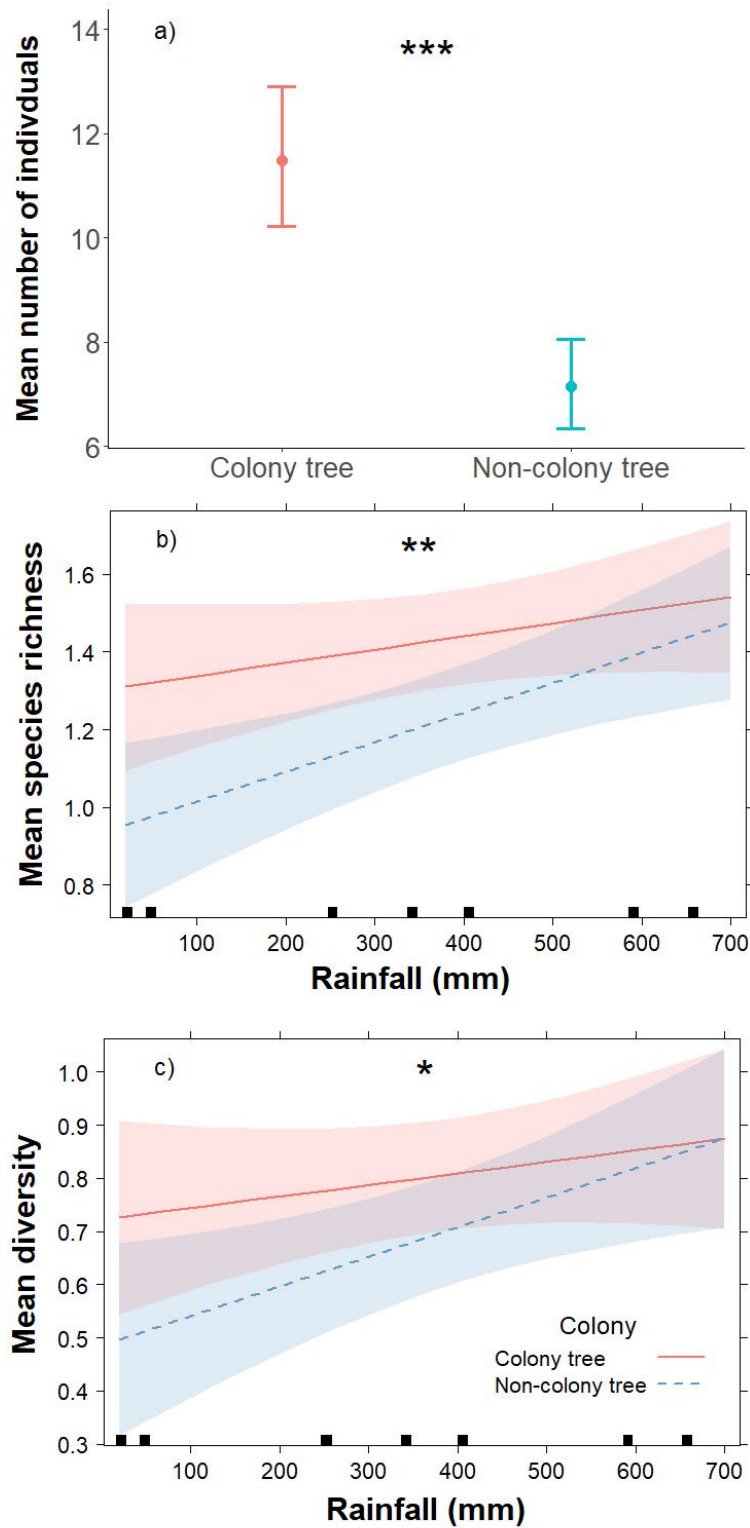


Figure 6. The relationship of rainfall on the terrestrial invertebrate abundance in terms of (a) number of individuals (raw data \pm 95% CI), (b) species richness (c) and Shannon diversity at colony and non-colony trees showing the colony presence by rainfall interaction in the data. (b) and (c) lines represent the model predicted values with 95% confidence intervals (* $p < 0.05$; *** $p < 0.001$).

Aerial invertebrates: A total of 2704 individuals (17.58 ± 1.17) were sampled in pan traps. Colony presence and rainfall explained significant variation for all response variables. Colony presence increased the number of individuals by 25% (Appendix 2.5a, Figure 7a), species richness by 27% (Appendix 2.5b, Figure 7c) and the Shannon diversity index by 17% (Appendix 2.5c, Figure 7c). Whereas across the rainfall range (22-732 mm), the number of individuals increased by 40% (Appendix 2.5a; Figure 8a), species richness increased by 40% (Appendix 2.5b, Figure 8b), and the species diversity index increased by 38% (Appendix 2.5c, Figure 8c). Tree characteristics and the interactions between colony presence and rainfall did not explain any of the response variables tested, with the interaction removed from the final model (Appendix 2.5).

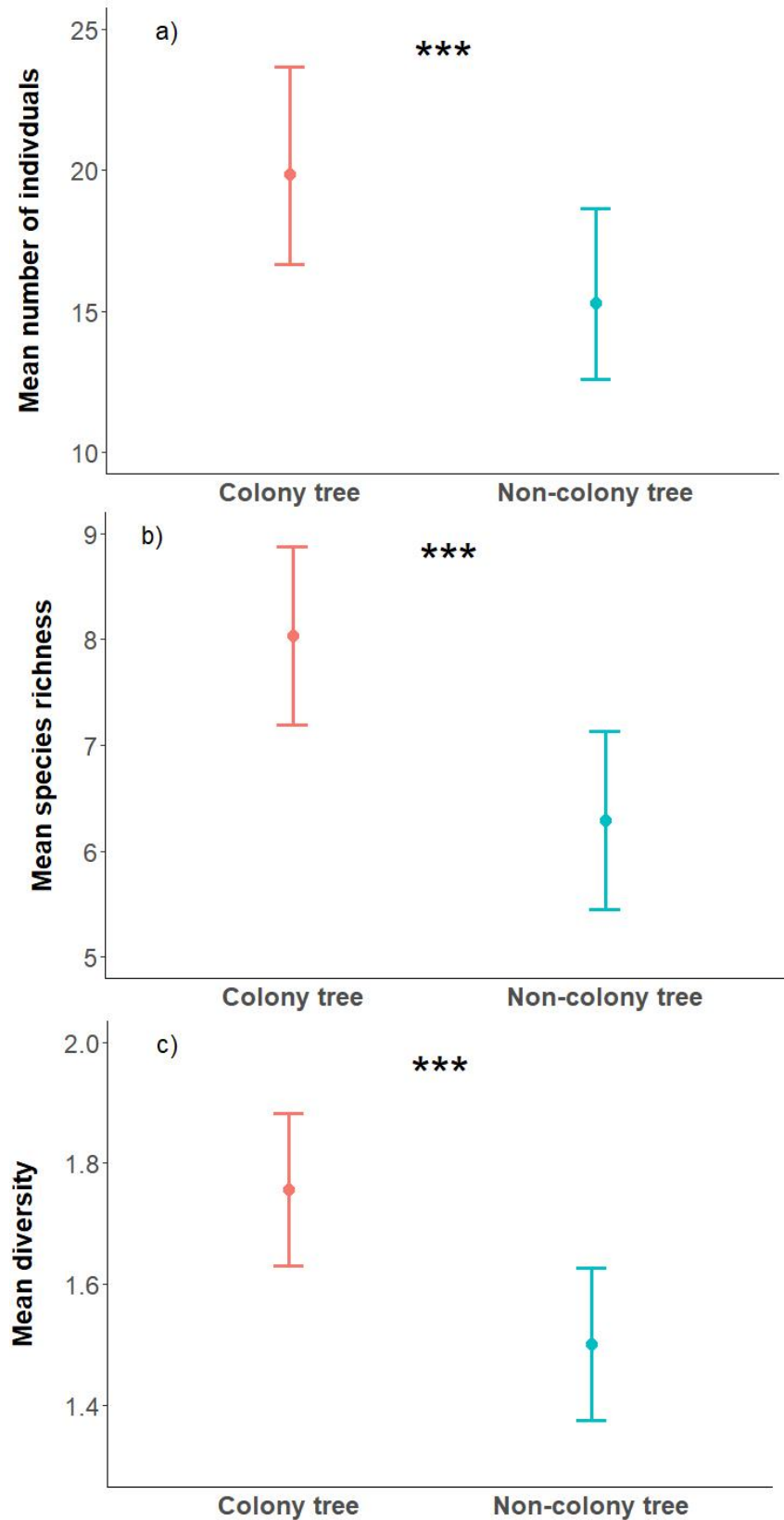


Figure 7. The effects of colony presence on aerial invertebrate abundance. The effects of colony trees (raw data \pm 95% CI) on (a) the number of individuals, number of species (b) and Shannon diversity (c) (***) indicates $p < 0.001$).

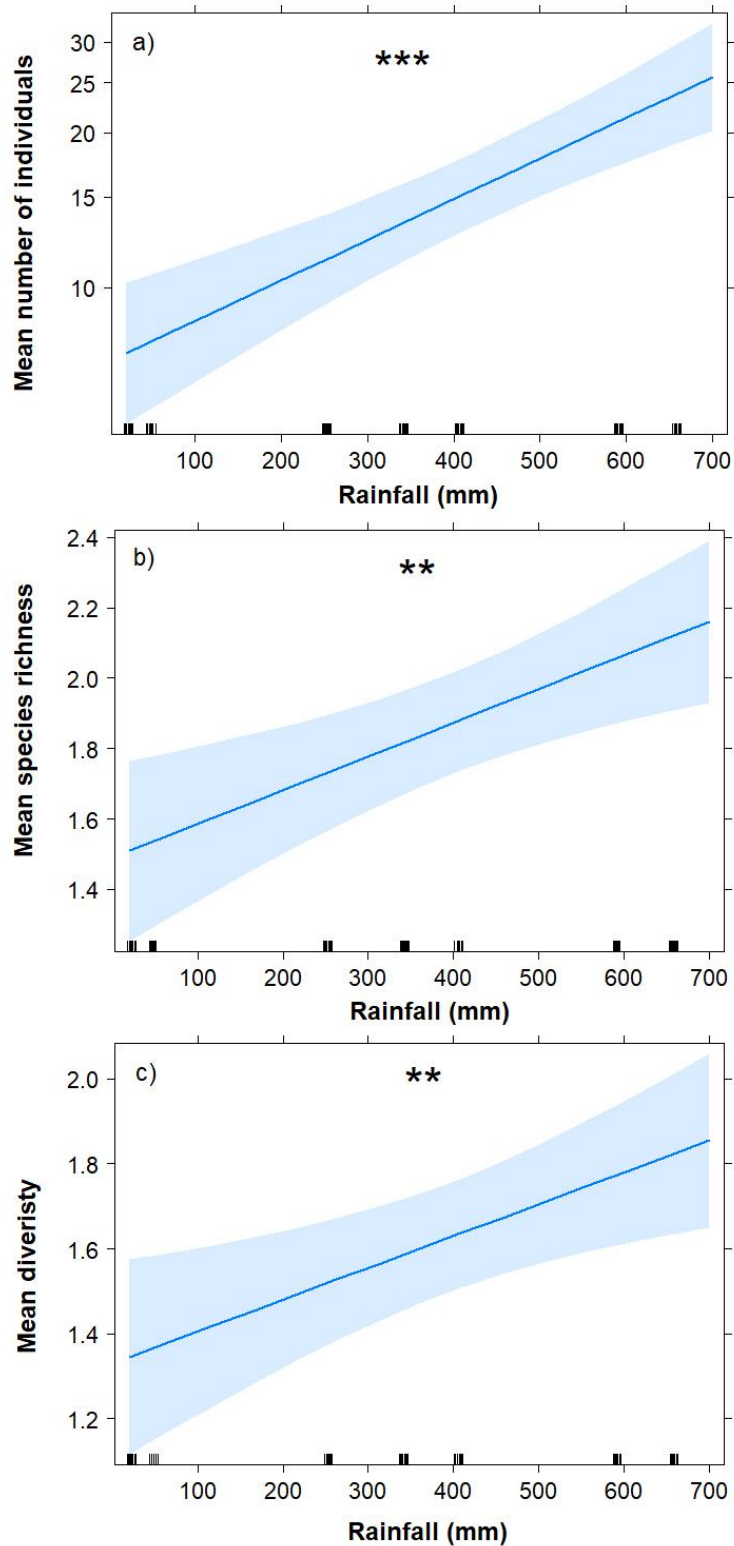


Figure 8. The effects of rainfall on aerial invertebrate abundance (model values \pm 95% CI), on the number of individuals (a), number of species (Y axes in log scale), (b) and Shannon diversity (c) (** indicates $p < 0.01$; *** indicates $p < 0.001$).

Night use of colony chambers

A total of 100 heterospecifics (1.6 individuals/colony ± 0.26), consisting of eight different bird species (0.68 species/colony ± 0.08) were observed during night visits to colony trees. Colony size explained significant variation in the number of species observed (Appendix 2.6b, Figure 8). Neither rainfall nor tree characteristics explained significant variation.

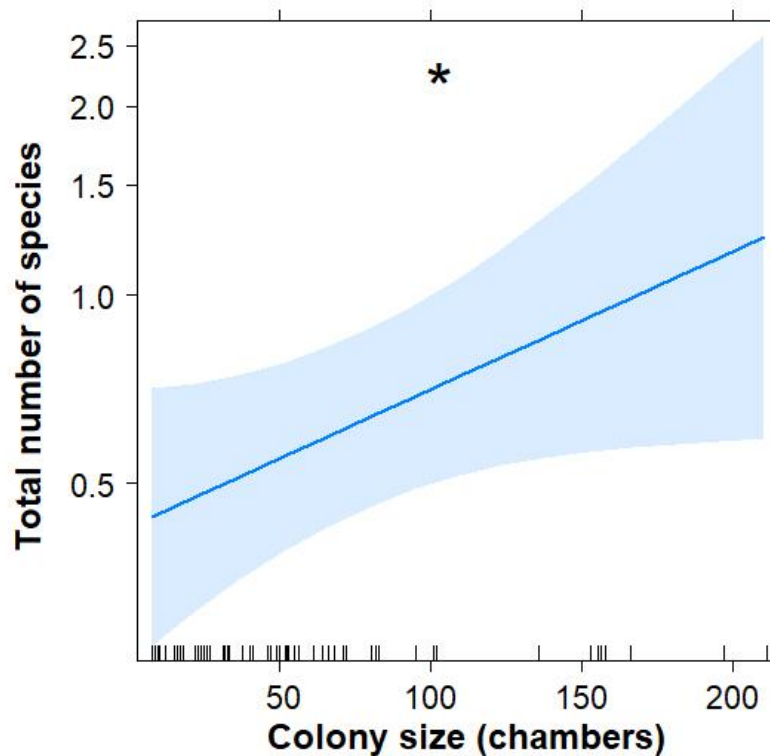


Figure 8. The effects of colony size on the number of heterospecific birds using colony chambers at night (model values \pm 95% CI; Y axes in log scale * denotes $p < 0.05$).

Discussion

Our study demonstrates that weaver colonies enhance local diversity across their range and that these strong associations are replicated and are a consistent feature of these structures. For all taxa sampled (invertebrates, birds, reptiles and mammals), we found increased numbers of individuals, species richness and diversity associated with camelthorn trees hosting weaver colonies. Importantly, our results suggest that weaver colonies within camelthorn trees were associated with increased events and diversity especially at the more arid sites for both birds and terrestrial invertebrates, while the difference compared to non-colony trees was not as strong at more benign sites. It is clear that weaver colonies create a valuable resource and

habitat to the surrounding animal communities, serving as an ecological engineer. These colonies are also utilised more by some groups of animals in harsher environments, providing support for a prediction of the stress gradient hypothesis.

The positive diversity impacts of colonies were most significant on birds and terrestrial invertebrates at sites with low rainfall. Relative to non-colony trees, colony presence increased the number of individuals and species richness only at low rainfall sites. However, the importance of associating with weaver colonies, measured as events happening at the trees, almost disappeared when environmental conditions became less severe. Thus, the impacts of colonies changed from positive in the more stressful sites to neutral at sites that deemed to be benign. Therefore, this study provides empirical support for the stress gradient hypothesis and compliments very recent research (Dangles et al. 2018, Bell and Cuddington 2019) using terrestrial animal communities that found evidence of increased importance of associative or facilitative interactions in harsh environments. Additionally, by demonstrating that some taxa have a higher association with colony trees in more arid climates than they do with non-colony trees, we provide support that facilitation by weaver colonies increases the niches of certain species in the driest areas (Armas et al. 2011, He and Bertness 2014). Furthermore, this is the first study to extend this hypothesis to free-ranging animals, as previous studies were tested under laboratory conditions (Dangles et al. 2018, Bell and Cuddington 2019). Our site visits were not carried out concurrently, and therefore may have some effects on our results. However, our study design of using paired trees should minimise these impacts. It is likely that such facilitation plays an important role, allowing multiple taxa to persist in environments that may otherwise be too harsh.

Invertebrates demonstrated a particularly strong association with colony trees. The main factors influencing the abundance of insects in arid environments are temperature, the availability of water and the presences of organic matter (Noy-Meir 1985). Organic matter collects underneath colonies in the form of guano and fallen nest material. With the potential of hundreds of individual birds residing in a given colony, faecal deposited on the ground below can form substantial faecal mats that would be an essential source of organic matter in these environments (du Toit 2016, Prayag 2016). The more arid an environment becomes, the greater the importance of this source of organic matter would be, and this would explain the difference between terrestrial invertebrate interactions with colony and non-colony trees across the environmental gradient.

In more arid sites, birds had an association for colony trees. In harsh environments, small to medium-sized birds will avoid high temperatures by seeking refuge (Willmer et al. 2009). Weaver colonies should provide permanent shade and the chambers have been shown to buffer against harsh temperatures (Maclean 1973c, van Dijk et al. 2013, Leighton and Echeverri 2014). All birds observed during point counts would fit into Willmer et al.'s (2009), small to medium-sized categories, suggesting that this kind of facilitation would explain the differences observed between the interactions with colony and non-colony trees across the environmental gradient. Additionally, insects are an essential food source, providing nutrition and water, for many bird species. Therefore, the increased number of invertebrates associated with weaver colonies may explain why we see more birds at colony trees in areas with low rainfall.

Mammals had an overall tendency for associating with colony over non-colony trees, but this did not differ across the sites. These trees received more visits, had longer stays and had greater mammal diversity. However, we did not see the same pattern between the interactions at colony and non-colony trees across the different sites as we did with birds and terrestrial invertebrates. Again, this could be explained by how engineers may provide facilitation towards these taxa. The terrestrial and arboreal mammals captured by camera traps would mostly be classified by Willmer et al. (2009) as endurers, and these species reduce their metabolic heat production by reducing activity during the hottest parts of the day. We have previously found that mammals use weaver colonies for shade (Chapter 1). However, this study did not include the hottest time of the year and as a result this behaviour was not frequently observed. We could speculate that if this study was repeated during summer, we might find that the interactions between colony and non-colony trees across the different sites may be similar to that observed for birds and terrestrial invertebrates.

Colonies presence increased the abundance of reptiles. Therefore, our findings support previous research, demonstrating that reptiles associate strongly with weaver colonies (Rymer et al. 2014). However, like mammals, we did not see a variation between the differences in colony and non-colony trees across the aridity gradient. The main factors that influence the abundance of reptiles are food availability and the ability to manage their thermoregulation. Reptiles, need to raise their body temperature by basking, but their priority is to minimise overheating (Corbalán et al. 2013), and colonies provide shelter to do so. Additionally, the two species observed, both tree skinks (*Trachylepis spp.*), are insectivores and invertebrate abundance is higher around colony trees. Therefore, colonies provide the primary resources needed by reptiles in arid environments and explain why colony trees have greater interactions

with reptiles than non-colony trees across all sites. The increase in numbers at wetter sites is likely driven by productivity leading to an increase in prey. Furthermore, snakes visit colonies more frequently after rains, when weavers are breeding (Chapter 3).

Weaver colonies provide different resources for different taxa, and in turn, create ecological hotspots around colony trees. Our results demonstrate that the importance of these resources, for specific taxa at least, increases as aridity increases. Consequently, colony presence at more stressful sites likely causes more isolated hotspots of life. Many species in harsh habitats have adaptations that allow them to survive with the extreme stresses associated with these environments (Schmidt-Nielsen et al. 1969, Bennett et al. 1984, Williams and Tieleman 2005). However, many of the species sampled use colonies as thermal refuges (Chapter 2). Therefore, our results suggest that, in a landscape that will become increasingly harsh as climate change advances (Akoon et al. 2011), these colonies will become critical ecosystem components that will buffer some of the harsh environmental conditions and allow some species to persist despite these tougher conditions. Therefore, to conserve biodiversity and reduce the impacts of climate change it is important to understand how facilitation within animal communities is undertaken and how the processes and interactions within ecosystems are maintained (Coggan et al. 2018). For example, as arid environments becoming increasingly harsh, the reduction of grass in an environment (Baez et al. 2013) may diminish the effectiveness of colony maintenance, and therefore the thermal function of weaver colonies become less effective. Additionally, if external temperatures exceed a threshold that colonies can no-longer sufficiently buffer against, this will have severe consequences for animal communities in these areas. Therefore, we must understand the role that engineers will play on maintaining ecosystems in an environment changing due to human-induced climate change and that this should be a priority for future research.

In summary, our findings add to the growing literature that ecosystem engineering is an essential biological interaction that can relieve stress in harsh environments (Hastings et al. 2007, Romero et al. 2015, Coggan et al. 2018). We also show the importance of Sociable weavers as a structural engineer and the significance of their colonies in structuring animal communities, throughout the weaver's range. Furthermore, facilitation by weavers increases in more harsh environments and, thus, the stress gradient hypothesis can be applied to animal-animal interactions. However, despite showing that colonies are more critical in harsh environments to birds and terrestrial invertebrates, we failed to show this in other taxa. This may be due to smaller sample sizes, resulting in a false-negative result. Thus, we cannot rule

out that the importance of weaver colonies on mammal and reptile communities does not match the stress gradient hypothesis. It may also be because this study was carried out as a snap-shot in time. If this study was undertaken over a more extended period, we might find that colonies in extremely harsh environments are more critical during the seasonal extremes (summer and winter). Therefore, we suggest further studies with a recommendation to increase sample sizes, and possibly over more extended periods. For example, camera trapping periods should be extended to a minimum of two weeks (Larsen 2016), and the number of trees used during reptiles counts should also be increased where possible. Nevertheless, we highlight the importance of weaver colonies and how its importance increases as environmental harshness increases, suggesting that colonies may mitigate some of the additional stresses experienced by associated wildlife as climate change advances.

Appendix 1. Loading scores from the Principle Component Analysis (PCA), comparing tree characteristics measured; tree height, canopy cover and circumference at chest height.

Principle Component	Percent variation
Loading score 1	95.8%
Loading score 2	4.2%
Loading score 3	0.0%

Appendix 2.1. Results from the generalised linear mixed models investigating mammal abundance variables to colony presence, rainfall and tree characteristics. A total of 128 trees were monitored (64 colony trees, paired with 64 non-colony trees), interactions with *p* values greater than 0.01 were removed from the final models.

Response variables	Explanatory variables	Estimate	± SE	χ^2	<i>P</i>
a) Animal events	Colony present (yes/no)	-0.617	0.204	9.10	<0.01
	Rainfall	0.546	0.106	26.21	<0.001
	Tree characteristics	0.086	0.107	0.65	0.42
Interaction removed					
	Colony present*Rainfall	0.215	0.213	1.03	0.31
b) Event duration	Colony present (yes/no)			6.87	<0.01
	Rainfall	0.31	0.18	2.85	0.09
	Tree characteristics	0.11	0.17	0.40	0.53
Interaction removed					
	Colony present*Rainfall	-0.38	0.37	1.01	0.30
c) Species richness	Colony present (yes/no)			1.37	0.24
	Rainfall	0.41	0.09	22.0	<0.001
	Tree characteristics	0.01	0.08	0.03	0.86
Interaction removed					
	Colony present*Rainfall	0.20	0.14	2.12	0.15
d) Shannon diversity	Colony present (yes/no)			10.33	<0.01
	Rainfall	0.14	0.04	13.51	<0.001

Tree characteristics	0.06	0.04	1.52	0.12
Interaction removed				
Colony present*Rainfall	-0.03	0.07	0.17	0.68

Appendix 2.2. Results from the generalised linear mixed model that investigated reptile abundance at colony and non-colony trees. In total 128 trees were monitored (64 colony trees, paired with 64 non-colony trees). The significant interaction between colony presence and rainfall was removed, due to post-hoc tests demonstrating differences to be none significant.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
Reptile abundance	Colony Present (yes/no)			4.71	<0.05
	Rainfall	0.41	0.41	0.99	0.32
	Tree characteristics	0.02	0.11	0.01	0.91
	Time	0.0001	0.02	0.00	0.99
Interaction removed:					
	Colony present*Rainfall	-0.599	0.341	3.07	0.08

Appendix 2.3. Results from the generalised linear mixed models investigating avian abundance variables to colony presence, rainfall and tree characteristics. In total, 126 trees were monitored (62 colony trees, paired with 62 non-colony trees), interactions with *p* values greater than 0.01 were removed from the final models. The significant interaction between colony presence and rainfall, resulting from the species diversity analysis (c), was also removed, due to post-hoc tests demonstrating differences to be none significant (250 point counts at 50 trees). All model terms, error distributions, transformation and zero-inflations are listed in Appendix 4.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Avian abundance	Colony present (yes/no)			6.48	<0.05
	Rainfall	0.101	0.213	0.22	0.64
	Tree characteristics	0.164	0.258	0.40	0.53
	Colony presence*Rainfall	0.729	0.244	8.87	<0.01
b) Species richness	Colony present (yes/no)			4.83	<0.05
	Rainfall	0.052	0.216	0.06	0.81
	Tree characteristics	0.10	0.227	0.19	0.66

	Colony presence*Rainfall	0.69	0.25	7.63	0.006
c) Shannon diversity	Colony Present (yes/no)			0.29	0.59
	Rainfall	0.06	0.04	1.61	0.20
	Tree characteristics	0.02	0.03	-0.31	0.58
Interaction removed					
	Colony present*Rainfall	0.10	0.06	2.93	0.09

Appendix 2.4 Results from the generalised linear mixed models investigating terrestrial invertebrate variables to colony presence, rainfall and tree characteristics. Interactions with p values greater than 0.10 were removed from the final models. In total, 128 trees were monitored (64 colony trees, paired with 64 non-colony trees), each having six pitfall traps placed below. Of which, 320 pairs ($n = 640$) were without interference.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Invertebrate abundance	Colony present (yes/no)			31.46	<0.001
	Rainfall	0.256	0.171	2.25	0.13
	Tree characteristics	0.030	0.048	0.39	0.53
Interaction removed					
	Colony present*Rainfall	0.056	0.078	0.52	0.47
b) Species richness	Colony present (yes/no)			33.03	<0.001
	Rainfall	0.086	0.063	1.87	0.171
	Tree characteristics	0.031	0.025	1.54	0.214
	Colony present*Rainfall	0.108	0.363	8.88	0.003
c) Shannon diversity	Colony present (yes/no)			11.56	<0.001
	Rainfall	0.055	0.053	1.07	0.300
	Tree characteristics	0.023	0.020	1.29	0.255
	Colony present*Rainfall	0.086	0.033	6.92	0.009

Appendix 2.5. Results from the generalised linear mixed models investigating aerial invertebrate variables to colony presence, rainfall and tree characteristics. We placed one trap at each of the 128 trees were monitored (64 colony trees, paired with 64 non-colony trees). We recovered 62 pairs without interference (n = 126). Interactions with *p* values greater than 0.01 were removed from the final models.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Invertebrate abundance	Colony present (yes/no)			13.57	<0.001
	Rainfall	0.45	0.083	29.78	<0.001
	Tree characteristics	0.094	0.058	2.57	0.108
Interaction removed					
	Colony present*Rainfall	-0.075	0.095	0.63	0.43
b) Species richness	Colony present (yes/no)			30.29	<0.001
	Rainfall	0.23	0.07	10.80	<0.01
	Tree characteristics	0.06	0.04	4.26	0.01
Interaction removed					
	Colony present*Rainfall	-0.006	0.071	0.009	0.922
c) Shannon diversity	Colony present (yes/no)			15.94	<0.001
	Rainfall	0.186	0.065	8.31	<0.01
	Tree characteristics	0.067	0.042	2.56	0.11
Interaction removed					
	Colony present*Rainfall	0.017	0.067	0.07	0.79

Appendix 2.6. Results from the generalised linear mixed models investigating the abundance of heterospecific species using the colonies at night. The number of individuals and species were compared to rainfall, tree characteristics and colony size.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Heterospecific abundance	Rainfall			0.19	0.66
	Tree characteristics	-0.04	0.17	0.06	0.79
	Colony size	0.003	0.004	0.57	0.45
b) Species richness	Rainfall	0.18	0.17	1.1	0.29
	Tree characteristics	-0.14	0.13	1.03	0.31
	Colony size	0.005	0.002	4.01	<0.05

Appendix 3. The number of animal events and the mean time spent (minutes) at colony and non-colony trees captured by camera traps at colony and non-colony trees

Terrestrial species		Total		Time (m)	
		Colony Present	No	Colony Present	No
Common Duiker	<i>Sylvicapra grimmia</i>	33	26	2	1.38
Large-spotted Genet	<i>Genetta tigrina</i>	26	2	110.89	1
Slender Mongoose	<i>Galerella sanguinea</i>	23	1	307.19	1
Sheep		14	10	2.57	2.9
Cattle		15	4	34.9	3
Greater Kudu	<i>Tragelaphus strepsiceros</i>	5	12	2.8	13.67
Black-backed Jackal	<i>Canis mesomelas</i>	12	5	1.41	1.8
Woodland Dormouse	<i>Graphiurus murinus</i>	4	10	7.5	2.4
Steenbok	<i>Raphicerus campestris</i>	4	9	1	1.33
Gemsbok	<i>Oryx gazella</i>	6	4	2.5	1.5
Springhare	<i>Pedetes capensis</i>	5	4	6.2	18.25
Cape Porcupine	<i>Hystrix africaeaustralis</i>	4	3	2.5	1.3
Vervet monkey	<i>Chlorocebus pygerythrus</i>	2	4	12	3
Springbok	<i>Antidorcas marsupialis</i>	3	3	1.67	34.3
Cape ground squired	<i>Xerus inauris</i>	5	1	1.2	1
Unknown		4	1	1	1
Cape fox	<i>Vulpes chama</i>	2	3	1	1
Other		24	10	14.03	9.5

Appendix 4. Complete list of models used, including response, explanatory and random effects. Distribution, transformations, zero inflations and overdispersion parameters are also shown. All models were carried out in the glmmTMB package using the glmmTMB function (Brooks et al. 2019).

Response variables	Model	Distribution	Explanatory variables	Random effects	Transformation	Zero inflation	Overdispersion parameter
<u>Abundance of terrestrial vertebrates</u>							
Camera trap events	GLMM	Negative binomial	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID/ Pair ID		Yes	1.93
Event duration (minutes)	LMM	Negative binomial	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No	0.486
Species richness	GLMM	Quasi-Poisson	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No	0.11
Shannon diversity	LMER	Gaussian	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID	sqrt	No	0.172
<u>Abundance of non-avian reptiles</u>							
Number of reptiles	GLMM	Poisson	Colony (present/absent)	Site ID / Pair ID		No	

Rainfall
 Tree characteristics
 Time of day
 Colony present * Rainfall

Abundance of avian fauna

Number of birds	GLMM	Quasi-Poisson	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID		No	0.651
Species richness	GLMM	Poisson	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No	
Species diversity	GLMM	Poisson	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID	sqrt	No	

Abundance of terrestrial invertebrates

Number of invertebrates	GLMM	Negative binomial	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No	1.42
Species richness	GLMM	Gaussian	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID	Log1 + 1	Yes	

Species diversity	GLMM	Gaussian	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID	sqrt	No
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Abundance of arboreal invertebrates

Number of invertebrates	GLMM	Quasi-Poisson	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No	2.75
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Species richness	GLMM	Gaussian	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID	log	No
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Species diversity	GLMM	Gaussian	Colony (present/absent) Rainfall Tree characteristics Colony present * Rainfall	Site ID / Pair ID		No
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Chapter 4

Eavesdropping between taxa: skinks use bird presence and alarm calls to manage predation risk and expand realised niche



Abstract

Eavesdropping on community members has immediate and clear benefits. However, little is known regarding its importance for the organisation of cross-taxa community structure. Furthermore, the possibility that eavesdropping could allow species to access risky foraging habitat, thereby expanding their realised niche, has been little considered. Kalahari Tree Skinks (*Trachylepis spilogaster*) associate with Sociable weaver (*Philetairus socius*) colonies, as do African pygmy falcons (*Polihierax semitorquatus*), a predator of skinks and weavers. We undertook observational and experimental tests to determine if skinks use eavesdropping to mitigate any increase in predation threat that associating with weaver colonies may bring. Observations reveal that skinks use information from weavers to determine when predators are nearby; skinks were more active, more likely to forage in riskier habitats and initiated flight from predators earlier in the presence of weavers. Playback of weaver alarm calls caused skinks to increase vigilance and flee, confirming that skinks eavesdrop on weavers. Furthermore, skinks at colony trees were more likely to flee than skinks at non-colony trees, suggesting that learning is mechanistically important for eavesdropping behaviour. Overall, it appears that eavesdropping allows skinks at colony trees to gain an early warning signal of potential predators, expand their realised niche and join communities, whose predators may otherwise exclude them.

Introduction

Eavesdropping is common in animal and plant communities (Bradbury and Vehrencamp 1998, Karban and Maron 2002, Vitousek et al. 2007) with information regarding predation threats being particularly valuable. Individuals that are able to eavesdrop on predator-related information gain immediate and clear benefits (Magrath et al. 2015), including enhanced predator detection and increased foraging efficiency resulting from reduced vigilance (Sullivan 1984, Doligez et al. 2002, McGraw and Bshary 2002, Vitousek et al. 2007, Oommen et al. 2009, Schmidt et al. 2010, Sharpe et al. 2010, Baigrie et al. 2014). However, little is known regarding the importance of eavesdropping for the organisation of community structure, including cross-taxa communities (Goodale et al. 2010). Nevertheless, what is known suggests that this importance is context-dependent (Oommen et al. 2009). Joining a community may expose individuals to increased risk (Götmark and Andersson 1984, Groom 1992), including from other community members. Eavesdropping could in principle offset such costs and facilitate community membership (Oommen et al. 2009). Furthermore, risk-related information from

heterospecifics within communities could increase access to higher-risk habitat and therefore expand species' realised niches (Goodale et al. 2010, Ridley et al. 2014, Martinez and Vredenburg 2018). Here we seek to identify whether eavesdropping allows individuals to join diverse taxonomic communities, whose predators may otherwise exclude them. We also seek to determine if community members use eavesdropping to expand their realised niche within communities by enabling them to exploit new habitat.

To date, research on eavesdropping has demonstrated that heterospecific alarm calls can elicit increased vigilance (Vitousek et al. 2007, Müller and Manser 2008, Kitchen et al. 2010), and increase the distance at which individuals flee from approaching predators (flight initiation distance (FID), (Ydenberg and Dill 1986). By contrast, non-alarm calls can indicate the lack of a predator, allowing individuals to increase foraging success by reducing vigilance when other species are present (Baigrie et al. 2014, Lilly et al. 2019). Eavesdropping could also affect spatial variation in perceived predation risk (Martinez et al. 2017), known as the landscape of fear (Brown et al. 1999, Laundré et al. 2001). By reducing the costs of accessing habitat with higher predation risk, eavesdropping could enable individuals to expand their realised niche to exploit areas from which they were otherwise excluded. This would be particularly valuable for organisms that make decisions to forage and/or move to unexploited environments that provide additional food (Gil et al. 2017). To date, this possibility has been largely overlooked, although research has demonstrated that some birds and reptiles expand their niche when associated with heterospecifics (Whiting and Greeff 1999, Ridley et al. 2014, Martinez and Vredenburg 2018). Therefore, it is not only of interest to determine if species eavesdrop on other species, enabling them to expand their realised niche, but also whether organisms also gain additional benefits when in the presence of heterospecifics on whom they eavesdrop.

By reducing predation risk, eavesdropping could enable organisms to join communities, including those where predatory members would otherwise exclude them (Oommen et al. 2009). For individuals to benefit from predator information within communities, eavesdropping must provide relevant and reliable information. Heterospecific alarm calls are only relevant if the calling species and eavesdropper are vulnerable to the same predators (reviewed by Magrath et al. 2015, Meise et al. 2018). For example, New Holland honeyeaters (*Phylidonyris novaehollandiae*) share more predators with white-browed scrubwrens (*Sericornis frontalis*) than superb fairy-wrens (*Malurus cyaneus*). Consequently, honeyeaters flee more often to scrubwrens, than fairy-wrens, alarm calls (Magrath et al. 2009a). Therefore,

the type of taxa that heterospecifics eavesdrop upon is less relevant, as long as they are able to mechanistically recognise the information.

Responding appropriately to relevant heterospecific alarm calls can either be learned or innate or potentially a combination of these behavioural mechanisms (Magrath et al. 2015, Meise et al. 2018). Innate responses would allow organisms to react to heterospecific alarm calls without previous experience, therefore reducing exposure to predators (Hollen and Radford 2009). Whereas, learned responses would mean that individuals may need to be exposed to associated species in order to be able to interpret the information and respond accordingly (Ramakrishnan and Coss 2000, Magrath et al. 2009b). Where learning plays a primary role, only individuals with an opportunity to learn would show full capacity for eavesdropping. Research on bird-bird and mammal-mammal alarm eavesdropping has considered whether responses result from shared phylogeny and similar alarm vocalisations, or learning (Magrath et al. 2009b, Randler 2012, Dutour et al. 2017, Meise et al. 2018). However, where eavesdropping occurs between phylogenetically distant taxa that exploit different communication modalities (e.g. sight, sound), they are unlikely to respond to other taxa's alarm signals due to overlap with species' own alarm systems. Such cross-taxa eavesdropping will more clearly result from innate or learnt mechanisms (Magrath et al. 2015).

Here we consider the interactions between Kalahari tree skinks (*Trachylepis spilogaster*), and sociable weavers (*Philetairus socius*), and African pygmy falcons (*Polihierax semitorquatus*), henceforth 'skinks', 'weavers' and 'falcons', respectively. These skinks occur in the arid savannah of southern Africa (Broadley 2000) and live in small groups of 3.9 ± 0.54 individuals on average (Brain 1969, Rymer et al. 2014). They largely forage on trees and on the ground close to trees but retreat to trees when disturbed, indicating that the ground represents a higher risk foraging habitat (Brain 1969). They are strongly associated with weaver colonies, being found in greater numbers on trees with colonies (Rymer et al. 2014). Skinks appear to gain substantially from weaver colonies, including through refuge, basking, and foraging benefits (Rymer et al. 2014). Weaver colonies vary in size, often increasing with age, and can contain between two and 250 nesting chambers housing hundreds of weavers (Figure 1) (Maclean 1973c). Weaver colonies host a wide range of other species, across multiple taxa, including falcons, whose diet largely consists of small lizards (Maclean 1970) including skinks, whose remains are often found under falcon nests when falcons are breeding (Lowney and Thomson, personal observation). However, trees with colonies inhabited by falcons do not have fewer skinks than colony trees without falcons (Rymer et al. 2014). Falcons do not build their own

nests, and in southern Africa rely solely on weaver colonies for breeding and roosting (Maclean 1970). Falcon territories may contain multiple colonies, with falcons often moving between these colonies throughout the year.



Figure 1. Sociable weaver colony. Large colonies can cause destruction to the host tree and it is not uncommon to observe broken branches associated with larger nests. These provide additional ground refuges for the diverse community of organisms associated with weaver colonies.

Weavers have the potential to provide information to skinks about predators through both their behaviour and vocalisations. Falcons likely present only a low threat to adult weavers given the low proportion of the falcon diet they make up (Maclean 1970), and the association between the species. Nevertheless, weavers alarm when a falcon is visible (Maclean 1970), and disperse when they approach (Lowney and Thomson, personal observation). Weavers usually occur in large groups around their colonies; their alarm calling when a falcon approaches the colony tree is conspicuous and unmistakable (Lowney, Thomson and Flower, personal observation). Skinks, therefore, have the opportunity to eavesdrop on predator presence information provided by weavers. Eavesdropping could facilitate their membership of this community in the face of predation risk by falcons. They might even exploit such information to expand their niche use

at the weaver colony by spending more time foraging on the ground, and further from the tree refuge.

Here we explore the association between skinks and weavers to identify distinct association benefits. To do this, we focus on whether skinks eavesdrop on weavers to gain information. Certain reptiles have been shown to eavesdrop on other species (Whiting and Greeff 1999; Vitousek et al. 2007). Broadley's flat lizards (*Platysaurus broadleyi*) use signals from red-eye bulbuls (*Pycnonotus nigricans*) and pale-winged starlings (*Onychognathus naboroupp*) to locate food (Whiting and Greeff 1999), while the Galapagos marine iguana (*Amblyrhynchus cristatus*) use alarm calls of Galapagos mocking bird (*Mimus parvulus*) as a warning that Galapagos hawks (*Buteo galapagoensis*) are nearby (Vitousek et al. 2007). The information gained from eavesdropping in the aforementioned studies have distinctively different benefits, and these are not typically considered together. Firstly, we investigate whether skinks use eavesdropping to expand their realised niche at colony trees by joining a cross-taxa community, despite the increased likelihood of a predator. Secondly, we test to determine if skinks gain early warning of predators from weavers and flee to cover earlier in response to approaching predators in the presence of weavers. Thirdly, we experimentally test whether skinks eavesdrop on weaver alarm calls to reduce predation risk. Finally, to determine whether eavesdropping is mechanistically dependent on learning through familiarity with weaver vocalisations we additionally compare alarm responses of skinks from colony versus non-colony trees.

Material and Methods

Field site

This study was carried out at Tswalu Kalahari, a reserve in the Northern Cape, South Africa (27°13'30"S and 22°28'40"E) that exceeds 100,000 ha (Mucina and Rutherford 2006, Tokura et al. 2018). Our main study area consists of 130 km² containing over 250 sociable weaver colonies, mostly in the two dominant tree species; camelthorn (*Vachellia erioloba*) and shephard's tree (*Boscia albitrunca*) (Rymer et al. 2014). Falcon occupation of weaver colonies averaged 14% (± 0.77 SE) annually of ~250 colonies monitored (Bolopo et al. 2019). Ground vegetation is patchily distributed and dominated by Kalahari sourgrass (*Schmidtia kalahariensis*) and small shrubs. We focussed our study on an area of 6 ha and on skinks at camelthorn trees only. All colonies used were within known falcon territories but did not host falcons at the time of the study. All observations are by AML. Additionally, the time of day

has been demonstrated to affect skinks behaviour (Huey and Prianka 1977). Therefore, we carried out balanced treatments that equally represented different times of day.

Skink abundance and movement

To investigate whether weaver presence expanded habitat use by skinks at colony trees, we counted skinks visible and whether they were on the ground or the tree, at times when weavers were present at their colony or absent. Skink counts were carried out between December 2016 and January 2017 at twenty colony trees. Skinks counts were undertaken from four locations around a colony tree, each lasting four minutes. Each observer location was at least 50 meters from the tree and after each count the observer moved to the next location, approximately 90 degrees around the tree. Once the full rotation of the tree had been carried out. A further five minutes was used for the observer to slowly walk towards and around the tree; this helped identify individuals on the floor, as these individuals were difficult to see from a distance of 50 meters and to clarify any uncertainties about whether some individuals may have been counted twice. Counts were undertaken using a spotting scope (Kowa TSN-881 and Kowa 20-60x eyepiece), and we noted the number of skinks (active and therefore exposed) and their position as either low risk (on the tree) or high risk (on the ground) when first observed. An entire tree count would last approximately 25 minutes. Counts were done twice at a given tree (paired); once with weavers present and once when absent. Paired counts were always done on the same day the order of counts was alternated between each paired count.

Skink Flight Initiation Distance (FID) in response to predators

Secondly, to investigate whether weavers facilitate earlier escape responses by skinks and therefore reduce predation risk, we used an approaching human as a model predator to generate FIDs for both weavers and skinks. We undertook trials at trees with colonies and weavers present, and to reduce habituation, we paired these with non-colony trees where weavers were absent. One trial was carried out at each colony tree and each paired non-colony tree. We chose non-colony trees as controls as this helped control for environmental differences. Time has been demonstrated to affect skinks behaviour (Huey and Prianka 1977), therefore, it was essential to carry out paired treatments as soon after one another as possible. However, we could not account for when and how long weavers would be at a given colony, therefore using skinks at non-colony trees as controls would reduce the influence of time on the skink's behaviour. Additionally, this also prevented habituation to the approaching 'predator'. To control for habitat differences, paired trees were always within 200 m of each other and both

trials were conducted within 60 minutes (21.2 minutes \pm 2.55). The order of trials at colony and non-colony trees was alternated between samples. With the control tree being within 200 m of the colony tree, we were able to observe when weavers were at the colony tree and therefore start counts at non-colony trees when control trials were first, thus increasing the likelihood of skinks still being at the colony tree when FID at the control was finished.

We searched for skinks from >50 m away using the spotting scope. Once a skink was located, the observer walked directly towards the skink at ~3 m/s, keeping the skink in sight. Weaver FIDs were also recorded at the colony trees where weavers were present, to determine whether this affected skink FIDs. Different colour markers were dropped to mark when skinks or weavers initiated escape and FID was measured (metres) after the trial.

Skink eavesdropping on weaver alarm calls

Recording of weaver calls

We used a playback experiment to confirm that skinks eavesdrop on weaver alarm calls and flee to cover in response and investigate whether this eavesdropping behaviour is learned or innate. To determine if skinks eavesdrop on weaver alarm calls, skinks at control trees were presented with playback stimuli of weaver alarm (alarm) and non-alarm contact vocalisations (control), when weavers were not present. These playbacks were repeated to skinks at non-colony trees, again making sure that no weavers were present at the time of experiment. Stimuli were created using recordings collected with a Sennheiser ME66 directional microphone attached to a tripod, placed 20 m from a colony tree that currently hosted falcons and coupled with a Marantz PMD660 recorder. Once the recording was started the observer moved to a distance of >50 m from the colony tree and noted when weavers were present, how many there were, and the context of any calls (when foraging, weaving, resting or when a predator approached). When alarm calls were produced, the species that triggered the alarm response was also noted. This allowed for the use of alarm calls produced specifically in response to approaching falcons. Non-alarm vocalisations were those produced when weavers were at the colony provisioning or weaving, and no predator was observed, nor weaver anti-predator behaviours.

During 59.5 hours of acquiring playback recordings, we observed falcons approaching colonies on 108 occasions. Weavers alarmed to 90% of all falcon approaches, and in 87% of these approaches, the birds flew away from the spot where they had been perched.

Playback stimuli

Recordings from twenty unique colonies were used to produce one alarm stimulus and one non-alarm playback stimulus paired for each colony (40 playback stimuli in total) in Raven 1.4 (www.birds.cornell.edu/raven). Each stimulus consisted of 30 s of silence followed by 30 s of vocalisation. The 30 s of vocalisation stimulus were created using sound segments from a single recording. Chosen segments were those that had the better signal to sound ratio. Where possible full 30 s segments were used (29/40), however where this was not possible smaller segments were pieced together. These were filtered with a high pass filter set at 500 Hz, with amplitudes standardised across recordings.

Experimental design and procedure

Playbacks trials were conducted at 40 different trees; 20 with a weaver colony and 20 without (paired). All paired trees were located within 250 m from one another. Each tree received two playback trials; one alarm and one non-alarm resulting in a total of 80 trials (20 paired trials at colony trees, and 20 at non-colony trees). We ensured that the recording playback pair was from a different colony to that where playbacks occurred.

Playback trials were undertaken using a wireless speaker (FOXPRO Fury GX7 Digital Game Call) positioned on the tree, where the experiment was carried out. The observer retreated to >25 m and used the scope to locate skinks. Once a skink was located on the tree, the observer would operate the speaker via a remote (TX-500) transmitter. To account for carry-over effects, the order of stimulus presented was changed between each experiment. Skink behaviour during each trial was observed through the scope. Response parameters were whether a skink ran from view (Yes/No), and the total number of vertical and lateral head movements. An increase in vigilance may result in an increase in the number of head movements as skinks scan for potential predators. This has been shown to be true with other reptiles (Ito and Mori 2010). An individual skink would be presented with two trials; one alarm and one non-alarm vocalisation. If skinks are shown to respond appropriately (increased vigilance to alarm calls but not change in behaviour when presented with the control) at colony trees but not at non-colony trees, then this would imply a role of call learning and not simply innate knowledge of weaver alarm vocalisations. If a skink fled during the first trial we would wait until a skink returned to the same area before repeating the process with the second trial. Occasionally, a skink would be quite distinct (missing part of a tail) and these would return to the same basking sites, suggesting that individuals have preferred locations and trials were conducted on the same

individuals. However, many skinks were indistinguishable, therefore we could not guarantee that the second trial was conducted using the same individual as the first. Nevertheless, random playback order ensures that any effect is balanced between treatments. Once a skink returned to the area, we waited 60 s before presenting the second stimulus. This was to allow the individual to resume foraging or basking behaviour. All trials were conducted when there were no weavers present. If weavers did appear during the trial, the experiment was abandoned and a different colony/non-colony tree pair was selected for the experiment.

Statistical analyses

All data were analysed using the R statistical package 3.4.0. (R Core Team 2017). Generalized linear mixed models (GLMMs) were undertaken using the glmmTMB package (Brooks et al. 2019). This package was used due to its ability to handle zero-inflated models. Where count data were over-dispersed models were fitted with either a quasi-Poisson or negative binomial distributions (Hara and Kotze 2010). Trees where paired treatments were undertaken were given unique ID's that were then used as random terms in the relevant models. For analyses where interactions were fitted, we explored interactions where p values were less than 0.1 using post-hoc tests. Those that had a value greater than 0.1, or where post-hoc tests revealed no significant differences were subsequently removed from the models. Tukey post-hoc tests were carried out using emmeans function (Lenth 2018). For each response variable, the full model terms and structure, and the error distribution used are detailed in Appendix 1.

To test whether weaver presence influenced skinks foraging site and behaviour. A negative binomial distribution was first fitted to test whether weaver presence influenced the number of skinks visible at colony trees. A Poisson distribution was used to compare the number of observed skinks foraging away from the tree when weavers were and were not present, fitted as an explanatory term (present/absent). Time has been demonstrated to affect skinks behaviour, with peak activity occurring earlier and later in the day (Huey and Prianka 1977) therefore, we included time of observation/experiment as an additional explanatory term in this and all subsequent models. Time was recorded in the 24-hour format and was converted to decimal (e.g. 12:30 became 12.5), before being used in the models. Colony was included as a random term.

A negative binomial GLMM was used to determine whether weaver presence influenced skink FID. Colony presence (present/absent) and time of day were used as explanatory terms. Paired

trees were given a unique pair ID and this was used as a random term. A Pearson's correlation was used to determine to what extent weaver FID influenced skink FID.

To test our assumption that skinks are able to eavesdrop on weaver alarm calls and whether this depended on their familiarity with weavers, we carried out GLMM's considering vigilance during playback trials fitted with a quasi-Poisson distribution. Our model used the number of head movements as the response variable and stimulus type (alarm/control), playback-period (pre/during), tree type (colony/non-colony) and time of day as explanatory terms. Paired and individual trees were given unique ID's and these were used as random terms; with Tree ID being nested within Pair ID. We fitted a three-way interaction between the playback period, stimuli type and tree type to determine whether skinks respond differently to the playback treatments.

We also tested the likelihood that skinks flee for cover to further identify whether skinks familiar with weavers more often show appropriate escape responses to alarm versus control calls. Again, this would imply a role for call learning and not simply innate knowledge of weaver alarm vocalisations. Here we used stimulus type (alarm/control), tree type (colony/non-colony) and time of day as explanatory terms. Tree ID nested within playback pair ID were used as random terms. We included an interaction between tree type and stimulus type to explore whether skinks familiar with weavers better distinguish control and alarm weaver calls.

Results

Skink abundance and movement

Consideration of whether weaver presence promotes skink activity on colony trees revealed that twice as many skinks were observed when weavers were present (Figure 2a, Table 1a). Furthermore, five times as many skinks were observed foraging on the ground when weavers were present compared to when weavers were absent (Figure 2b, Table 1b).

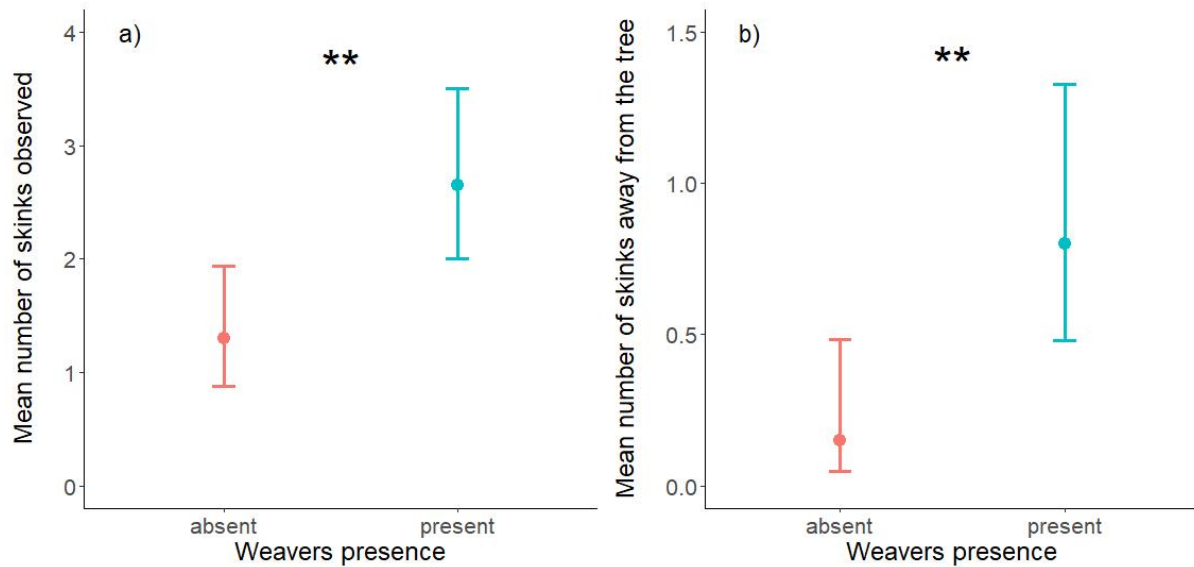


Figure 2. Mean (\pm 95% CI) number of skinks when weavers were present and absent at colony trees: a) total skinks observed; b) proportion foraging away from the tree (** = $p < 0.01$).

Table 1. GLMM (Negative binomial and Poisson, respectively) of whether the number of skinks observed is influenced by the presence of sociable weavers; (a) at colony trees only and (b) around colony trees.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	P
a) Total number of skinks n=20	Weavers Present (yes/no)	0.778	0.24	10.38	<0.01
	Time	0.066	0.03	3.63	0.06
b) Skinks away from the tree n = 20	Weavers Present (yes/no)	1.70	0.63	7.17	<0.01
	Time	0.02	0.07	0.08	0.78

Skink Flight Initiation Distance (FID) in response to predators

In total 68 FID experiments were undertaken; 34 at colony trees with weavers present and 34 at paired non-colony trees with weavers absent. The human ‘predator’ could approach significantly closer to skinks at non-colony trees, before skinks fled for cover, compared to colony trees with weavers present (Figure 3, Table 2). There was a strong positive correlation between the weavers and skinks FID (Pearson’s correlation coefficient $|r| = 0.85$). Both species initiated their escape at the same distance in 23 of the 34 trials. During the other eleven trials, the weavers always dispersed first.

Table 2. GLMM (Negative binomial) of whether sociable weaver presence influenced skink FID in response to predators

Response variables	Explanatory variables	Estimate	± SE	χ^2	<i>P</i>
Skink FID	Weavers Present (yes/no)	0.838	± 0.17	24.23	<0.001
n=68 (34 paired)	Time	0.004	± 0.031	0.02	0.89

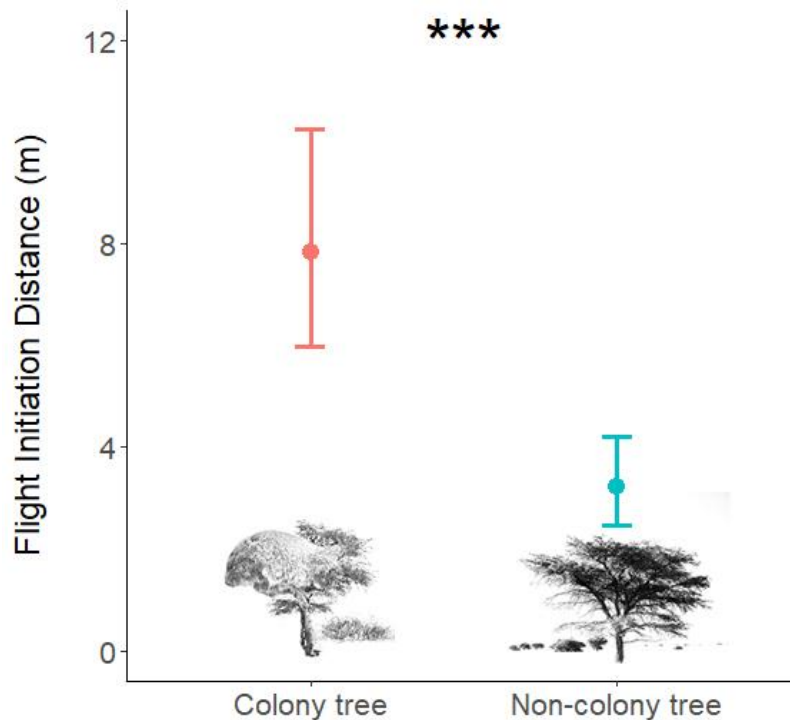


Figure 3. Mean (of the raw values ± 95% CI) flight initiation distance of Kalahari Tree Skinks at non-colony trees compared to when weavers were present at colony trees (***) = $p < 0.001$).

Skink eavesdropping on weaver alarm calls

Vigilance response to playback stimulus

In response to weaver call playbacks, the interaction between playback period, stimulus type and colony presence explained much of the variation (Table 3; Figure 4). Post-hoc tests revealed that skinks significantly increased their vigilance when presented with an alarm

stimulus compared to the pre-playback period at colony (type, $z = -5.501$, $P = <0.001$; Figure 4a) and non-colony trees (type, $z = -5.741$, $P = <0.001$). However, skinks at colony trees did not increase their vigilance when presented with a control stimulus (type, $z = -1.653$, $P = 0.716$; Figure 4b); whereas skinks at non-colony trees did (type, $z = -3.832$, $P = <0.01$; Figure 4d). Skinks were significantly more vigilant when presented with an alarm than a control stimulus at both colony (type, $z = -4.410$, $P = <0.01$; Figure 4) and non-colony trees (type, $z = 3.121$, $P = <0.05$; Figure 4). Comparison between skinks at colony and non-colony trees, when presented with an alarm stimulus revealed no differences in vigilance. However, an increase in vigilance was observed in response to the control stimuli by skinks at non-colony trees (type, $z = -2.841$, $P = 0.09$; Figure 4).

When comparing the vigilance responses between skinks at colony and non-colony trees, analyses showed that skinks at non-colony trees were significantly more vigilant when presented with a control stimulus, than those at colony trees ($z = -2.86$, $P = 0.03$; Figure 5a). Skinks responded similarly at colony and non-colony trees when presented with an alarm stimulus (Figure 5a), being significantly more vigilant when presented with an alarm stimulus compared to a control at colony ($z = 4.7$, $p = <0.001$) and non-colony ($z = 3.42$, $= <0.01$) trees suggesting an elevated response to alarm stimuli despite lower familiarity at non-colony trees.

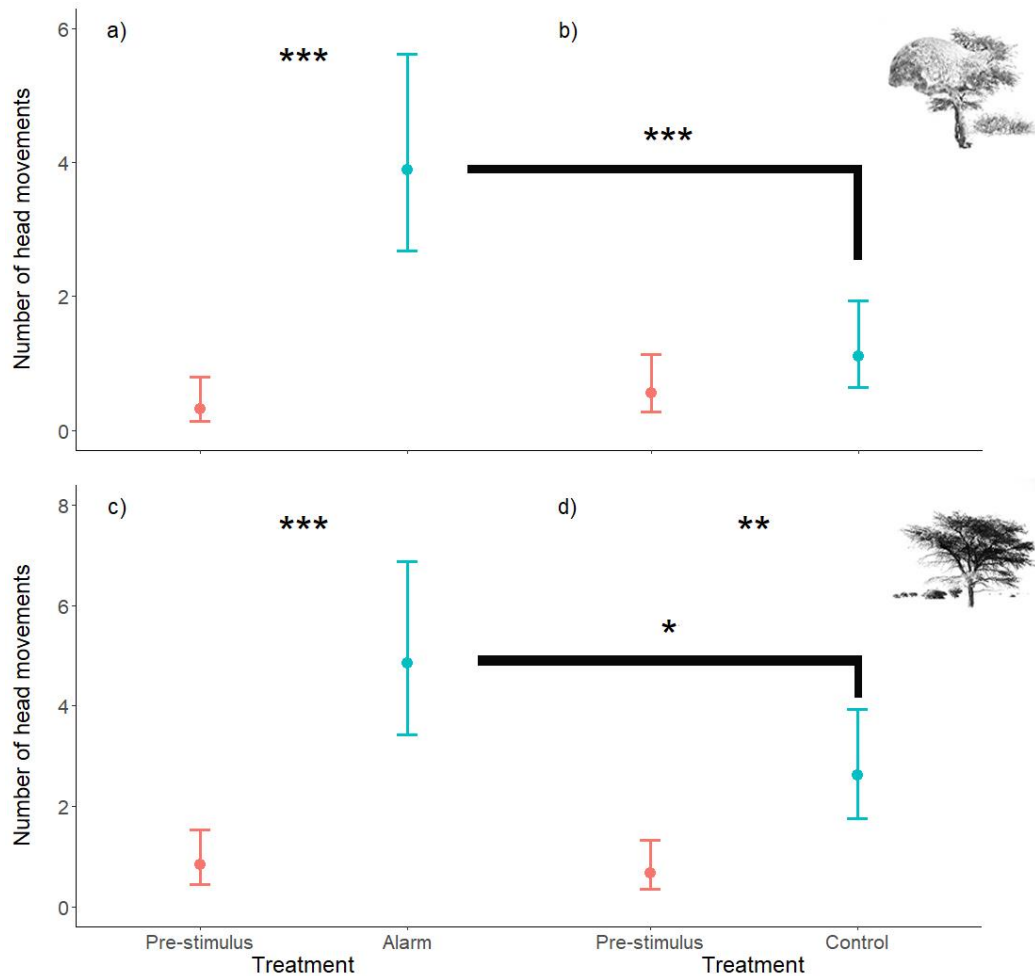


Figure 4. Skink vigilance measured as head movements (mean \pm 95% CI). (a) Skink vigilance significantly increased when presented with the alarm call playback stimulus at colony trees, but not control playbacks. Vigilance was also significantly greater to alarm than control playbacks. However, vigilance did not significantly change when presented with a control stimulus. Whereas, at non-colony trees (b) vigilance significantly increased when presented with either stimulus. Vigilance was also significantly greater to alarm than control playbacks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Likelihood skinks flee when presented with different playback stimuli

Our model testing the likelihood skinks flee for cover when presented with weaver call stimuli, revealed that skinks at colony trees were more likely to flee when presented with an alarm stimulus than skinks at non-colony trees ($z = -2.943$, $P = <0.05$; Figure 5c, Table 3). No difference was observed when comparing responses to the control stimuli. Post-hoc tests also revealed that skinks at colony trees are more likely to flee when presented with an alarm than

a control stimulus ($z = 2.689$, $P = <0.05$; Figure 6a & 6b, Table 3), but at non-colony trees, no significant difference was observed.

Table 3. Skink response to playback stimuli (quasi-Poisson and binomial respectively), Skink vigilance (a) and the likelihood that skinks flee (b) when presented with alarm and control stimuli in response to playback stimuli.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Vigilance n=160	Playback period (pre/stimuli)			71.1	<0.001
	Treatment (alarm/control)			19.97	<0.001
	Colony tree (yes/no)			8.02	<0.01
	Time of trial	0.03	0.04	0.67	0.41
	Treatment order (first/second)			0.77	0.38
	Playback period*Treatment	-0.41	0.47	6.22	<0.05
	Playback period*Colony tree	0.73	0.55	0.01	0.93
	Treatment*Colony tree	0.76	0.67	1.33	0.25
	Playback period * Treatment* Colony tree	-1.40	0.77	3.30	0.069
	b) Flee (yes/no) n=80	Treatment (alarm/control)			1.04
Colony tree (yes/no)				5.45	<0.05
Time		-0.73	0.73	1.02	0.31
Treatment order (first/second)		4.50	2.98	2.29	0.13
Treatment*Colony tree		-20.62	8.88	5.49	0.02

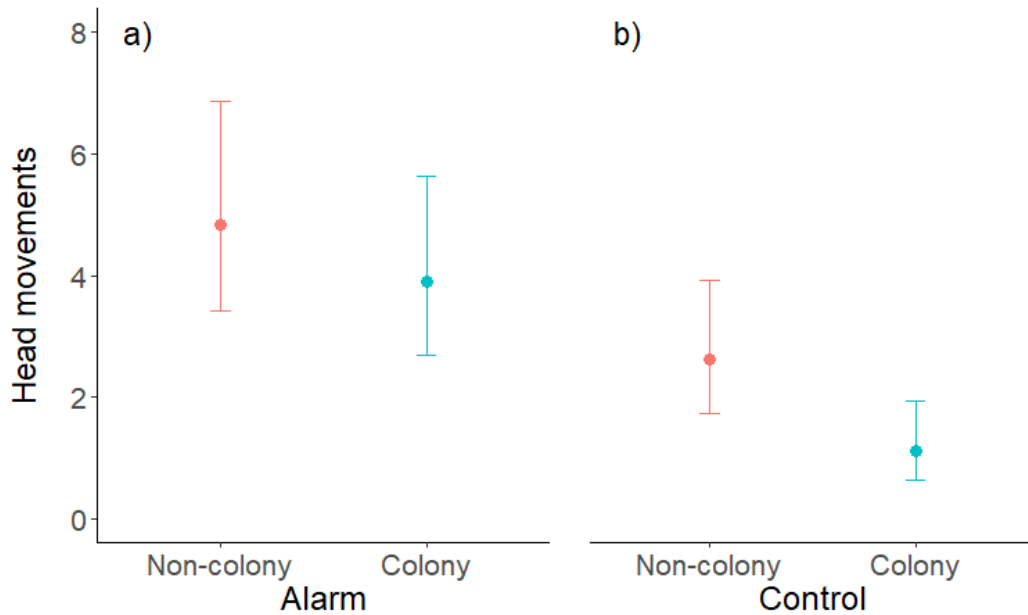


Figure 5. Skink vigilance (mean \pm 95% CI) in response to alarm (a) and control (b) stimuli. (a) Skinks at colony and non-colony trees were more vigilant in response to alarm than control stimuli, but skinks at non-colony trees showed greater vigilance to control stimuli (b).

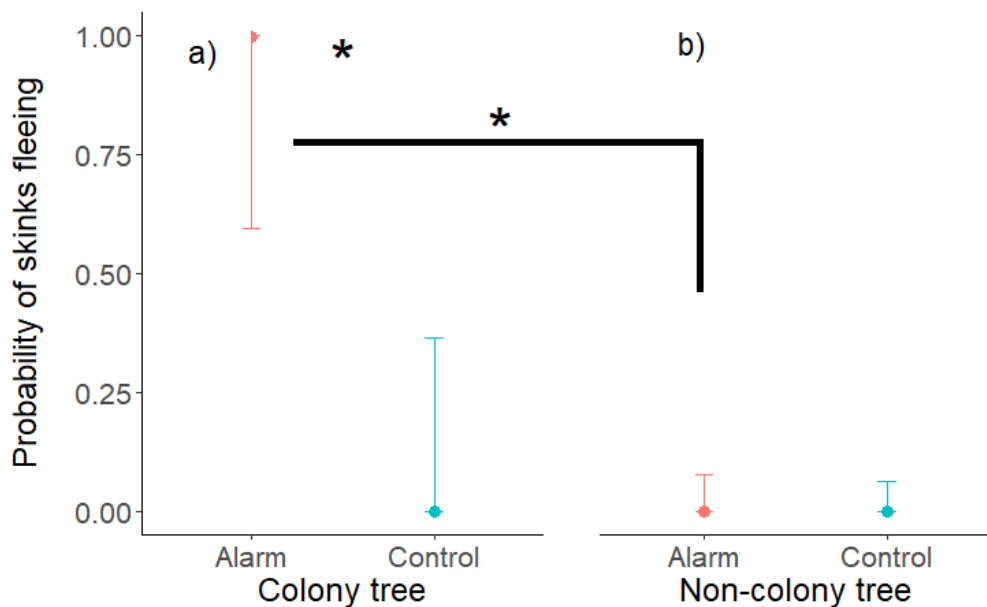


Figure 6. The likelihood (\pm 95% CI) of skinks fleeing during playback periods at colony and non-colony trees. Skinks at colony trees were more likely to flee in response to alarm stimuli than control stimuli, but skinks at non-colony trees did not show this relationship. Furthermore, in response to alarm stimuli, skinks at colony trees were more likely to flee to cover than skinks at non-colony trees (** = $p < 0.01$).

Discussion

Our results suggest that associating with weaver communities and eavesdropping on alarm vocalisations enables skinks at colony trees to reduce predation risk and exploit riskier habitat, despite exposure to a predatory community member, the pygmy falcon. Associating with weavers facilitates skink foraging and basking, by allowing them to increase activity, venture further from refuges, and sit in more exposed locations. We show experimentally that skinks respond decisively to weaver alarm responses and specifically eavesdrop on weaver alarm calls. Furthermore, eavesdropping appears to be at least in part learnt, since skinks at colony trees respond more strongly to weaver alarm calls than controls and show appropriate escape responses, while skinks at non-colony trees do not clearly distinguish controls and alarms. It is possible but highly unlikely that there is a sub-population of ‘weaver specialist’ skinks within the species with a genetically driven weaver alarm response and preference for weaver colonies. However, this explanation appears less parsimonious given the lack of evidence for reproductive isolation between trees. Together, our results demonstrate that skinks eavesdrop on weaver alarm vocalisations towards falcons, which enables them to reduce predation risk and expand their realised foraging niche, potentially mitigating the costs of living with a predatory community member.

Many studies have focused on responses of eavesdroppers to alarm signals, but here we emphasise that eavesdropping may allow organisms to expand their realised niche (Magrath et al. 2015). By foraging in the presence of weavers, skinks can reduce their risk in the ‘landscape of fear’. This could enable skinks to reduce vigilance, as demonstrated for other species (Sullivan 1984, Doligez et al. 2002, McGraw and Bshary 2002, Schmidt et al. 2010, Sharpe et al. 2010), and/or expand the area of habitat or resources exploited for a given risk threshold as we demonstrate here. The skink’s strategy will be a trade-off between gaining more protection and exploiting the weavers to get more food which likely depends upon skink energetic state with less satiated individuals more likely to exploit foraging benefits for an equal predation risk (Heithaus et al. 2007). We suggest that further research assess when animals exploit eavesdropping to expand their habitat use and/or foraging in comparison to reduced exposure to predators.

Skinks eavesdropping on weavers illustrates how exploitation of beneficial relationships within communities can mitigate the costs of negative interactions with other community members. Skinks may gain numerous benefits from joining weaver communities, including through

increased foraging returns and by mitigating risk. However, association with weavers likely exposes them to enhanced predation by pygmy falcons. Nevertheless, skinks can mitigate the risk through additional eavesdropping interactions with weaver community members. Therefore, we may expect to see that when animals join mixed-species associations, natural selection will favour the evolution of beneficial species interactions that specifically mitigate the costs of negative interactions with other community members. For example some bird species nest near a potential predator, who by forming a protective umbrella around its own nest can exclude mutual predators (Bogliani et al. 1999).

Skinks may not only eavesdrop on signals but also attend to weaver cues, including foraging and flight behaviour. In non-alarm contexts, skinks may use weaver chatter signals or foraging/weaver behaviour as cues that predation risk is low. Studies have suggested that heterospecifics taking flight in response to an approaching predator should also be a reliable cue in alarm contexts (Morse 1977), yet few studies have indicated that relaxed behaviour can be used as a reliable cue (Sullivan 1984, 1985, Ridley et al. 2014, Lilly et al. 2019). Although we did not test for this, we did observe fewer false responses to control calls at colony trees and, therefore, suggest that this be explored in future studies. Moreover, to the best of our knowledge, only one study has explicitly determined through experimentation that heterospecific relaxation is a cue to the absence of a predator (Lilly et al. 2019). Such behaviour is likely widespread in mixed-species assemblages and research to explore this possibility would represent an exciting new avenue to determine how community members exploit both heterospecific signals and cues to moderate risk in the landscape of fear.

Skinks use cross-taxa eavesdropping to avoid predation, further demonstrating that eavesdropping is likely driven by shared information value rather than phylogeny. Eavesdropping is commonly used in species associations, especially between species within the same taxonomic and functional group (Lea et al. 2008). Eavesdropping will be favoured by any organism when information from the environment reliably correlates with a context in the environment that affects individual fitness (Danchin et al. 2004, Shettleworth 2010). Intuitively, between taxa eavesdropping should, therefore, be no less likely than within taxa eavesdropping, assuming that signal detection is possible and predators overlap. However, studies have mainly focussed on within taxa eavesdropping (Kitchen et al. 2010, Baigrie et al. 2014, Ridley et al. 2014, Meise et al. 2018). In particular, research has considered how the alarm calls of different bird species often share acoustic similarities which may facilitate heterospecific recognition (Marler 1957, Hurd 1996). Overlap in information value and sensory

systems to detect signals may be less likely between taxa, nevertheless, for organisms of the same trophic level, requiring similar habitat and which share predators, overlap might be high (Goodale et al. 2010).

The mechanism behind skink eavesdropping appears to be in part learnt through familiarity, but other factors may contribute. Our finding that skinks at colony trees better-discriminated alarm and control stimuli, and were more likely to show flee responses to alarm calls, indicates that learning plays a role in the acquisition of eavesdropping responses appropriate for signal context. By contrast, skinks at non-colony trees showed limited discrimination, nor an appropriate flee response to alarms. The overall high response to alarm and control signals at non-colony trees may result from a low threshold for unfamiliar sounds. The lack of evidence for reproductive isolation between trees suggests that individual skinks may change location, develop in different places and also experience weaver flocks in their territory providing opportunities for learning. Overall, our results demonstrate the benefits available from a learning mechanism that enables individuals to exploit available information within a heterogeneous environment (Griffin 2004). Such learning mechanisms likely play an important role for species that exploit mixed-species associations where community membership may be variable, especially across a species' range.

In summary, we demonstrate how across-taxon eavesdropping allows skinks to expand their realised niche and join communities including predatory members, that may otherwise exclude them. Such habitat use expansion may be an important aspect of mixed-species assemblages that are facilitated by eavesdropping. Eavesdropping is likely possible through learning in skinks, and more generally, a learning mechanism may allow individuals to be flexible in response to changes in local community composition (Griffin 2004). Our study highlights the broad benefits of eavesdropping for risk management, specifically through niche expansion, thereby highlighting its potential importance in facilitating community associations and habitat use.

Appendix 1. Complete list of models used, including response, explanatory and random effects. Distribution, zero inflation and overdispersion parameters are also shown. All models were carried out in the glmmTMB package using the glmmTMB function (Brooks et al. 2019). Analyses reported in this article can be reproduced using the data provided by Lowney et al. (2020).

Response variables	Model	Distribution	Explanatory variables	Random effects	Zero inflation	Overdispersion parameter
<u>Skink abundance and movement</u>						
a) Total number of skinks	GLMM	Poisson	Weavers present (yes/no) Time	Colony ID	No	
b) Skinks away from the tree	GLLM	Poisson	Weavers present (yes/no) Time	Colony ID	No	
<u>Skink Flight Initiation Distance (FID) in response to predators</u>						
Skink FID		Negative binomial	Weavers present (yes/no) Time	Paired ID	No	2.25

Skink eavesdropping on weaver alarm calls

a) Skink vigilance	GLLM	Quasi-Poisson	Playback period (pre/stimuli)	Pair ID	No	0.577
			Treatment (alarm/control)	Tree ID		
			Colony tree (yes/no)			
			Time of trial			
			Treatment order (first/second)			
			Playback period*Treatment			
			Playback period*Colony tree			
			Treatment*Colony tree			
			Playback period * Treatment* Colony tree			
b) Skinks fleeing (yes/no)	GLLM	Binomial	Treatment (alarm/control)	Pair ID		
			Colony tree (yes/no)	Tree ID		
			Time			
			Treatment order (first/second)			
			Treatment*Colony tree			

Chapter 5

Sleeping with the enemy: African pygmy falcons provide colony defence but inflict apparent direct costs on weaver reproductive output



Abstract

Coevolution is often described as an ‘arm-race’ between two interacting species evolving reciprocal adaptations that determine fitness outcomes. While antagonistic effects may dominate these interactions, there may be positive outcomes that are fitness-enhancing and the benefits that may accrue are likely to be context-dependent on particular biotic and abiotic conditions therefore, protective associations between a predator and prey species represent a scenario where typically antagonistic interacting species may confer facilitative benefits to each other. African pygmy falcons (*Polihierax semitorquatus*) are obligate nest associates of Sociable weavers (*Philetairus socius*), using weaver colonies exclusively to breed and roost. Falcons have been reported to occasionally prey on weavers, but may also have the potential to defend colonies from predators. We undertook observational and experimental tests to determine if falcons can deter snakes from weaver colonies and if so, investigated if this leads to an increased reproductive output for weavers that shared colonies with falcons. Additionally, we followed falcon breeding attempts and compared the success of falcon nests that overlapped with weaver breeding and those that did not. Observations reveal that snake encounters were reduced at colonies with falcons, but increased when weavers were breeding. Our experiments showed that falcons are more aggressive towards a snake stimulus than a control stimulus, but only when falcons were breeding. Despite this, overall weaver breeding success did not increase at colonies that hosted falcons. In fact, weaver egg predation rates decreased when falcons were breeding, but chick predation rates did not differ. Falcon defence of colonies likely leads to this enhanced weaver nest survival at the egg stage; however, this gain is offset after hatching due to active chick predation by falcons. Interestingly, when weavers were breeding, falcon nests suffered increased in snake predation, whereas when weavers were not breeding falcon breeding attempts mainly failed due to reasons other than predation (e.g. lack of provisioning), but overall falcon breeding success was not explained by whether weavers were breeding. This suggests that both weavers and falcons incur costs and benefits of their close association, with net effects likely to depend on the exact conditions in a particular breeding season (i.e. snake predation pressure or food availability).

Introduction

Coevolution is often described as an ‘arm-race’ between two interacting species evolving reciprocal adaptations that determine fitness outcomes (Dawkins and Krebs 1979). ‘Arms-race’ suggests that coevolution is driven by negative interactions, which is supported by theoretical

(Yoder and Nuismer 2010) and empirical studies that focus on predator-prey (reviewed by Ruxton et al. 2004), competitive (Abrams 2000) or host-parasite interactions (Thorogood et al. 2019). However, while antagonistic effects may dominate these interactions, there may be positive outcomes within these close interactions that are fitness-enhancing (e.g. Canestrari et al. 2014). Benefits that may accrue in otherwise combative interactions are likely to be context-dependent on biotic and abiotic conditions. Understanding these environmental contexts is essential in a changing world, but these remain mostly unexplored.

Protective associations between a predator and prey species represent a scenario where normally antagonistic interacting species may confer facilitative benefits to each other. This phenomenon is often described in avian systems, where timid species choose to nest near aggressive species that form a protective umbrella around their own nest thereby excluding mutual predators (Bogliani et al. 1999, Sergio and Bogliani 2001, reviewed by Quinn and Ueta 2008). Regularly, the protective species is a potential predator of the protected associate or could cause reproductive failure (Burger 1984, Bogliani et al. 1999, Quinn and Kokorev 2002). However, despite this threat, the protected species actively chose to breed close to these potential predators (Norrdahl et al. 1995, Bogliani et al. 1999, Thomson et al. 2006, Väänänen et al. 2016), a decision which ultimately enhances their mean reproductive success (Bogliani et al. 1999; Sergio and Bogliani 2001). The benefits gained through these interactions may be context dependant on prevailing environmental conditions, for example, nest predation pressure (Gotmark 1989, Larsen and Grundetjern 1997). In addition, to gain any protective benefit, protected species need to time their breeding to overlap with the breeding of the protective species, because aggressive behaviours are mainly for nest defence (Bogliani et al. 1999; Ueta 2001). However, the interplay between these costs and benefits have not been quantified.

For the protective ‘aggressive’ species, there are potential cost-benefits trade-offs of associations with timid species too (Quinn and Ueta 2008). Protective species may have additional access to food by preying on the protected species chicks or eggs (Norrdahl et al. 1995; Young and Titman 1986) of their nesting associates. However, more species nesting nearby may attract more predators, resulting in the increased likelihood of having their own nesting attempts or even themselves succumb to predation. They may also spend more time and energy exhibiting defensive behaviour, which can negatively affect their reproductive output (Groom 1992). Nonetheless, of the studies that have investigated the costs and benefits to protective species (Wiklund 1979, Groom 1992, Larsen and Moldsvor 1992, Lindell 1996,

Olson et al. 2001, Beier and Tungbani 2006), only Wiklund (1979) revealed any benefits. Merlin's (*Falco columbarius*) provide protection for fieldfares (*Turdus pilaris*), an already aggressive passerine, and when both species nest together they both gain greater reproductive success than non-associated pairs (Wiklund 1979, 1982). However, only rarely do protective associates actively choose to nest near a timid species, which may happen when the protective associate requires the timid species to alter the physical habitat in this landscape. Studying such systems would allow for a greater understanding of this association and determine how such behaviours may evolve.

Ecosystem engineers are species that strongly alter the physical environment and can cause cascading effects on other biotic and abiotic factors (Jones et al. 1994, Hastings et al. 2007). By modifying habitats and altering the availability of resources, engineers may increase local environment carrying capacity and enable range expansions (Kylafis and Loreau 2008, Krakauer et al. 2009). Interactions between species associated with a resource can create “engineering webs” that, along with recognised trophic interactions, regulate ecosystem functioning (Jones et al. 1994). Considering that biotic interactions may increase the rate of adaptation, speciation and coevolution, we would expect greater relevance to these types of interactions (Schemske et al. 2009), especially between species that coexist in such close proximity. Therefore, when engineers modify their physical habitat, they may also modify selection on other species that depend on these physical changes (Laland and Feldman 2003). This may then drive behavioural adaptations, coevolution, strengthen or relieve competition, influence the probability of coexistence, and produce macroevolutionary trends (Krakauer et al. 2009, Laland et al. 2016). As a result, this may allow species to become members of communities where competitive or predatory behaviours would otherwise preclude their membership.

Here, we aim to describe the nature of the interaction between two species in an unconventional nesting association. Our extraordinary study system involves an obligatory nesting parasite, the Pygmy falcon (*Polihierax semitorquatus*; henceforth “falcons”) and its nest-building host, the Sociable weaver (*Philetairus socius*; henceforth: “weavers”). Weavers are ecosystem engineers that build extensive colonies (Chapter 2 and Chapter 3). Falcons breed and roost exclusively within weaver colonies causing their distribution in southern Africa to overlap with the presence of weavers (Maclean 1970). Both weavers and falcons use the colonies year-round, creating an extreme nesting association. The literature on this system has speculated on the benefits and costs to both species (Maclean 1970), although these relied on anecdotal

observations at colonies (Spiby 2014). We explore the reproductive outcomes of both species under different contexts and try to identify the mechanisms that allow these species to coexist in such close proximity. Providing the first quantitative measure of success in such a novel system provides insight into the coevolution of such an extreme nesting association.

Weavers appear to resent the falcons and instantly alarm when a falcon is visible (Maclean 1970) and often disperse when falcons approach (Chapter 4). Falcons have been reported to prey on weavers adults and chicks, but to what extent is unknown (Maclean 1970, Covas et al. 2004, Spiby 2014). Maclean (1970) states that he never observed snakes in colonies that host falcons and that there was no evidence to suggest that any of the monitored falcon breeding attempts were predated by snakes. This is extraordinary considering, up to 70% of weaver breeding attempts are predated (Covas 2002, Covas et al. 2004); mainly by snakes (Maclean 1973b, Covas 2002). In this study, we investigate if falcons can defend colonies from predators, particularly snakes, and reduce nest predation rates. If so, we investigate if this protection leads to increased weaver's reproductive success? Additionally, what benefits and costs do falcons incur by being an associative species?

Materials and Methods

Study site and data collection

This study was carried out at Tswalu Kalahari, a reserve in the Northern Cape, South Africa (27°13'30"S and 22°28'40"E). Our main study area consists of 130 km² containing over 250 weaver colonies, mostly in the two dominant tree species; camelthorn *Vachellia erioloba* and shephard's tree *Boscia albitrunca*. There are between 29 (11%) and 39 (17%) active falcon territories in the study area annually that occupy one (rarely two) weaver colonies. Falcon groups and territories have been observed since 2011, with all adults colour-ringed from 2015 onwards (Boloipo et al. 2019).

Snake encounter rates

To determine if falcon presence influenced the likelihood of encountering snakes at a colony, we recorded snake presence at weaver colonies that hosted falcons and at paired weaver colonies that did not host falcons. The number of colonies visited, varied between years due to the fluctuation in the number of falcon territories; 36 colonies in 2015-2016 and 2016-2017, and 26 colonies in 2017-2018. Falcons have multiple colonies within a territory and can move between colonies from year to year. In addition, colonies are also dynamic and can increase in

size from year to year or completely collapse (R. Thomson, unpublished data). Therefore, a falcon occupied colony paired with a control in one year may be paired with a different colony the following year potentially causing an unequal number of colonies observed despite the paired design. Paired colonies were on average 699 m apart (± 102 m SE, range 58 – 2300 m; all means, unless otherwise stated are presented with standard error), and were of similar size (mean 82 chambers ± 4.37 , range 12 - 238) and matched for tree species. We used the number of chambers as a proxy for colony size as these positively correlate with the size of the structure (Leighton and Echeverri 2014), and recorded colony height above ground. We visited these colonies at least once every seven days during the peak breeding seasons (October – March) between 2015 and 2018, with paired colony trees being visited on the same day immediately after each other.

Pygmy falcon reaction to model predators?

To understand how falcons potentially respond to predators at weaver colonies, we fixed plastic toy snakes to colonies that hosted falcons. We conducted experiments at twelve different colonies that contained breeding falcons. All falcon nests contained three-week-old chicks (see below). We used two different model snakes, each at six colonies. They were 46cm long and $\text{\O}2\text{cm}$. A small soft football was used as the control ($\text{\O}8\text{cm}$). The order of presentation between the snake and the control changed between each experiment. Stimuli were attached to colonies using plastic wire ties. To prevent habituation, the second stimulus was presented three days after the first.

Once a stimulus had been attached to a colony, a video camera (Legria HF R 606) filmed the falcon's response for forty-five minutes. The researcher left the area, eliminating any influence an observer had on the falcon's behaviour. The camera was mounted on a tripod with unobstructed views of the colony and stimulus. Data extracted from the videos included: 1) if falcons responded aggressively (yes/no), defined as a falcon mobbing the stimulus, and 2) the level of aggression defined by the number of times a falcon physically struck the stimulus.

These experiments were repeated using the same individual falcons, three months later, when falcons had finished breeding. The falcons received the same decoy snake and presentation order as before. However, two falcon groups were excluded because they had moved to a colony that was too high to attach the stimuli.

Weaver and falcon breeding success

We inspected nest chambers of falcons and weavers, in 48 unique colonies, every 4-7 days throughout the breeding season to detect the laying of clutches. Due to the size of many of our colonies (up to 238 chambers), it was impossible to monitor every weaver chamber in each colony. Therefore, we monitored a subset of chambers (mean 29, range 12 – 42), with the same number of chambers monitored at paired colonies. We focused on chambers around the centre of the colony structures because this is where the dominant weaver individuals roost and nest and where most of the breeding occurs (van Dijk et al. 2013). All falcon occupied chambers were monitored because falcons mark their chambers with a conspicuous white faecal mat allowing easy identification of their chambers (Maclean 1970, Krochuk et al. 2018). Each chamber was inspected using a Rolson 60515 Two LED Telescopic Inspection Mirror. Once a weaver or falcon breeding attempt was recorded, these chambers were monitored closely to determine fledging success.

Weavers lay up to six eggs (Maclean 1973d, Covas 2002), and incubation lasts around fifteen days, usually starting after the first egg has been laid (Covas 2002). To determine exact hatching dates, the frequency of nest visits increased near the hatching date. Weaver nesting period is 21-24 days (Maclean 1973d); however, chicks may fledge prematurely if disturbed from day 18 onwards. Therefore, the last time we checked a nest was when the oldest chick was 17 days old. If the oldest chick survived to day 17 then we assumed then that the brood was said to have fledged and that breeding attempt was recorded as a success. Falcon nests hatch after around 28-days and chicks remain in the nest for a further four to five weeks. From day 24, chicks are large enough to see from the ground without using the mirror, and if the chamber appeared empty, we would then scan the territory looking for fledged chicks. If only some of the chicks were seen, we would check colonies at night with a torch. We could then record how many chicks had returned to the nesting chamber or were now using a different chamber. These methods allowed us to accurately determine the number of chicks that successfully fledged.

To assess nest predation of both weaver and falcon nests, we classified the disappearance of nest contents as predated if the contents of two or more adjacent breeding chambers were discovered empty (Covas 2002). If falcons were breeding but weavers not, then falcon nest predation would be classified only when the full falcon nest contents disappeared. Therefore,

if only one or two chicks or eggs disappeared, but the other/s remained, then this would not be recorded as nest predation. In addition, all chambers that were found empty the day after a snake was observed at a colony was also classified as predation (Covas 2002).

Statistical analysis

All data were analysed using R statistical package 3.4.0 (R Core Team 2017). We used generalised linear mixed models (GLMM) to test all response variables using the glmmTMB package (Brooks et al. 2019). Poisson distributions were used to analyse count data. When this was over-dispersed models were fitted with negative binomial distributions (Hara and Kotze 2010). During 2017 we did not record a single weaver breeding success, meaning that the response variable for this year only contained zeros. This affected our ability to undertake robust statistical tests, therefore we omitted year from our explanatory variables. Colony size has been shown to influence weaver breeding success, with weavers from larger colonies producing more offspring than weavers from smaller colonies (Covas 2002); therefore, using the number of chambers as a proxy for colony size (Leighton and Echeverri 2014) we entered this as an explanatory variable in all models testing for breeding success of weavers or falcons. For each response variable, the full model terms and structure, the error distribution used, and any data transformation performed are detailed in Appendix 1.

To determine if falcon presence explained the probability of encountering a snake at a colony, we used the binomial response variable ‘snake presence’ (yes/no). The model included explanatory terms, falcon presence (yes/no), weavers breeding (yes/no), colony size (number of chambers) and height of colony above ground. Colony ID was nested within paired colonies ID as a random effect to account for non-independence for multiple nests within the same colony and paired spatial dependence between paired colonies. To test if active falcon breeding explained the probability of snake encounters, we subset the data to only include colonies that hosted falcons, therefore only Tree ID was used as a random effect.

We examined falcon behaviour to the different stimuli using falcon response to a stimulus (yes/no) and the level of aggression (contact made with stimulus, yes/no). These models with binomial error distributions included the explanatory variables, treatment (snake or control stimuli), the order of treatments (first or second) and the number of chicks that were in the nest. Group ID was used as a random effect to account for non-independence for the multiple trials a group experienced.

We examined how falcon presence explained weaver breeding success by using binomial response variables, ‘nest success’ (failed/success) and stage-specific nest success, ‘clutch hatched’ (yes/no), and for the subset of hatched nests ‘brood lost to nest predator’ (yes/no). Falcons presence (yes/no), colony size and colony height were used as explanatory terms with colony ID being nested within pair ID included as a random term.

To examine how falcon breeding may explain weaver breeding success (same response variables as above), we subset the data to only use colonies that hosted falcons, and included falcon breeding (eggs or chicks in the nest, yes/no) and colony size as an explanatory variables, with colony ID being used as a random effect. Colony height failed to explain any of the variation observed when testing falcon presence on weaver breeding, and was, therefore, omitted from these analyses.

Lastly, we examined if weaver breeding explained falcon breeding success or probability of falcon nest predation using binomial response variables, falcon nest success (at least one chick fledged, yes/no), and falcon nest predated (yes/no). To determine if weaver breeding explained the probability of a falcon nest being predated or failed for other reasons, we tested two further response variables. These were predation (was the nesting attempt predated yes/no) and failure due to reasons other than predation (for example, lack of provisioning or abandonment, yes/no). Explanatory variables used in the model were, weavers breeding (at least one active weaver nest in the colony, yes/no), colony size and colony height. We compared the number of falcon chicks that successfully fledged when weavers were and were not breeding, with Gaussian distributed mixed-effects model using the glmmTMB package (Brooks et al. 2019).

Results

Snake encounter rates

A total of 2090 visits to 48 unique colonies were carried out, with thirty-two snakes being observed. The probability of encountering a snake at a colony was significantly explained by weaver breeding, falcon presence and colony size (Figure 1a; Table 1a). The probability of encountering a snake when weavers were breeding was nearly seven times greater than when they were not (0.016 ± 0.008 of $n=1255$ checks vs 0.002 ± 0.001 of $n = 835$ checks). In colonies that hosted falcons, the probability of encountering a snake more than halved compared to colonies without falcons (0.004 ± 0.002 vs. 0.010 ± 0.03 , $n = 1045$ checks for each). The probability of encountering snakes also increased at larger colonies (0.001 to 0.05 across a range of 12 to 238 chambers; $n= 2090$; Table 1a). The probability of snake encounters was not

statistically explained by active falcon breeding attempts, in a subset of colonies that all contained falcons (Figure 1c; Table 1b). Colony height did not explain snake encounter rates and was removed from the final models (Table 1).

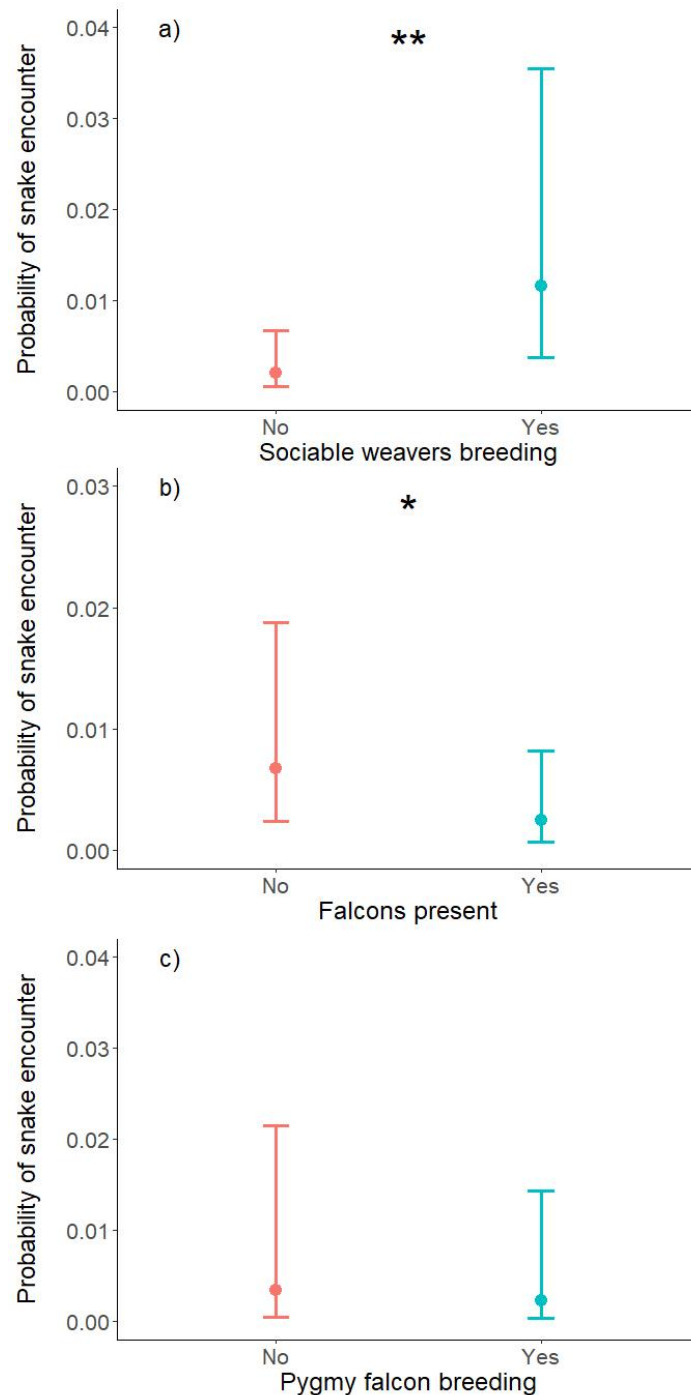


Figure 1. The probability of encountering snakes (model predicted values \pm 95% CI) at sociable weaver colonies when (a) weavers are and are not breeding, (b) when pygmy falcons are and are not present, and (c) at colonies that host breeding or non-breeding falcons (** denotes $p < 0.01$, * denotes $p < 0.05$).

Table 1. Results from the generalised linear mixed models investigating factors that may impact the probability of (a) snake encounters at all colonies and (b) for a subset of colonies hosting falcons.

Response variables	Explanatory variables		χ^2	<i>P</i>
	Estimate	\pm SE		
a) Snake encounters n=2090	Falcons present		5.86	<0.05
	Weavers breeding		9.80	<0.01
	Colony size	0.54 0.25	4.8	<0.05
Removed variable:	Colony height	0.01 0.01	1.04	0.31
b) Snake encounters n=1034	Falcons breeding		0.28	0.60
	Weavers breeding		4.26	<0.05
	Colony size	0.52 0.38	1.83	0.18
Removed variable:	Colony height	0.20 0.42	0.21	0.64

Pygmy falcon responses to model snakes

Falcons responded to stimuli during nine, of the 24 experimental trials, when they were breeding. However, falcons failed to respond to a single stimulus when they were not breeding. This lack of response to either stimulus when falcons were not breeding precluded statistical analyses, therefore we subset the data to carry out statistical analyses on experiments only when falcons were breeding. Stimulus type significantly explained the probability of aggressive falcon attacks (Table 2a). Falcons showed aggressive responses in 58% (7 of 12) of the trials when presented with a snake stimulus and 17% (2 of 12) when presented with the control stimulus, being three times as likely to respond aggressively towards a snake stimulus than the control (Figure 2a). When responding aggressively, falcons would attack the snake stimuli more often than the control (mean 2.0 times \pm 1.06 for snake vs 0.08 \pm 0.08 for control; Table 2b; Figure 2b) and would attack a given stimulus more often when they had more chicks to defend (Table 2b; Figure 2c).

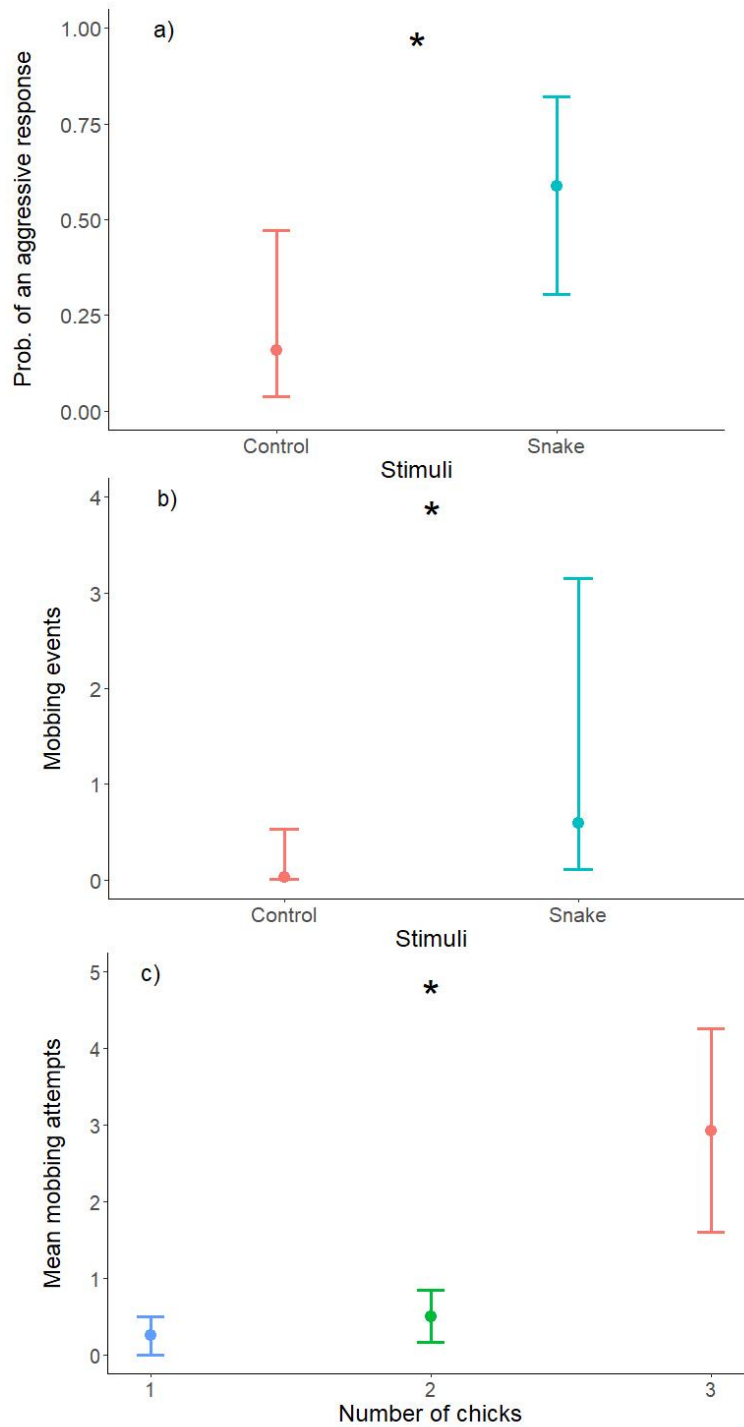


Figure 2. The probability (model predicted values \pm 95% CI) of (a) falcons responding aggressively towards presented stimuli, (b) the mean number of times falcons physically attacked the stimuli, and (c) the mean number for times the falcons attacked a stimulus in response to the number of chicks inside the nest. (* denotes $p < 0.05$, ** denotes $p < 0.01$).

Table 2. Results from the generalised linear mixed models investigating (a) the probability of an aggressive falcon response to the different stimuli placed at their breeding chambers, and (b) the level of aggression displayed.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Aggression n=24	Stimuli			4.09	<0.05
	Order of stimulus presentation			0.25	0.62
	Number of chicks	0.51	0.66	0.6	0.44
b) Level of aggression n=24	Stimuli			5.21	<0.05
	Order of stimulus presentation			0.92	0.34
	Number of chicks	2.62	1.32	3.90	<0.05

Sociable weaver breeding success

A total of 812 weaver breeding attempts were monitored (mean per colony 16.9 ± 1.61). A total of 756 attempts (93%) were unsuccessful at producing any fledged offspring (mean per colony 15.58 ± 1.51), 375 hatched (46 %; mean per colony 7.8 ± 0.8), and 56 (6.9%) were successful at producing at least one chick (mean per colony 1.2 ± 1.4).

Falcon presence at a colony did not explain the probability of weavers breeding (Figure 3a, Table 3a), nor did it explain the likelihood of weaver nests hatching (Table 3b). Raw data reveals that 48% (200 out of 411) of weaver nests in colonies with falcons hatched, similar to the 43% (175 out of 402) in colonies without falcons. For hatched nests only, falcon presence did not explain the probability of chick predation (Figure 3c, Table 3c). Despite this, our model predicted a 19% higher probability of chick predation in colonies with falcons compared to those without. Furthermore, the probability of nests being successful (fledging at least one offspring) was not explained by falcon presence (Figure 3c, Table 3c). Raw data reveals that 9% (36 out of 411 attempts) of breeding attempts at colonies without falcons were successful compared to 5% (20 out of 411 attempts), at colonies with falcons.

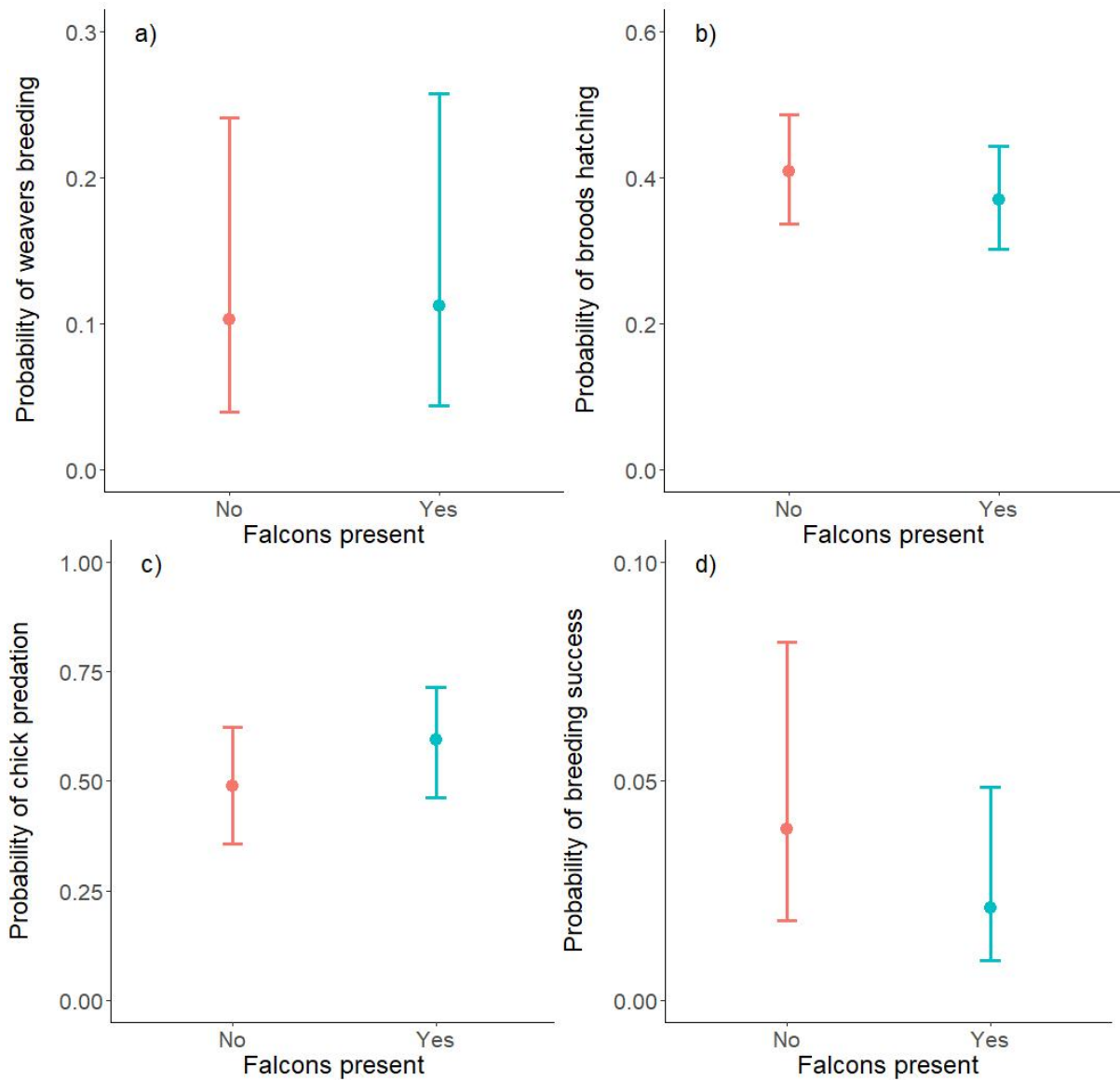


Figure 3. Probability (model predicted values \pm 95% CI) of (a) weaver breeding attempts, (b) broods hatching, (c) chicks being predated, and (d) breeding success at colonies with and without pygmy falcon's present.

Table 3. Results from the generalised linear mixed models investigating weaver breeding success compared to whether falcons were or were not present in colonies; (a) the likelihood of weavers breeding, (b) the likelihood of broods hatching, (c) predation of chicks, (d) and the (d) successful attempts.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Weavers breeding	Falcons present (yes/no)			0.14	0.71
(yes/no)	Colony size	0.24	0.22	1.21	0.27
	Colony height	-0.01	0.22	0.004	0.95
b) Hatched (yes/no)	Falcons present (yes/no)			0.66	0.42
	Colony size	0.21	0.11	3.94	<0.05
	Colony height	-0.12	0.10	1.34	0.25
c) Predation of chicks	Falcons present (yes/no)			1.28	0.26
(yes/no)	Colony size	-0.33	0.20	2.80	0.09
	Colony height	-0.23	0.18	1.58	0.21
d) Breeding success	Falcons present (yes/no)			1.72	0.19
(yes/no)	Colony size	0.47	0.25	3.44	0.06
	Colony height	0.23	0.26	0.79	0.37

For the subset of colonies that hosted falcons, the probability of weavers breeding, and their probability of hatching success were significantly explained by whether falcons were breeding (Figure 4; Table 4). The probability of weavers breeding almost halved when falcons were breeding (0.23 ± 0.23) compared to when falcons were not breeding (0.37 ± 0.34 ; Figure 4a; Table 4a). Weavers were also nearly five times more likely to be observed breeding in larger colonies (0.73 ± 0.81) than in smaller colonies (0.16 ± 0.49), across a range of colony sizes (12 – 238 chambers; Table 4a). Weaver clutches were nearly twice as likely to hatch at colonies when falcons were breeding (prob. 0.58 ± 0.22) compared to when they were not (prob. 0.30 ± 0.17 ; Figure 4b; Table 4b). Despite this, falcon breeding did not explain the likelihood of weaver chick predation (Table 4c) or the likelihood of fledging at least one offspring (Table 4d).

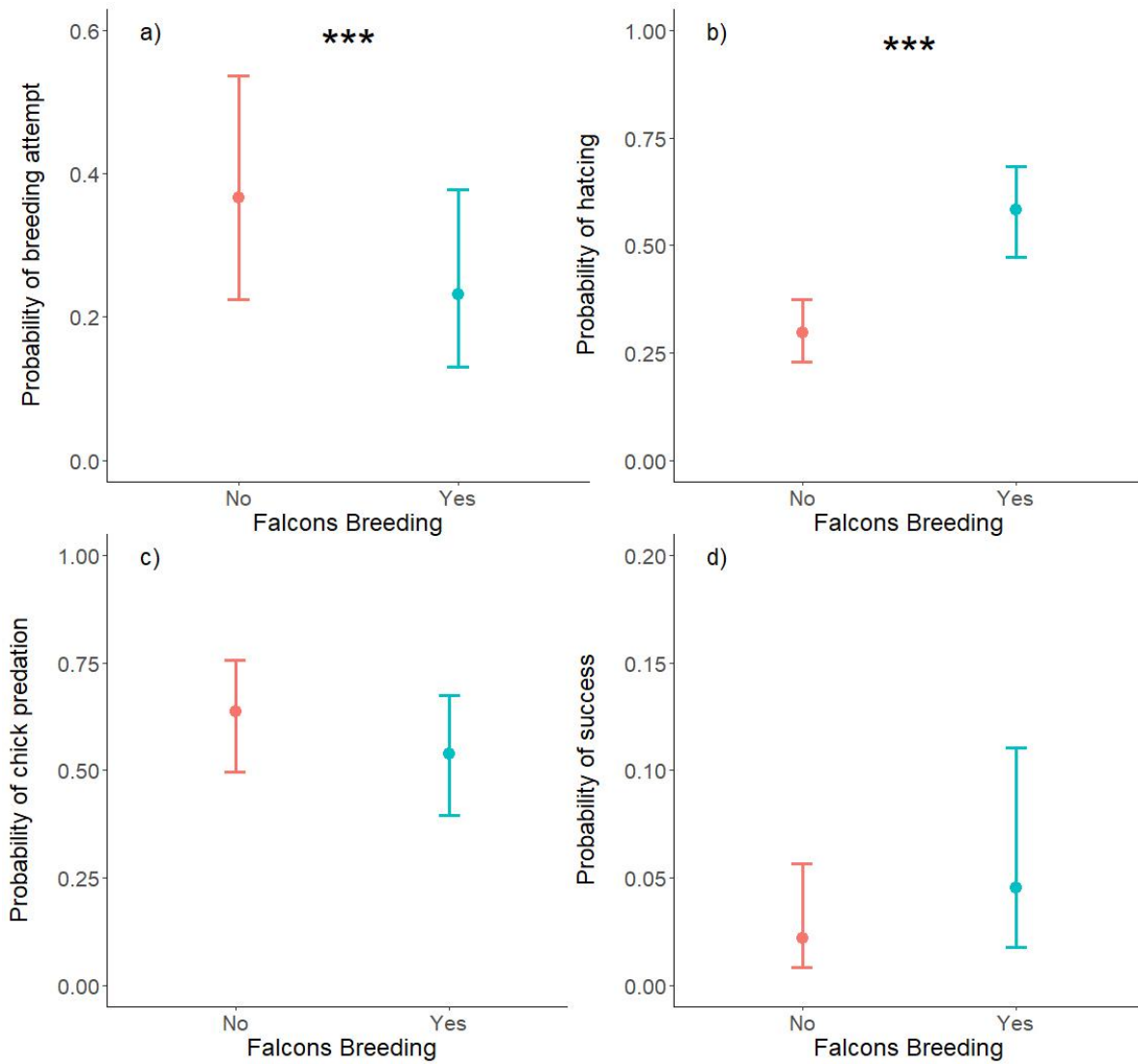


Figure 4. Probability (model predicted values \pm 95% CI) of (a) weavers breeding, (b) weaver broods hatching, (c) weaver chicks being predated, and (d) overall success at colonies where falcons are and are not breeding (***) p < 0.001).

Table 4. Results from the generalised linear mixed models investigating weaver breeding success in colonies that hosted falcons were explained by whether falcons were or were not breeding; (a) the likelihood of weavers breeding, (b) the likelihood of broods hatching, (c) predation of chicks, (d) and the successful attempts.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Breeding attempts (yes/no)	Falcons breeding (yes/no)	-0.65	0.16	17.58	<0.001
	Colony size	0.01	0.004	6.18	<0.05
b) Hatched (yes/no)	Falcons breeding (yes/no)			22.0	<0.001
	Colony size	0.002	0.003	0.50	0.48
c) Nest predated (yes/no)	Falcons breeding (yes/no)			1.23	0.27
	Colony size	-0.01	0.004	1.82	0.18
d) Breeding success (yes/no)	Falcons breeding (yes/no)			2.2	0.14
	Colony size	0.53	0.33	2.56	0.11

Pygmy falcon breeding success

In total 59 falcon breeding attempts were observed, of which 12 were predated, 19 failed due to reasons other than predation and 28 successfully fledged at least one chick. The probability of falcons breeding was not explained by whether weavers overlapped in breeding with falcons (0.44 ± 0.21 weaver breeding overlapping vs 0.46 ± 0.21 not overlapping; Figure 5a; Table 5a). However, the reasons behind falcon nesting failure were explained by whether weaver breeding overlapped (Table 5b; Figure 5b & c). All predated falcon nesting attempts took place while weaver breeding overlapped. The lack of any falcon nest predation when weavers were not breeding means that this data precluded statistical analyses. The probability of nesting failure due to reasons other than predation was significantly greater when weavers were not breeding (prob. $0.49 \pm$ SE 0.36), compared when weavers were breeding (prob. 0.14 ± 0.54). Falcon breeding success was not explained by whether weavers were (0.43 ± 0.39) or were not (0.51 ± 0.36) breeding (Figure 5d, Table 5c). Additionally, weaver breeding did not affect the mean number of chicks that successfully fledged from a given attempt. Raw data reveals that,

on average, 2.0 ± 0.60 and 1.81 ± 0.65 falcon chicks fledge when falcon and weaver breeding do and do not overlap, respectively (Table 5d).

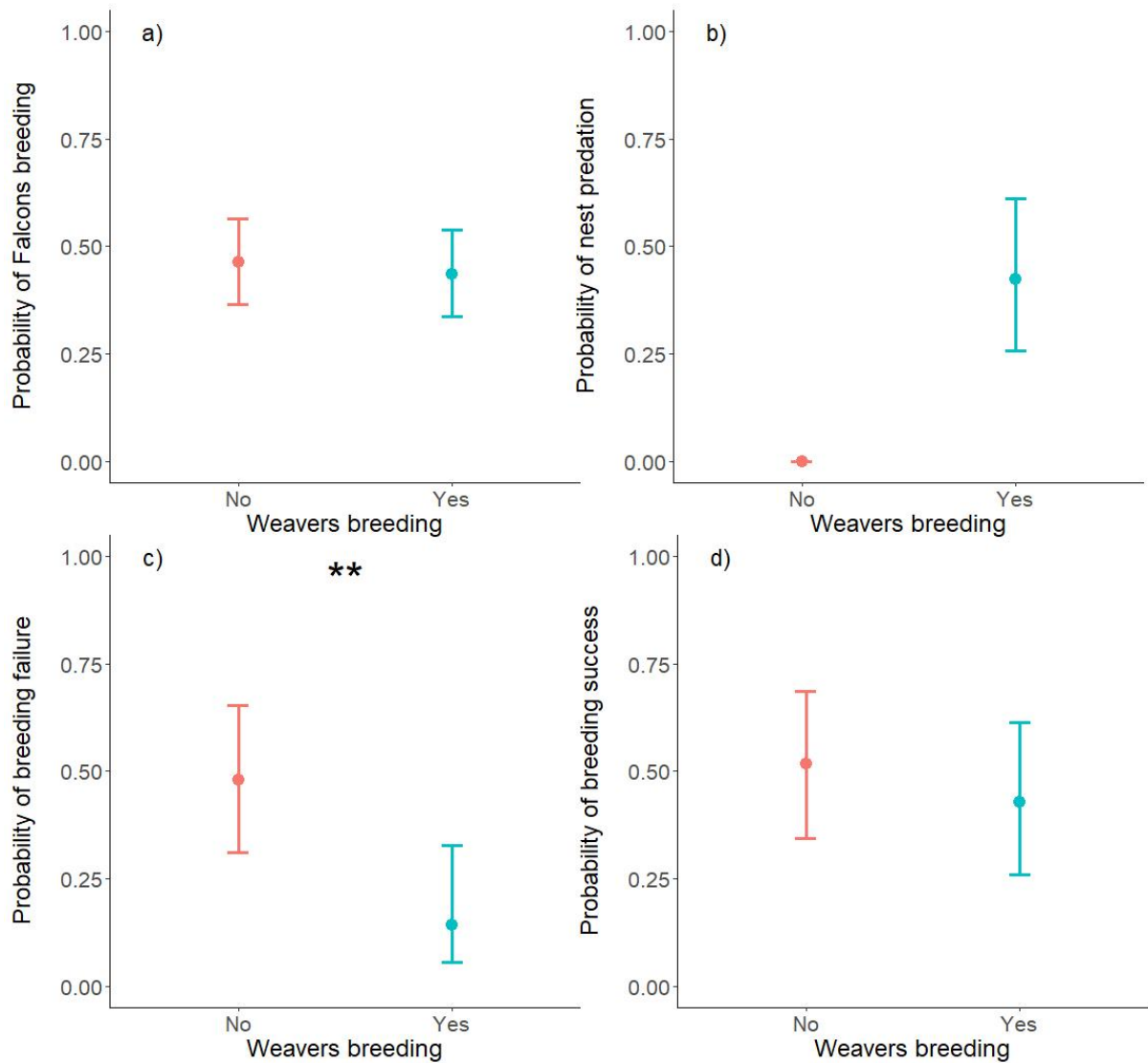


Figure 5. Probability (\pm 95% CI) of (a) falcon breeding attempt, (b) brood predation, (c) brood failure due to reasons other than predation, (d) and breeding success at colonies where falcons are and are not present (** p < 0.01). Due to the lack of evidence of brood predation when weavers were not breeding, this data could not be statistically tested.

Table 5. Results from the generalised linear mixed models comparing falcon breeding success in colonies when weavers were and were not breeding. (a) The likelihood of falcons breeding, (b) the likelihood of nest failure due to reasons other than predation, (c) breeding success and (d) the average number of chicks that fledged.

Response variables	Explanatory variables	Estimate	\pm SE	χ^2	<i>P</i>
a) Breeding attempts (yes/no)	Weavers breeding (yes/no)			0.54	0.46
	Colony size	-0.25	0.18	1.90	0.16
	Colony height	0.08	0.20	0.18	0.68
b) Nest failure, other than predation (yes/no)	Weavers breeding (yes/no)			6.80	<0.01
	Colony size	0.11	0.31	0.12	0.73
	Colony height	0.14	0.32	0.19	0.67
c) Breeding success (yes/no)	Weavers breeding (yes/no)			0.45	0.50
	Colony size	0.19	0.28	0.44	0.51
	Colony height	-0.07	0.28	0.05	0.82
d) Number of Chicks fledged	Weavers breeding (yes/no)			0.14	0.7
	Colony size	-0.04	0.18	0.53	0.82
	Colony height	-0.0001	0.17	0	0.997

Discussion

Snakes were detected at lower frequency in colonies with resident falcons, coupled with the falcons increased aggression towards the snake stimuli suggest that pygmy falcons can provide protection against snake predation. However, this did not materialise into measurable fitness benefits for those weavers breeding in colonies that hosted these obligate associates. Pygmy falcons deterred snakes from foraging at weaver colonies, but this only occurred when falcons were breeding. This protection provided by breeding falcons translated into reduced nest predation rates on weaver nests during the egg stage (egg-laying and incubation). However, after hatching of the weaver nests, the nest predation rates during the chick rearing phase did not differ in colonies without and without falcons, which suggests that falcons are preying on weaver chicks in the nest. Therefore, there seems to be an interplay of costs and benefits in this

forced association, with our data suggesting the weaver breeding output suffers net costs in most years. Furthermore, there were also costs and benefits for the falcons. Despite the additional availability of food, in the form of weaver chicks, there was no measurable effects on the reproductive output of falcons as there was an increased likelihood of snake encounters at colonies when weavers were breeding, and therefore an increased risk of nest predation.

Aggressive attacks on snake stimuli suggest that falcons deter snakes from entering and predating weaver colonies. This is supported by the far lower snake encounter rates at colonies with falcons. However, we found that falcons do lose nests to snake predation, meaning that aggressive defence against these predators is not always successful. This is in concordance with previous research revealing that woodpigeons (*Columba palumbus*) that nest near hobby's (*Falco subbuteo*), still had suffered from nest predation despite the hobbies aggressive behaviour towards other predators (Bogliani et al. 1999). Bogliani et al. (1999) were also able to show that certain hobbies were more aggressive than others, and were more likely to successfully deter predators. We did not set out to answer this question, however this would be an interesting focus for future research into this system. Our results suggest that snakes will attempt to access colonies that host falcons, and are therefore not actively avoiding these particular structures. Furthermore, falcons only behave aggressively and defend colonies when they are breeding. The lack of aggression towards either stimulus when falcons were not breeding suggest that any benefits that weavers may derive from falcons are limited to the period when falcons are breeding, providing further support for previous studies (Ueta 1994, Bogliani et al. 1999), and is also supported by the increase in weaver nesting attempts hatching during this period and provides.

Weaver broods are more likely to hatch at colonies with breeding falcons; however, this advantage does not translate in higher fledging rates at the colonies. This suggests that falcons are successful at defending colonies from snakes, thus improving the initial survival of weaver nests (at the egg-stage), but the disappearance of this protective benefit at the chick stage suggests falcons are predating on weaver chicks. Falcon predation on weaver chicks has been documented (Maclean 1970, Covas et al. 2004) but has been suggested to be rare or at best infrequent. However, our current results and increasing observational data (A. Lowney, unpublished) suggests that the nest predation pressure imposed by falcons on weaver chicks is significant. Therefore, any benefit gained from nest defence is reduced/cancelled by chick predation. There is no evidence to suggest that falcons eat weaver eggs; the two snake predators, cobras (*Naja nivea*) and boomslang (*Dispholidus typus*) in our study area, will

consume the entire contents of a weaver nest at any stage (Covas 2002). In light of this we suggest that further studies need to be undertaken to quantify and gain an understanding of the temporal aspects of this falcon predation of weaver nests. Currently, this 'enforced protective' association is a net cost to the weaver. However, in years of high nest predation pressure by snakes and other potential diurnal predators, there may be benefits of co-inhabiting a colony with falcons (Quinn and Ueta 2008, Canestrari et al. 2014).

Pygmy falcons have evolved to obligately exploit Sociable Weaver colonies due to the assumed benefits of this association, but we documented clear costs too. When weaver breeding overlapped with falcon breeding, falcon nests suffered higher nest predation rates, most likely due to the attraction of snakes to the weaver colonies. In contrast, when weaver breeding did not overlap with falcon breeding, falcon attempts failed due to reasons other than predation. These failures typically appeared to be from a lack of provisioning, although there was no clear evidence that the availability of weaver chicks impacted falcon reproductive success. Overall, our result shows the costs that the aggressive protector species may encounter in nesting associations, even though the falcon-weaver association is exceptional in that the falcon actively selects to nest in the colonies. Falcons do not invest time or energy in building and maintaining nests and gain a nesting chamber that is buffered from temperature extremes. When weavers are breeding, food (in the form of weaver chicks) is available nearby, although that also attracts destructive snake predators. With a breeding period that is double the length of the weavers, falcons would also be unable to avoid breeding in overlap with weavers, and weavers could initiate breeding long after falcons and overlap would still occur. This cost to protector species, especially species which are actively sought by timid species requires more study, as do the adaptations to avoid these costs if they do exist.

Weaver breeding is highly influenced by rainfall (Covas 2002). Therefore, our results suggesting weavers tend to time their nesting attempts so that they do not overlap with the breeding of falcons, is likely untrue. Avoidance of breeding overlap may be driven by the additional predation pressure of falcons provisioning for their chicks. However, species in harsh environments have less flexibility, and they usually have relatively small windows in which to breed and successfully raise their young. Therefore, it is more likely that weavers are not "choosing" to breed so that they do not overlap with the falcons, but that breeding of both species simultaneously only occurs if rainfall has occurred before the falcon breeding season.

In summary, our findings add to the growing literature with regards to the coexistence of predator and prey species pairs. We also provide evidence of costs and benefits for both protected and protective species, the latter of which is often overlooked (Bogliani et al. 1999). Weaver colonies provide nesting and roosting sites for falcons, thus expanding the falcons realised niche. Falcons demonstrate aggressive behaviours towards potential predators, thus providing a protective association for weavers. However, falcons are not always successful at defending colonies with the increase in predation of weaver chicks compared to eggs, suggesting that falcons may exacerbate weaver predation risk by feeding on chicks at rates higher than previously assumed. Additionally, it may be that falcons in our study site select larger colonies (D. Bolopo, A. Lowney & R. Thomson, unpublished data) and this may help dilute their impact on a colony population. Falcons breeding at the same time as weavers may be more likely to completely fail or produce full broods and are less likely to fledge only one or two chicks from larger clutches. Whereas, when breeding and weavers are not, falcons may be less likely to have full broods successfully fledge.

Our study demonstrates the costs and benefits that protective and protected species incur due to their close association. We reveal how certain biotic changes can affect these costs and benefits, including how falcon defensive behaviour changes, and how weaver breeding success does not differ between times when falcons are and are not breeding. However, other changes to biotic and abiotic conditions, that may affect the outcomes of this associate relationship, were not tested (Gotmark 1989, Larsen and Grundetjern 1997). For example, predation pressure by snakes and falcons may change due to other environments conditions, especially in arid environments where resource availability fluctuates between abundant and scarce (Hillel and Tadmor 1962, Rosenzweig 1968). During times when resource availability is low, predation pressure on weavers may increase. Falcon populations also fluctuate between years (Bolopo et al. 2019), and an increased number of falcons in a landscape may increase competition for resources, adding to weaver predation pressure. These aspects of costs and benefits to these associates needs further investigation and should be a focus of future research.

In this study we have described behaviours of pygmy falcons that enables them to coexist with their protected associate and potential prey. Unlike other studies where protected species have selected to nest near a protector, this novel system has allowed us to analyse the interactions between a species pair, where the predator requires the presence of the protective species to occur within a landscape. By modifying its physical habitat, the weavers may also have modified selection on falcons, that may have driven coevolution and influenced the likelihood

of coexistence. As a result, the overall net outcome of these interactions is unlikely to be negative. These interactions demonstrate that “engineering webs” occur between falcons and weavers and likely expand to other species that associate with colonies.

Appendix 1 Complete list of models used, including response, explanatory and random effects. Distribution and overdispersion parameters are also shown. All carried models were carried out using in the glmmTMB package using the glmmTMB function (Brooks et al. 2019).

Response variables	Model	Distribution	Explanatory variables	Random effects	Overdispersion parameter
<u>Snake encounters rates – falcons present and weavers breeding</u>					
Snake encounters	GLMM	Binomial	Falcons present (yes/no) Weavers breeding (yes/no) Colony size Colony height	Pair ID/Tree ID	
<u>Snake encounter rates – falcons breeding</u>					
Snake encounters	GLMM	Binomial	Falcons breeding (yes/no) Colony size Colony height	Pair ID/Tree ID	
<u>Falcon response to stimuli – Breeding season</u>					
Aggression (Yes/No)	GLMM	Binomial	Stimuli (Snake/Ball) Stimuli Order Number of chicks	Falcon territory ID	
Mobbing attempts	GLMM	Negative binomial	Stimuli Order Chicks	Falcon territory ID	0.457

Weaver breeding compared to falcon presence

Weavers breeding (yes/no)	GLMM	Binomial	Falcons present (yes/no) Colony size Colony height	Pair ID/ Colony ID
Hatched (yes/no)	GLMM	Binomial	Falcons present (yes/no) Colony size Colony height	Pair ID/ Colony ID
Predation after hatching	GLMM	Binomial	Falcons present (yes/no) Colony size Colony height	Pair ID/ Colony ID
Success (yes/no)	GLMM	Binomial	Falcons present (yes/no) Colony size Colony height	Pair ID/ Colony ID

Weaver breeding success compared to whether or not falcons were breeding

Weavers breeding (yes/no)	GLMM	Binomial	Falcons present (yes/no) Colony size	Colony ID
Hatched (yes/no)	GLMM	Binomial	Falcons present (yes/no) Colony size	Colony ID
Predation after hatching	GLMM	Binomial	Falcons present (yes/no) Colony size	Colony ID
Success (yes/no)	GLMM	Binomial	Falcons present (yes/no)	Colony ID

Colony size					
<u>Falcon breeding success compared to whether or not falcons were breeding</u>					
Failed (yes/no)	GLMM	Binomial	Weaver breeding (Yes/No)	Colony ID	
			Colony size		
			Colony height		
Success (yes/no)	GLMM	Binomial	Weaver breeding (Yes/No)	Colony ID	
			Colony size		
			Colony height		
Number of chicks fledged	GLMM	Negative binomial	Weaver breeding (Yes/No)	Colony ID	0.395
			Colony size		
			Colony height		

Chapter 6

Synthesis and conclusions



The overall objective of this thesis was to investigate the importance of Sociable weaver (*Philetairus socius*) colonies to animal species diversity, abundance and community structure. I further wanted to understand these impacts within changing environmental contexts and tested how colony use varied in response to seasonal and spatial changes in environmental harshness. Lastly, I set out to describe the nature of the interactions between Sociable weavers and their recognised close associates. I aimed to understand how multiple species can coexist at colonies and what affects these may have on Sociable weavers. Before this study, relatively little was known regarding how birds can distribute resources within a given landscape and how this affects whole animal communities (Natusch et al. 2016, Coggan et al. 2018). Furthermore, previous studies that have investigated terrestrial animals as ecosystem engineers have failed to look at either spatial or temporal scales, therefore, failing to understand the full impacts of these animals throughout their distribution, and whether their impacts differ as environmental conditions change. This study provides several novel findings and provides a greater understanding of the importance of birds as ecosystem engineers and how associate species interact. Additionally, it shows the importance of Sociable weaver colonies as a resource in an arid environment and how this resource may potentially become increasingly important as climate change advances.

This final chapter aims to highlight the primary outcomes of this thesis and discuss their significance and limitations. I describe the impacts of Sociable weaver colonies and the importance of these structures to the surrounding animal community as a whole, and document how the influence of weaver colonies increases as environments become more arid. Furthermore, I discuss behavioural adaptations that allow competing species and predators to coexist at the same resource. I show novel between-taxa eavesdropping of alarm calls and suggest the weaver colonies may also be centres of information, here conspecifics and/or heterospecifics may be able to gain information regarding resource availability and predatory threats. The presence of obligate predator associates allowed me to show the interplay of costs and benefits in a unique avian protective nesting association. Lastly, I make recommendations for future research that may enable further understanding of the importance of ecosystem engineers and how they may mitigate the effects of climate change.

Sociable weavers as ecosystem engineers

My results show that the presence of a Sociable weaver colony creates localised biodiversity hotspots and that this pattern is replicated across the weaver's range. These colonies create

habitat, alter community structure and increase habitat heterogeneity; resulting in increased animal diversity at trees housing colonies for all the taxa sampled. The physical characteristics of the colony structure appear to provide resources for reptiles, birds, and mammals, thus creating a focal point of animal activity within the broader landscape. Importantly, our results show that the association between weaver colonies and birds, and terrestrial invertebrates increases as environments become more arid, while these associations appeared to weaken at benign sites. Furthermore, the frequency of terrestrial mammal use of colonies for shade increased as temperatures increased, which not only demonstrates the importance of weaver colonies to the animal community but also suggests that the importance of positive associations and facilitation increases as environmental harshness increases. These weavers are, therefore, a clear-cut case of an ecosystem engineer and one that can reduce stress and may allow species to persist in an environment that is predicted to become harsher, due to global climate change.

My thesis demonstrates that, through altering habitat, birds can influence whole animal communities. Yet birds have been mainly overlooked as ecosystem engineers. Of the 9956 estimated bird species only 13 have been identified as ecosystem engineers (Coggan et al. 2018), this is surprising as bird nests can take many shapes and sizes (Mainwaring et al. 2015). Furthermore, recent research has revealed that bird nests can provide resources for multiple species and influence the distribution of local animal communities (Natusch et al. 2016, Delhey 2018), suggesting that the number of bird species identified as ecosystem engineers is highly under representative. There have been numerous studies investigating the importance of cavity creating birds to other animals (Jones et al. 1994, Martin and Eadie 1999, Aitken and Martin 2007, Drever et al. 2008, Cockle et al. 2011). However, very few studies investigate the importance of other built bird nests. Cavities can remain in the environment for multiple years (Cockle et al. 2011, Pakkala et al. 2018), whereas bird nests generally do not last longer than a single nesting event (Deeming and Reynolds 2015). Yet, nests of some species can remain within the landscape for multiple years, with some of these being utilised by other species (Martella and Bucher 1973), further suggesting that the importance of birds as ecosystem engineers, and how this affects local animal communities is a topic of research that remains mostly unstudied. Understanding the impacts of birds as ecosystem engineers, especially, among different habitats and different environmental gradients may be necessary for the management of species with conservation concern, and I suggest that this is an area of research that needs further attention.

The increase in the importance of weaver colonies to heterospecific birds and terrestrial invertebrates at sites with low rainfall supports the stress gradient hypothesis (Bertness and Callaway 1994). This study is the first to provide empirical evidence that supports this hypothesis in free-ranging terrestrial communities and complements recent research undertaken within controlled environments (Dangles et al. 2018, Bell and Cuddington 2019). However, with regards to mammals and reptiles, I found no difference of associating with colony trees between harsh and benign sites. Why colony association of some taxa fit the stress gradient hypothesis while others appear not to may be explained by how engineers provide facilitation. Colonies offer refuge from the extreme temperatures that can be utilised by birds and insects alike (Maclean 1973c, van Dijk et al. 2013, Leighton and Echeverri 2014). Additionally, in oligotrophic landscapes, the substantial faecal input underneath colonies would be an import source of organic material, required for invertebrates to persist in arid environments (Noy-Meir 1985). Furthermore, insects are an essential source of nutrition and water for many bird species. Therefore, the increased number of invertebrates associated with weaver colonies may also explain why I see more birds at colony trees in areas with low rainfall.

Mammals had a tendency for associating with colony over non-colony trees, but the magnitude of this association did not differ across sites or between seasons. However, the reasons for utilising colony resources did vary between seasons. Again, this is likely explained by how colonies facilitate these taxa. Mammals tended to use the physical structure of the colony as a resource. Terrestrial mammals used the shade to manage their metabolic heat production during the hottest times of the day (Figure 1), while smaller arboreal mammals slept inside the thatched structure during winter, supporting predictions of the stress-gradient hypothesis. Large cats use the top of larger colonies as platforms for vantage points (Lowney and Charlton 2017), and smaller predatory mammals, were frequently recorded on top of these structures. These may be predated on small arboreal rodents that were also often observed on top of weaver colonies. Across the sites, the length of time that arboreal mammals spend on weaver colonies reduces as NDVI increases, suggesting that these colonies as a resource are less needed/critical when there are resources elsewhere. Resources provided by these colonies change as abiotic factors change; yet, the colony influence on structure and diversity of animal communities is maintained throughout the temporal and spatial gradients. Unfortunately, the study design only allowed for camera traps to be set for seven days, but Larsen (2016) recommends that camera

traps should be set for a minimum of two weeks. Therefore, our study design may have led to a lack of power, increasing the likelihood of a false-negative result.



Figure 1. Greater Kudu (*Tragelaphus strepsiceros*) using a sociable weaver colony for shade to manage their metabolic heat production during the hottest times of the day.

Reptile abundance followed the same pattern as mammals, with higher association to colony over non-colony trees, and that the magnitude of this association did not differ between sites. This again may have been impacted by our study design as our site visits were not carried out concurrently, and therefore our last site was visited eight weeks after the first. This may affect species activity patterns, especially with regards to reptiles. Reptile activity is heavily influenced by environmental factors, especially the time of day and temperature (Huey and Prianka 1977). Average daily temperatures may have differed from the start to end of the study period. However, our study design of using paired trees and the incorporation of time of day into our statistical models should minimise this impact. Furthermore, I observed a strong association with colony trees, suggesting that reptiles were active and my results supported the findings of earlier work carried out on Kalahari tree skinks (*Trachylepis spilogaster*, Rymer et al. 2014). To increase activity, reptiles need to raise their body temperature by basking, but they also need to prevent themselves from overheating (Corbalán et al. 2013). Therefore, reptiles are likely to gain the most from the thermal buffering provided by weaver colonies. Additionally, the majority of the reptiles observed (*Trachylepis spp.*) were insectivores that

mainly forage on the ground (Brain 1969). Consequently, these species are also likely to benefit from the strong association of terrestrial invertebrates at weaver colonies, suggesting that a complicated ecological web of interactions occur at weaver colonies.

Associate interactions at engineered resources

My investigations into the interactions between Sociable weavers and two of their recognised close associates, Kalahari tree skinks and African pygmy falcons (*Polihierax semitorquatus*), revealed intricate behaviours that allow these species to coexist and utilise the resources provided by weaver colonies. I found that skinks were able to eavesdrop on weaver signals enabling them to reduce their predation threat from pygmy falcons and expand their own realised niche. When weavers were present, skinks would bask in the open and forage further away from the safety of the tree. If a potential predator approached, and weavers fled for cover, then skinks also fled for cover. Consequently, skinks at colony trees fled sooner in the presence of weavers. Furthermore, skinks at colony trees were also able to use weaver vocalisation to manage their predation risk. Skinks at colony trees would increase vigilance and be more likely to flee when they were presented with weaver alarm vocalisations. Whereas, skinks at non-colony trees were unlikely to flee in response to any vocalisation but demonstrated increased vigilance to both alarm and control stimuli. Intriguingly, this suggests that the ability to interpret information encoded within weaver vocalisations is learnt through the increased frequency of interactions between weavers and skinks. Being able to manage their predation threat in such a way, allows skinks to access colonies and gain the benefits associated with these structures, despite the increased risk of predation by pygmy falcons.

I have shown that skinks at colony trees manage the predation risk by eavesdropping on Sociable weavers and that by doing so gain access to a thermal refuge and increased insect abundance. However, I have not determined how this affects the overall fitness of skinks. Are skinks at colony trees healthier than those at non-colony trees and do they obtain a higher reproductive output? To fully understand the benefits that skinks receive from associating with colony trees, these questions should be researched further. Furthermore, eavesdropping is common between species (review by Magrath et al. 2015), and I show how this allows species to join communities that predators may otherwise exclude. However, I have also shown that there are multiple species that associate with colony trees (*Acacia* pied barbets, *Tricholaema leucomelas*; pygmy falcons, *Polihierax semitorquatus*; ashy tits, *Melaniparus cinerascens*; scaly-feathered finches *Sporopipes squamifrons*). Therefore, weaver colonies have the

potential to be information hotspots. If these associates are also able to eavesdrop on Sociable weavers as well as other colony associates, then these species would gain further benefits than those identified in this thesis (e.g. thermal refuge) and is a topic that would be interesting to investigate further.

Both weavers and falcons incurred costs and benefits due to their close association. Falcons do not build nests and in southern Africa rely solely on weaver nesting chambers for breeding and roosting (Maclean 1970); therefore, gaining nests free of the energy and time in building such a structure. Snakes are attracted to these colonies, especially when Sociable weavers are breeding, and snakes take up to 70% of all weaver nesting attempts (Covas 2002). Consequently, snakes are also a threat to falcon nesting attempts. However, falcons can actively defend their reproductive investment and do deter snakes from colonies; this inadvertently provides protection for breeding weavers. Yet, this does not increase the reproductive success of weavers. This is partly because falcons only defend colonies when they, themselves, are breeding and partly because they also predate weaver chicks. Falcons whose breeding overlapped with weavers did not gain an increase in the probability to be successful, despite the availability of weaver chicks, as an additional food source and is likely due to increased nest predation by snakes when weavers were breeding. Even though falcons can defend colonies, they are not always successful. As a result, breeding concurrently with weavers leads to increase in predation of falcon nests. However, falcons whose breeding did not overlap with weavers gained a reduction in nest predation but were more likely to suffer from nest failure, for reasons other than predation (e.g. lack of provisioning). Therefore, the benefits appear to offset the costs of this forced association and enable pygmy falcons and Sociable weavers to coexist within such close proximity.

I have started to reveal some of the intricacies between the weaver and falcon interactions. But many more go unexplored. For example, weavers resent falcons, alarm calling when falcons are close by (Maclean 1970), and fleeing when they approach (Lowney and Thomson, personal observation). Therefore, research into the behavioural adaptations that weavers have evolved to counter this intrusion, would be of interest. Furthermore, when comparing egg predation rates to chick predation rates, there is evidence to suggest that falcons may predate on weaver chicks far more than previously accepted, although this was not quantified this specifically. Environmental variability is stark in this Kalahari system, and it would be interesting to investigate if falcon predation of weaver chicks is explained by these prevailing conditions (biotic or abiotic). The seasons encapsulating my study were dry and relatively harsh, and I

could speculate that weaver chick predation was higher than usual because of these difficult conditions. These are questions that would be exciting to explore, and are highly recommended with regards to future research.

Predator and prey species that are positively influenced by the same ecosystem engineer, can coexist at the same resource (Rymer et al. 2014). This thesis reveals some of the mechanisms that allow this coexistence to occur. Focal species developed novel behaviours that not only allow them to manage their increased predation risk but also expand their own realised niche. These behaviours are likely driven by the increased frequency of interactions between associates, which you would expect when species coexist at a given resource. I also show via these studies that there are both costs and benefits to close associations of a single resource and that these costs and benefits are context-dependent. Therefore, when engineers modify their physical habitat, they may also modify selection on other species that depend on these physical changes (Laland and Feldman 2003), and this can lead to an increased rate of adaptation, speciation and coevolution (Schemske et al. 2009). These interactions demonstrate that “engineering webs” occur between associates at weaver colonies and these enable niche and range expansion and along with recognised trophic interactions, likely regulate ecosystem functioning (Jones et al. 1994).

Concluding remarks

This thesis adds to the growing literature that ecosystem engineering is an essential biological interaction that can relieve stress in harsh environments (Hastings et al. 2007, Romero et al. 2015, Coggan et al. 2018). I show the importance of Sociable weavers to local animal communities, revealing that weaver colonies provide resources for all taxa tested and that the importance of these colonies increases as environmental harshness increases. I show that colonies in drier environments are more important to birds and terrestrial invertebrates, and during hotter seasons colonies provide important shade for large terrestrial mammals. Additionally, arboreal vertebrates increasingly utilise the top of colonies while landscape productivity was at its lowest. The response of bird and terrestrial invertebrates provides support for the stress gradient hypothesis for these taxa and is the first study to test this hypothesis at the animal community level. Furthermore, I show that a complex ecological web of interactions occurs between weavers and their associates and that by altering the physical habitats, Sociable weavers enable niche and range expansion and along with recognised trophic interactions, likely regulate ecosystem functioning.

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