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The Impacts of Cattle Grazing on Arboreal Reptiles

Thesis submitted by

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Title page photographs

Top: Australian native house gecko, *Gehyra dubia*

Left: Eastern spiny-tailed gecko, *Strophurus williamsi*

Right: Northern velvet gecko, *Oedura castelnaui*

Bottom: Brahman bull, *Bos indicus*

All photographs by Eric J. Nordberg

Statement of Contributions and Ethics Declaration

This thesis would not have been possible without the help and contribution of others. My primary supervisor, Lin Schwarzkopf, is a co-author on all of my data chapters in this thesis. She has provided invaluable advice throughout my project on experimental design, statistical analysis, and editing of manuscripts resulting in this body of work. My secondary supervisor, Ross Alford, is a co-author on Chapter 4, and has also helped me with statistical analysis and troubleshooting in R throughout my candidature. Professor Jeremy VanDerWal and Heather Neilly are co-authors on Chapter 2. Jeremy helped with editing drafts of the manuscript, while Heather Neilly and I designed the study, collected and analyzed data, wrote and edited the manuscript. Paul Murray is a co-author on Chapter 4, in which he helped me collect and analyze both field and lab data. Lexie Edwards is a co-author on Chapter 6, in which she helped collect field data and edit the manuscript. I am indebted to many of my lab mates and volunteers for helping me collect field data.

I have been supported by an International Postgraduate Research Scholarship from the Australian government as well as a Doctoral Completion Award through James Cook University throughout my candidature. My Research funds were provided by a grant to Lin Schwarzkopf from Meat and Livestock Australia (B.ERM.0088), a Holsworth Wildlife Research Endowment to Heather Neilly, and funding I obtained through the College of Science and Engineering at James Cook University. Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Ethics approvals and permits

All data was collected within the guidelines for ethical treatment of animals and approved by James Cook University (animal ethics permit # A2050) and the Queensland Department of Environment and Heritage Protection (research permit # WISP14656614).

Preface

The following publications have come to light as a result of this thesis.

Chapter 2; **published** – Nordberg and Schwarzkopf. 2015. Arboreal cover boards: using artificial bark to sample cryptic arboreal lizards. Herpetologica, 71(4):268–273. https://doi.org/10.1655/HERPETOLOGICA-D-15-00016

Chapter 3; **published** – Neilly, H., E.J. Nordberg, J. VanDerWal, and L. Schwarzkopf. 2017. Arboreality increases reptile community resistance to disturbance from livestock grazing. Journal of Applied Ecology, 2017:1–14 (available online). https://doi.org/10.1111/1365-2664.12982

Chapter 4; **published** – Nordberg, E.J., P. Murray, R. Alford, and L. Schwarzkopf. 2017. Abundance, diet, and prey selection of arboreal lizards in a grazed tropical woodland. Austral Ecology. (available online). http://doi.org/10.1111/aec.12570

Chapter 5; **under review** – Nordberg, E.J., and L. Schwarzkopf. *Under review*. Alternative prey availability, not predator abundance, determines predation risk. Ecology.

Chapter 6; **under review** – Nordberg, E.J., L. Edwards, and L. Schwarzkopf. *Under review*. Terrestrial invertebrates: an underestimated predator guild for small vertebrate groups. Food Webs.

Chapter 7; **under review** – Nordberg, E.J., and L. Schwarzkopf. *Under review*. Mechanisms allowing generalist species to benefit from habitat homogenization. Functional Ecology.

Acknowledgments

As many people have said before me, “a Ph.D. is not the work of a single person, but a contribution of many” – I could not agree more, as many people have helped me towards earning my degree. I have received assistance in many forms, ranging from financial assistance to fund my research projects, intellectual discussions about research questions and experimental design, and hours of editing manuscripts trying to make me a better story-teller.

I am extremely grateful to my primary supervisor, Lin Schwarzkopf, who was kind enough to invite me to join her lab from the United States. Working in Australia has not only been a dream of mine, but I am extremely privileged to have had the opportunity to work in a lab full of such great scientists. Lin has had her work cut out for her, continually trying to make me a better writer, but more importantly, a “scientific story-teller”. She has constantly provided helpful and insightful comments and recommendations on my manuscripts to improve my writing skills as an early-career researcher. Lin hosts a great number of students in her lab, ranging from undergraduates to postdocs, yet she always has time to talk with students about projects, papers, problems, or lizards. Lin has been an excellent mentor, and I am very grateful for the opportunity to have trained under her supervision. Ross Alford has always been a wealth of knowledge regarding experimental design, statistical analyses, troubleshooting in R, and general discussions of ecological concepts. Ross has been a great secondary supervisor in which I was able to bounce ideas off and get advice on interpreting complex data sets. Many times, I have sat at my computer, stumped by some error message in R – Ross has always been someone who was more than willing to dissect my code and, not only find the problem, but suggest better, more efficient, or just ‘cooler’ ways of analyzing the data.

I feel extremely lucky to have worked with such a diverse group of scientists while in Lin’s lab, many of which have turned into valuable friendships. Lin attracts the best and brightest students across multiple disciplines, which makes her lab full of diverse skills and backgrounds. Lin’s weekly “Lizard Lunch” lab meetings provided a platform for many group discussions, critiques on analyses, and practice talks for conferences. Thanks to Heather Neilly, Ben Muller, Don McKnight, Lexie Edwards, Deb Bower, Juan Mula, Jendrian Reidel, Rishab Pillai, Jodie Nordine, Kirilly O'Reilly, Roderick Budd, Courtney Meek, Cat Kelly, Sheryn Brodie, Ayano Fushida, Sasha Greenspan, Richard Duffy, Rachel Duffy, Stephen Zozaya, Stewart Macdonald, Conrad Hoskin, and Ben Hirsch for comments and suggestions throughout my candidature. Many people in the lab have contributed to my fieldwork, and I am indebted to the "Wambiana gang" for their constant reliability and hard work. First and foremost, I would like to thank Heather Neilly. Heather and I both started our Ph.D.'s at the same time, with projects at Wambiana. We have spent countless (probably hundreds) hours talking about everything from trapping techniques, to fieldwork paperwork issues, to ideas for joint papers. Heather has also been great at receiving grants, and more importantly, sharing the funds with me – without her, I would not have been able to fund as many field trips as I have, so thanks Heather! Lexie Edwards, Ben Muller, Don McKnight, Roderick Budd, and Kirilly O'Reilly were always reliable to join me on field trips. I am thankful for their exceptional lizard catching abilities. A big thank you to Cam De Jong, Hannah Jones, Courtney Meek, Friedrich Rittner, Rishab Pillai, Elizah Nagombi, Paul Murray, Lauren Heilbronn, Peit Stutterheim, Richard Duffy, Vinay Udyawer, Jodie Nordine, Sarah Hart, Josh McIntrye, Jendrian Riedel, and Jess Waugh for their assistance in the field.

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While moving to Australia to pursue my Ph.D. has been a tremendous privilege, it has been tough being so far from friends and family. Over the last four years, I have missed countless birthdays, anniversaries, weddings, births, memorial services, and other social gatherings. My family has been extremely supportive as I moved across the United States, and then to Australia in pursuit of academic degrees and research projects. I want to thank both my parents, Mike and Teresa Nordberg, and my two brothers: Gannon and Taylor, for their endless support and enthusiasm. Although it has been a challenge to coordinate late night/early morning Skype and What's App communication, keeping in contact with my family has helped me overcome the distance. I would also like to thank my in-laws, for I have taken their daughter, Sarah, across the world with me on this journey. They too have provided endless support to both Sarah and I as we pursue our careers overseas. Tim, Patty, Pete, Ben, Annalynne, and Audreya Reddington, Lindsay and Chuck Holland, Hannah and Jared Bohrer, thanks for your support.

Lastly, but certainly not least, I want to thank my wife Sarah Reddington for coming on this journey with me. Sarah has always had my back, and encouraged me to follow my dreams, take opportunities when they arise, and travel the world. I would not have been able to complete my Ph.D. without Sarah – she has provided me with emotional and financial support (being a poor graduate student for most of my career), and has endured hours and hours of talk about reptiles, manuscripts, research ideas, and the dramas of university paperwork for the better half of four years. In the beginning of my project, Sarah joined me on every fieldtrip to Wambiana and quickly became a vital lizard catcher. More importantly, she has constantly helped me organize gear and prepare food for my long field trips. Without her organizational skills working behind the scenes, I would have been a mess in the field. Thank you Sarah for your constant love and support! ☺

Abstract

Habitat disturbances, such as grazing by livestock, can have major direct and indirect impacts on the structure and complexity of both vegetation and faunal communities. Changes to habitat structure and resource availability often lead to changes in biodiversity. While the impacts of livestock grazing has been well studied in vegetation communities, fewer studies have focused on wildlife. Further, terrestrial (ground-dwelling) communities have generally been the focal group of interest, whereas the impacts of grazing on arboreal systems have often been overlooked.

Arboreal reptiles are generally difficult to capture due to their cryptic nature and tendency to flee when encountered. Further, they often shelter under loose, peeling tree bark, or in hollows, making them difficult to capture without damaging their microhabitat. I implemented and used arboreal cover boards (ACBs) as “artificial bark” made from closed-cell foam cover boards to try and increase the capture rate of arboreal lizards. I tested the difference in capture success using standard visual encounter surveys (VES) and the use of arboreal cover boards as survey methods to sample small, cryptic arboreal lizards. Diurnal and nocturnal (spotlight) VES resulted in lower capture success compared to ACB surveys. While nocturnal VES showed a bias towards adult geckos, the use of ACBs captured individuals from all age classes. Further, ACBs were successful in monitoring non-target species, and even broad taxonomic groups. The use of ACBs extends beyond just a useful survey technique, but also provides the potential for long-term monitoring and restoring damaged or degraded microhabitats.

Domestic livestock alter ground-level vegetation structure due to grazing, but little is known about the effects on arboreal habitats. Similarly, the effects grazing has on ground-dwelling wildlife populations has been examined to some extent, yet the potential impacts to arboreal groups have received little attention. I examined the responses of arboreal and terrestrial reptile communities and their respective habitats to domestic livestock grazing. Terrestrial reptiles were generally negatively associated with heavy grazing, as their primary habitat (ground-level) was heavily impacted. Terrestrial reptiles were strongly associated with ground-level habitat complexity,

which was greatly reduced in areas with heavy grazing. Alternatively, arboreal reptiles were generally resistant to the impacts of even heavy grazing, and were positively associated with arboreal tree structures, such as peeling bark and tree hollows. While terrestrial and arboreal reptiles showed opposing trends (negative and positive association with grazing, respectively), individual species within these groups showed varied responses. I highlight the importance of retaining trees in rangelands as an overarching management guideline, as trees provide primary habitat for arboreal species, but also provide shade, leaf litter, and woody debris for terrestrial species.

Two species that showed resistance (i.e., no negative effects, or showed positive effects to livestock grazing) were a diurnal skink, the inland snake-eyed skink (*Cryptoblepharus australis*) and a nocturnal gecko, the Australian native house gecko (*Gehyra dubia*). Snake-eyed skinks showed no effect of livestock grazing on their abundance, while native house geckos were more abundant in sites with heavier stocking rates. I tested whether food availability was a driving mechanism that allowed these species to persist in areas with high levels of grazing. I quantified the invertebrate prey community available to both lizards using ACBs and light trapping. The invertebrate prey community composition was not significantly different among the four grazing regimes or habitat types. While both lizard species are habitat generalists, they were fairly selective in their diets, consuming prey disproportionally to their availability. Both snake-eyed skinks and native house geckos showed strong selection for beetles, spiders, and scorpions, resulting in high dietary niche overlap. While native house geckos and snake-eyed skinks both occupy similar microhabitats and consume similar prey items, they are temporally segregated by activity time (native house geckos = nocturnal; snake-eyed skinks = diurnal). Although not significantly different, the heavily grazed sites showed the greatest abundance of the most preferred prey items (beetles, spiders, scorpions), which may contribute to the high abundances of native house geckos in these sites.

Predator–prey dynamics play a vital role in shaping population structure and community assemblages. Predator–prey interactions have been of interest to biologists for hundreds of years, yet most studies focus on the perspective of the predator (examining functional and numerical responses), or from the perspective of the prey (examining direct mortality or non-consumptive effects). Few studies have measured predation risk in relation to the abundance of both predators and prey. I tested two competing hypotheses regarding predation risk: i) predation risk is predator-density dependent (i.e., more predators result in greater predation risk); and ii) predation risk follows the alternative prey hypothesis (e.g., predation risk is dependent on alternative prey availability). I used a combination of surveys (for predators, alternative prey (invertebrates), and lizards) and physical models (n = 800) to estimate predation risk on lizards. Predation risk on lizards was greatest in the dry season, when predator abundance and alternative prey populations were lowest. Alternatively, predation risk on lizards was lowest during the wet season, when predator abundance and alternative prey availability was greatest. This suggests that predation risk to lizards is not predator-density dependent, as predation risk was lowest when predator abundance was highest, and vice – versa. Our data also indicates that predation risk follows the alternative prey hypothesis, as predation risk to lizards was greatest when alternative prey populations (invertebrates) were lowest, and vice – versa.

Although predator–prey dynamics are important in shaping wildlife community composition, predation events are rarely observed. In many cases, our perception of what constitutes “predators” or “prey” may be biased towards anecdotal observations or studies that have documented predation events. In many ecosystems, vertebrates constitute a majority of what we consider “predators”, but large invertebrates exist across much of the world, especially in tropical regions, that may be formidable predators to small vertebrate groups. I conducted 500 man-hours of visual searches, compiling observations of *in situ* predation events, and deployed 800 model lizards to measure attack frequency and identify potential predators. Observing a predation event *in situ* was rare: I observed 9 predation events in total (4 instances of vertebrates eating another vertebrate; and 5 instances of invertebrates eating a vertebrate). This suggests that while observing any predation event is rare, invertebrate predators (e.g., large spiders, mantids) may contribute to similar levels of predation to more traditional vertebrate predators (e.g., snakes, birds). Further, large invertebrates (predominantly huntsman spiders) contributed to up to 23% of attacks on model lizards. I highlight the potential importance of large predatory invertebrates as predators to small vertebrates, especially herpetofauna, in comparison to more “traditional” predator groups, such as birds and snakes. Predatory invertebrates have largely been overlooked in the literature as potential predators, with exception to anecdotal observations. Their importance as predators in shaping community assemblages should be reconsidered.

Environments with greater habitat complexity support high biodiversity because they have abundant and diverse resources, which may reduce competition among species. Habitat disturbances, such as livestock grazing, often reduce habitat complexity and structure, resulting in a simplified, or homogenized environment. I tested if reduced competition, as a result of a homogenization from livestock grazing, acted as a mechanism that allowed native house geckos to thrive in heavily grazed environments. I compared the habitat utilization of three co-occurring arboreal geckos, native house geckos (*G. dubia*), northern velvet geckos (*Oedura castelnaui*), and eastern spiny-tailed geckos (*Strophurus willsiamsi*). All geckos displayed resource partitioning among tree species and tree structural characteristics. I found evidence of interspecific competition between geckos, in which native house geckos shifted their preferred habitat of dead trees, to Silver-leaf ironbark trees (*Eucalyptus melanophloia*) and complex trees with peeling bark in the presence of velvet geckos. Native house geckos were more resistant to the negative effects of grazing (low habitat complexity) than either velvet or spiny-tailed geckos. Native house geckos were more abundant in heavily grazed areas. In contrast, velvet and spiny-tailed geckos were rarely found in heavily grazed sites, and were more abundant in areas with lower grazing pressure. My data suggests that grazing by livestock homogenized the environment, and in turn, homogenized the arboreal reptile community. A lack of competition allowed native house geckos, a microhabitat generalist, to persist and even increase in abundance, where microhabitat specialists, such as velvet and spiny-tailed geckos, declined.

Habitat disturbances, such as livestock grazing, have detrimental effects on plant and animal communities. While many studies focus on species that decline in response to disturbance, it is just as important to understand how and why some species respond positively. This thesis is focused around the positive response of an arboreal lizard, *G. dubia*, to try and understand what mechanisms were responsible in allowing them to persist in environments where other species declined. I tested a series of potential mechanisms, including food availability, habitat availability, predation pressure, and competition, to try and identify their effects on native house gecko populations. While my data indicates that a reduction in competition as a result of habitat simplification is a major contributor, it is likely that no stand-alone mechanism is responsible. Rather, a combination of these mechanisms contribute to their success in heavily grazed environments.

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Figure 4.4. Prey selectivity for *Gehyra dubia* among the two habitat types (top; Reid River box and Silver-leaf ironbark), and among four grazing regimes (bottom; HSR = heavy stocking regime, MSR = moderate stocking regime, ROT = rotational stocking regime, and VAR = variable stocking regime). Values approaching +1 indicate a positive selection, values near 0 indicate random selection, and values approaching -1 indicate a negative selection or avoidance.

Figure 5.1. The native house gecko, *Gehyra dubia* (a), is an arboreal, nocturnal gecko found throughout northeast Australia. We used Blu-Tack® to make physical models of *G. dubia* for deployment in various macro- and microhabitats to test predation risk in lizards (b and c). Due to its pliable nature, attacks on models can be inferred from indentations remaining after predation events (c; indentations from a bird beak).

Figure 5.2. Expected and observed results of our two hypotheses: i) that predation risk (skull and crossbones) is predator density-dependent, i.e., predation risk increase with an increase in predator abundance (a); or, ii) is predation risk is inversely dependent on the abundance of alternative prey, i.e, the alternative prey hypothesis (b). The observed values for the predator-density dependent predation risk (c) indicate that predation risk was not predator-density dependent, as the mean number of attacks (Attacks; red) and the mean abundance of predatory birds (Pred.Birds; blue) show an inverse relationship to each other. Alternatively, the observed values for the alternative prey hypothesis (d)

indicate that predation risk on lizards (Attacks; red) was inversely related to the mean abundance of invertebrate (alternative) prey (Invert.Prey; blue), showing support for the alternative prey hypothesis.

Figure 5.3. Attack frequencies on Blu-Tack® model lizards vs. control models (patternless spheres). Predators attacked lizard shaped models significantly more often than control models (*t* = -3.394, df = 13, *P* = 0.004), yet there was no difference in the attack frequency during the day vs. night (*t* = 0.289, df = 13, *P* = 0.776).

Figure 6.1. Blu-Tack® model (A) tacked to the main trunk of a Silver-leaf ironbark (*Eucalyptus melanophloia*) to estimate predation on lizards. Blu-Tack® models were made to resemble the Australian native house gecko (*Gehyra dubia*; B). Photographs (A and B) taken at Wambiana Grazing Trial, QLD, Australia by E. Nordberg.

Figure 6.2. Predatory invertebrates consuming vertebrate prey. (A) Centipede (Scolopendridae) consuming an adult Australian native house gecko (*Gehyra dubia*); (B) Huntsman spider (Sparassidae) consuming a sub-adult *G. dubia*; (C) Praying mantis (Mantidae) consuming a sub-adult green tree frog (*Litoria caerulea*). (A) photographed by E. Nordberg near Charters Towers, QLD Australia; (B) photographed by L. Edwards and (C) photographed by R. Pillai in Townsville, QLD, Australia.

Figure 7.1. Eastern spiny–tailed gecko (*Strophurus williamsi*; (a)), Northern velvet gecko (*Oedura castelnaui*; (b)) and Australian native house gecko (*Gehyra dubia*; (c)). All photographs by E. Nordberg 2017.

Figure 7.2. Abundance (mean ± SE) of three arboreal geckos native house geckos (*Gehyra dubia)* [a], Velvet geckos (*Oedura castelnaui)* [b], and spiny tailed geckos (*Strophurus williamsi*) [c]) in four grazing regimes and two habitat types. Stocking regimes range from heavy – light from left to right; heavy stocking – HSR, variable stocking – VAR, rotational wet season spelling – ROT, and moderate stocking – MSR. Habitat represents woodland types, Reid River box (*Eucalyptus brownii*; Box) and Silver-leaf ironbark (*Eucalyptus melanophloia*; Ironbark).

Figure 7.3. Variation in habitat availability relevant to geckos among four grazing regimes (canonical scores and confidence ellipses (50% = solid; 95% = dashed)) (Heavy stocking [HSR] = red; variable stocking [VAR] = green; rotational wet-season spelling [ROT] = blue; and moderate stocking [MSR] = purple). Vectors indicate tree species or habitat cover measures (*Eucalyptus melanophloia* [Ironbark]; dead trees [Dead]; *Eremophila mitchellii*

[Sandalwood]; *Corymbia clarksoniana* [Bloodwood]; *Eucalyptus brownii* [Box]; *Carissa ovata* [C.ovata]; grass cover [grass.cover]; course woody debris [CWD]; fine woody debris [FWD]; bare ground [BG]). Grazing treatments show significant separation based on available habitat (Type II MANOVA Tests: Pillai test; $F_{33,36}$ = 1.818, P = 0.040).

Figure 7.4. Habitat use (canonical scores and confidence ellipses (50% = solid; 95% = dashed)) for three gecko species (*Strophurus williamsi* = blue; *Gehyra dubia* = red; and *Oedura castelnaui* = green). Vectors indicate tree species (a) and tree structural complexity measures (b). All three species are statistically separated by differences in selection (Manly selection ratios) of tree species and structural complexity features (MANOVA; (a) $F_{18,62}$ = 7.857, P < 0.001; (b) $F_{18,62}$ = 3.461, P < 0.001).

Figure 7.5. Principal component analysis of Manly selection ratios for different habitat attributes for geckos alone and in co-occupancy. Vectors indicate habitat selection by each species (first letter) when they are occupying sites with other species (second and third letters – indicate those species are also present). For example, the blue vector “S.G” indicates the selection of *Strophurus williamsi* (S) when *Gehyra dubia* (G) are also present. Points represent arboreal habitat features.

List of Equations

Equation 4.1. Levins Niche Breadth

$$Levins\ Niche\ Bredth: \quad B = \frac{1}{\sum P_i^2} \quad ; \quad B_{adj} = \frac{B-1}{n-1}$$

Equation 4.2. Pianka's Niche Overlap

$$Pianka's\ Niche\ Overlap: \quad O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum {P_{ij}}^2 {P_{ik}}^2}}$$

Equation 4.3. Shannon Diversity Index

$$Shannon\ Diversity\ Index: \quad H' = \sum_{i=1}^{S} -(pi * \ln pi)$$

Equation 4.4. Jacobs Selectivity Index

$$Jacobs\ Selectivity\ Index: \quad D = \frac{r-p}{r+p-2rp}$$

Equation 5.1. Survival (Trent and Rongstad 1974)

$$Survival: \quad Sn = \left(\frac{x-y}{x}\right)^n$$

Chapter 1 – General Introduction

Disturbance ecology

Changes in habitat structure and resource availability affect biodiversity indirectly, including species richness, and community assemblages (Tilman 1982; Landsberg et al. 2003; McIntyre et al. 2003; Kutt and Woinarski 2007; Ribeiro et al. 2009; Read and Cunningham 2010). Natural habitat disturbances such as wildfires or severe storms can be beneficial to some ecosystems by creating new microhabitats (Murphy and Legge 2007) or increasing ground-level light exposure for plants and animals (Greenberg 2001; Roznik et al. 2015; Greenspan et al. 2017). Many anthropogenic disturbances to the environment such as deforestation, urbanization, or grazing by livestock also alter existing microhabitats, yet many of these practices are negative for wildlife and biodiversity (Fleischner 1994; Rottenborn 1999; Martin and McIntyre 2007). Habitat disturbances are generally associated with negative effects, but not all habitat disturbances have detrimental effects on the environment. Intermediate levels of habitat disturbance can be beneficial to some species, and often increase species richness and diversity (Connell 1978). Many taxonomic groups benefit from intermediate habitat disturbances through the creation of heterogeneous habitat patches and a mosaic of microhabitats (Read 1995; Hódar et al. 2000; Germaine and Wakeling 2001).

Habitat disturbances change the structure, composition, and complexity of vegetation communities (Landsberg et al. 2003; Dorrough et al. 2004; Dias et al 2007). Habitats with high levels of disturbance, such as heavy livestock grazing, produce habitats with low grass and leaf-litter cover, increased bare ground, and lower habitat complexity (Landsberg et al. 2003; Neilly et al. 2017). A decrease in microhabitat complexity often causes lower species richness and diversity, leading to habitat homogenization (McKinney and Lockwood 1999). Environmental homogenization is widespread throughout disturbed landscapes (Olden 2006; McKinney 2006), changing species composition and assemblage diversity (Hendrickx et al. 2007; Mester et al. 2015). Homogenized environments support less biodiversity and less species-rich wildlife communities, and render different ecosystems more similar, reducing turnover

(Ekroos et al. 2010; Clavel et al. 2011), yet few studies have examined the mechanisms that drive these changes in species richness and abundance. Biotic homogenization has become a well-established ecological concept (McKinney and Lockwood 1999), but the actual processes leading to homogenization, including species interactions that may lead to species declines or spread, are typically not well studied in fauna.

Environmental impacts of livestock grazing

Grazing by livestock is one of the world's leading land uses, encompassing 25% of the world's land surface (Asner et al. 2004). In areas such as Australia, livestock grazing occurs on upwards of 56% of land areas, a much greater area than land designated for wildlife conservation and natural areas (6%; NLWRA, 2001). Therefore, if properly managed, rangelands could potentially be used for wildlife conservation, supported by long-term and sustainable grazing strategies (Neilly et al. 2016; Neilly et al. *In press*).

One of the major conservation concerns in relation to livestock grazing is the impact it has on the environment. While both native and domestic animals graze, domestic livestock are generally more numerous and site-restricted than native wildlife. The consumption of vegetative material leads to changes in vegetation community composition, structure, and diversity (Landsberg et al. 2003; McIntyre et al. 2003). Increasing perennial grass cover is thought to be one of the most important strategies increasing biodiversity, maintaining long-term sustainability, and ecosystem function (Dorrough et al. 2004). Intense grazing pressure can lead to desertification, increased soil temperature from sun exposure, decreased soil structure and drainage ability (Fleischner 1994; Yates et al. 2000; Castellano and Valone 2007) and declines in riparian habitat quality and structure (Kauffman and Kruger 1984; Szaro 1985; Belsky et al. 1999).

Impacts of grazing on terrestrial and arboreal fauna

Grazing by livestock not only changes vegetation structure and communities (Landsberg et al. 2003; McIntyre et al. 2003), but also indirectly affects faunal communities and assemblages (Bock et al. 1990; Fleischner 1994; Smith et al. 1996; Hayward et al. 1997). Sustainable management practices of grazing properties should become a priority for graziers for two main reasons: 1 – sustainable management practices reduce the risk of overgrazing and long-term degradation to land quality, and 2 – good land condition can support and maintain biodiversity, which could increase land productivity, or provide supplemental income from ecotourism or wildlife enthusiasts. Poorly managed properties with sustained overgrazing cause the land to become less profitable over time, more homogenized, and support less diverse wildlife populations (Fleischner 1994; Fuhlendorf and Engle 2001; O'Reagain et al. 2011; Neilly et al. *In press*).

Studies investigating the effects of grazing on wildlife have typically focused on ground-dwelling organisms (Jones 1981; Hayward et al. 1997; Bromham et al. 1999; James 2003; Knox 2010; Brown et al. 2011), likely because their primary habitat is most susceptible to degradation. Although few studies of fauna and grazing include arboreal organisms, some suggest arboreal species may be buffered from the direct effects of grazing because they mostly avoid affected habitat structures (Beutel et al. 2002; Neilly et al. 2017).

The presence of livestock in the environment may have significant indirect impacts on arboreal organisms. Although livestock do not generally alter foliage and leaf cover in the canopy, they may influence tree composition by consuming or trampling saplings and early successional tree species (Webb 1979; Jones 1981; Pitt et al. 1998; Ludwig et al. 2000; McIntyre et al. 2003; Kutt and Woinarski 2007). While large trees are not likely to be altered by livestock foraging, long-term grazing may affect tree morphology, composition, diversity, or dieback due to soil compaction, reduction in water filtration, or nutrient composition (Fleischner 1994; Ludwig et al. 2000; Castellano and Valone 2007). Cattle and other livestock rub the bark off trees; this behaviour may affect arboreal organisms that depend on rough or loose bark for refugia (Kauffman and Krueger, 1984; McCreary and George, 2005). Trees and arboreal systems support a wide variety of organisms including invertebrates, reptiles, mammals, and birds (Gibbons and Lindenmayer 2000). Small reptiles are sensitive to changes in habitat (Huey et al. 1983) and therefore may be indicators of ecosystem function (Bock et al. 1990; Trainor and Woinarski 1994; Valentine and Schwarzkopf 2009).

Arboreal reptiles are particularly abundant in Australian woodlands, an aspect of the high diversity of lizards, especially geckos and skinks. In our study system, the most abundant arboreal reptiles include Australian native house geckos (*Gehyra dubia*), northern velvet geckos (*Oedura castelnaui*), eastern spiny-tailed geckos (*Strophurus williamsi*), and inland snake-eyed skinks (*Cryptoblepharus australis*). In addition, less abundant species include: pale-headed snakes (*Hoplocephalus bitorquatus*), brown tree snakes (*Boiga irregularis*), common tree snakes (*Dendrelaphis punctulata*), frill-necked lizards (*Chlamydosaurus kingii*), eastern bearded dragons (*Pogona barbata*), freckled monitors (*Varanus tristis*), and tree skinks (*Egernia striolata*). A few previous studies (e.g. Woinarski and Ash 2002, James 2003) have indicated that arboreal reptiles, including native house geckos, respond positively (are “increaser” species), or show no effect of grazing on their abundance. To my knowledge, there have been no studies that have tried to identify the mechanisms that allow native house geckos (or other species) to respond as “increasers”. There are many possible ecological mechanisms that may contribute to a species persistence, increase, or decline in an environment, including habitat and prey availability, competition, predator–prey dynamics, thermal suitability, or oviposition-site availability. To identify and test these potential mechanisms, we need to understand the ecology and natural history of target species. Despite their high abundance and wide distribution across eastern Australia, to date, there are few (if any) studies on the natural history of any of the species I have listed above, aside from short descriptions in field guides (Wilson 2015, Cogger 2014). Therefore, my thesis aims to describe the natural history and ecology of these lizards, with particular interest in native house geckos, to identify the mechanism(s) allowing some of them to respond as an “increaser” species in the face of disturbance by livestock.

Lizards as a model system

Small reptiles are abundant in many landscapes across the world and have proven to be excellent model systems to study a variety of ecological and evolutionary processes (Huey et al. 1983; Vitt and Pianka 2014). Heterogeneous and complex habitats provide a multitude of refuge areas allowing small reptiles to avoid predators (Dickman 1992; Shepard 2007), find diverse microclimates for thermoregulation (Burrow et al. 2001; Singh et al. 2002), and a range of food sources (invertebrates; Abensperg-Traun et al. 2000; Hansen 2000; Hendrickx et al. 2007), and minimize inter- and intraspecific competition (McCoy and Bell 1991; Petren and Case 1998). Essentially, lizards rely on habitat structure for almost all aspects of their life (Huey et al. 1983). Lizards are likely to respond to even subtle changes in the environment, as they depend on habitat structure for so many physiological and behavioral activities. Aside from the aforementioned reasons, lizards are also very abundant and (relatively) easy to capture. Lizards represent a perfect study system to assess changes in natural history (abundance, habitat selection, diet, predation, competition, etc.) in response to livestock grazing.

Importance of natural history

Natural history and field ecology data are the backbone of our understanding of the natural world. Without natural history data, we would be unable to answer large scale questions about species distribution models, the impacts of climate change, pollution, urbanization, or a suite of other questions. Yet, over the last few decades, natural history and field ecological data has unfortunately been labeled a “dead” or “a dying field”, presumably because some people see this information as purely descriptive or lacking broad interest or implications (Greene 1994; Bury 2006; McCallum and McCallum 2006). While many of these data are indeed descriptive or narrowly focused, it is critical to document them so others may use the information in ways not have previously intended. This is the entire premise of publishing our work, so that others may use the information we have gathered to build upon and answer further questions. Few scientists have campaigned for the importance of natural history data and its value (Greene 1994; Herman 2002; Bury 2006; Greene 2005; Trauth 2006), while researchers and journals fail to see the value in natural history studies and observations, causing a reduction in these types of studies.

To adequately answer the questions surrounding the impacts of livestock grazing on arboreal reptiles, we must investigate a series of ecological questions targeting the influence of grazing on their natural history. Few studies have investigated broad impacts of grazing on reptiles in general (reviewed in the following chapters), but little is known about arboreal reptiles in response to disturbances such as grazing, and for many species their natural history is largely unknown. My primary objective was to help close this knowledge gap, by answering questions regarding the response of arboreal reptiles to livestock grazing, and in doing so, to also describe their natural history in terms of habitat use, diet, predation risk, and competitive interactions.

Study site – Wambiana Grazing Trail

My research took advantage of a long-running experimental grazing property run by the Queensland Department of Agriculture and Fisheries. The studies presented in the following chapters were conducted on the Wambiana Grazing Trial (WGT), a 1040 ha trial located on Wambiana Cattle Station, approximately 70 kms southwest of Charters Towers, Queensland, Australia. The WGT was set up in 1997 to test the long-term profitability and sustainability, in terms of land condition and beef production, of a series of grazing strategies and their response to weather (rainfall) variability. I used four of the five replicated grazing regimes in the WGT, all of which comprised of two major savanna woodland habitat types, Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*). A total of twenty-four, 1-ha sites were selected with equal numbers on all four grazing treatments and located in both habitat types (Figure 1.1). The four grazing regimes included: moderate stocking (MSR) – relatively consistent stocking at the long-term carrying capacity (8–10 ha per adult steer [450kg animal]); rotational stocking (ROT) – relatively consistent stocking at about 50% above the long-term carrying capacity in stocked paddocks, where 1/3rd of the paddock is spelled (rested) during the wet season on a rotational basis (7–8 ha per adult steer); variable stocking (VAR) – stocking rates adjusted annually at the end of the wet season depending on how much remaining pasture feed is available in the paddocks (3–12 ha per adult steer); and heavy stocking (HSR) – relatively consistent stocking at twice the long-term carrying capacity (4–5 ha per adult steer). Management justifications for each grazing regime are as follows: for the MSR, conservative stocking rates are thought to maintain land condition and minimize financial losses in drought years or when there is poor rainfall; the ROT grazing style is thought to buffer against rainfall variability by only grazing 2/3rds of the paddock in the wet season, and permitting 1/3rd of the paddock to regrow without grazing pressure, ensuring there is ample grass available during dry periods; the VAR grazing style takes advantage of periods with high pasture yield by increasing stocking rate, and minimizing overgrazing by removing stock during low rainfall years; and finally the HSR has high potential profitability and beef production in good years, but high risk of financial losses as cattle must receive supplementary feed in poor rainfall years.

Thesis chapters outline

This thesis aimed to answer the overarching question "How does cattle grazing affect arboreal reptiles?", but to adequately answer this question, a series of more specific questions had to be addressed. Therefore, my thesis is structured as a series of stand-alone publications that target specific questions about identifying the effect of cattle grazing on various aspects of the ecology, behavior, and natural history of arboreal reptiles. First (Chapter 2), I determined a method to successfully sample arboreal reptiles. This included comparing the efficacy, efficiency, and broad-scale use of traditional visual encounter surveys and a novel method using arboreal cover boards to monitor populations of arboreal reptiles. I then (Chapter 3) determined the impacts cattle grazing had on terrestrial and arboreal reptile abundance, richness, community structure and composition in relation to the different grazing regimes described above. This included identifying the influence of each grazing strategy on vegetation structure and complexity, and their influence on reptile assemblages. In Chapter 4, I described the abundance, diet, and prey availability of two abundant arboreal lizards, and the impacts cattle of grazing on their invertebrate prey community composition. In Chapter 5, I quantified predator–prey system dynamics including measuring the relationship between predator abundance and predation risk and, in Chapter 6, I highlighted the impact of underestimated predator groups on population structure of small vertebrates. Finally, in Chapter 7, I identified the mechanisms that lead to habitat homogenization in this grazing trial, and ultimately the changes to lizard community structure by examining habitat selection, competition, and resource partitioning. I conclude with a general discussion and synthesis, management implications and recommendations, and over-arching conclusions (Chapter 8).

FIGURES

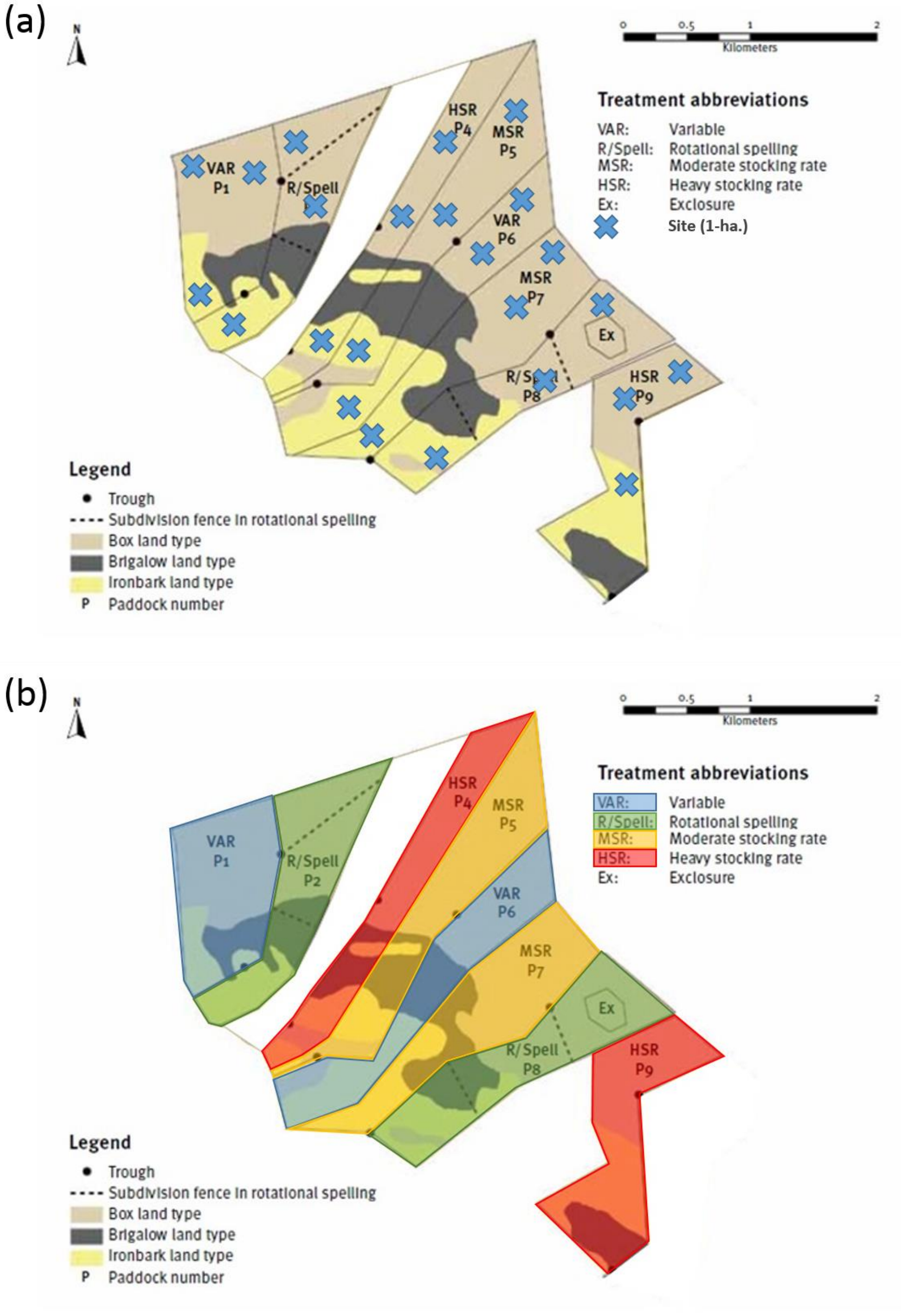

Figure 1.1. Site map of Wambiana Grazing Trial, indicating habitat types and site locations (a) and grazing treatments (b). Adapted from O'Reagain and Bushell 2011.

Chapter 2 – Arboreal Cover Boards: Using Artificial Bark to Sample Cryptic Arboreal Lizards

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ABSTRACT

Arboreal reptiles are often difficult to capture because of their cryptic nature and propensity to flee out of reach when approached. In addition, arboreal lizards often seek refuge under loose or peeling tree bark; therefore researchers often remove it to catch them, thereby potentially damaging habitat. Using arboreal cover boards, or "artificial bark," might reduce damage to natural shelter sites, allowing repeated surveys. We compared capture success and population structure of samples obtained by two capture methods—active searches (visual encounter surveys [VES]) and arboreal cover boards used as artificial bark—on two species of arboreal lizards, inland snake-eyed skinks (*Cryptoblepharus australis*) and Australian native house geckos (*Gehyra dubia*). Two types of arboreal cover boards (cardboard and closed-cell foam) were strapped around the main trunks of trees with elastic straps. Systematic VES during the day (for *Cryptoblepharus*) and at night (for *Gehyra*) were conducted in conjunction with monitoring of arboreal cover boards. Diurnal VES for *Cryptoblepharus* had low capture success (17.1% of observed animals) compared to arboreal cover boards (49.6%). Nocturnal spotlight surveys for *Gehyra* resulted in a high number of observations, but low capture success (44.9% of observed animals) compared to arboreal cover boards (83.5%). There was no difference in the capture success between cover board materials. Using arboreal cover boards as artificial bark increased hand captures of arboreal lizards, and preserved natural bark shelters that would have otherwise been destroyed by peeling bark during visual encounter surveys.

KEYWORDS

Active searches; Methods; Reptiles; Spotlighting; Trapping

INTRODUCTION

Because of their cryptic nature, reptiles are often difficult to study and observe (Fitzgerald et al. 2002; Bell 2009). Although some trapping and monitoring techniques can have relatively high capture rates, they might be seasonally biased, or influenced by habitat type or behavior (Dorcas and Willson 2009). Both active and passive capture methods have proven successful for monitoring reptiles. Passive capture techniques are generally thought to be an unbiased trapping method because animals are not attracted to the traps, but trapping success rather depends on the chance that an animal encounters one. Passive techniques, such as pitfall and funnel traps, can be time-consuming to monitor because they must be checked regularly to ensure that trapped animals do not starve, dehydrate, escape, or become injured or killed by predators or conspecifics (Dorcas and Willson 2009). Alternatively, one can use indirect passive monitoring techniques that do not require an observer to physically capture the animal, but rather indicate an animal's presence by searching for signs such as footprints, scats, or hair, or images on motion-sensitive or infrared camera traps.

Active monitoring techniques often rely on the skills of the observer, and therefore might result in a higher observer bias. Active survey methods include actively searching the environment for target organisms (visual encounter surveys [VES]), line transects, road or aerial surveys, or flipping artificial cover objects. Active trapping techniques, such as the use of artificial cover objects (e.g., cover boards), provide shelter for terrestrial animals (including reptiles, amphibians, small mammals, and invertebrates) that can be collected or captured by an observer when the shelter is removed (Grant et al. 1992; Monti et al. 2000; Lettink et al. 2011; Batson et al. 2015). Surveys using artificial shelters typically require much less monitoring than other passive traps because they can be left in place for months or years without causing mortality, as the animals are not physically restrained. A potential limitation of artificially adding shelter sites, especially if left in place for long periods, is that these sites might artificially enhance habitat for the species of interest, which may be undesirable for some types of studies, such as habitat assessments. On the other hand, artificial refugia can improve degraded habitats when permanently installed (Webb and Shine 2000; Souter et al. 2004; Francke 2005; Croak et al. 2013), increasing habitat suitability for threatened or rare species.

Arboreal organisms are notoriously difficult to sample, and are often underrepresented in studies using traditional sampling methods such as pitfall traps and funnel traps because many arboreal species rarely come to the ground where they would encounter a trap (Barker and Pinard 2001). The superior climbing ability of arboreal specialists, such as some geckos, might also allow them to avoid capture by climbing out of terrestrial pitfall traps (Towns and Elliot 1996). Other methods have been used to survey arboreal reptiles, such as VES (Michael et al. 2012; Vanderduys and Kutt 2012), artificial cover objects (Bell 2009), and arboreal nets or traps (Hamilton et al. 2007; Davis et al. 2008). Diurnal arboreal reptiles are often surveyed by walking transects or conducting systematic searches or random point searches through habitat (Lovich et al. 2012), whereas nocturnal reptiles are often surveyed by spotlighting while searching for eye-shine at night (Ribi 1981). While these types of VES often do not allow the observer to capture every animal, abundances and presence/absence data can be inferred from the total number of animals observed. Small arboreal organisms often take refuge under loose tree bark for shelter and thermoregulatory purposes (Werner 1990). Techniques for surveying for cryptic arboreal species often include peeling back loose tree bark in search of sheltering animals (Bustard 1968; Werner 1990; Valentine 2006). Peeling or removing tree bark might destroy the natural habitat used by arboreal lizards for shelter, thermoregulation (Bustard 1967), and oviposition sites (Ineich 2010), potentially reducing habitat suitability. Long-term effects of removing habitat to search for individuals might lead to habitat degradation and encourage species to relocate (Goldingay and Newell 2000; Goode et al. 2004, 2005). Artificial cover objects have been used successfully to monitor terrestrial reptiles and amphibians (Croak et al. 2013), but less so for arboreal species (Francke 2005; Bell 2009). Artificial cover objects have been used to monitor arboreal invertebrates (Hodge et al. 2007; Bowie et al. 2014) and nocturnal geckos (Francke 2005; Bell 2009) in New Zealand. Because it obviates bark removal to catch animals, artificial cover might serve as a non-destructive and sustainable technique to capture cryptic arboreal species that are often underrepresented in other traditional survey methods.

We compared the difference in capture success between VES (diurnal and nocturnal) and the use of artificial bark (arboreal cover boards) to capture two different species of arboreal lizards, one diurnal and one nocturnal. In addition, we compared the capture success of two types of artificial bark (cardboard and closed-cell foam) to establish a method for repeated sampling of these species.

METHODS

This study was conducted at Wambiana Cattle Station (20.554666°S, 146.110317°E; datum = WGS84), a commercial cattle property located approximately 70 km southwest of Charters Towers, northern Queensland, Australia. Wambiana is located in dry tropical savanna dominated by three tree species, Reid River Box (*Eucalyptus brownii*), Silver-leaf Ironbark (*Eucalyptus melanophloia*), and Bendee (*Acacia catenulata*). Research sites were on the Wambiana Grazing Trial, a 1040-ha section of the Wambiana Cattle Station established by the Queensland Department of Agriculture and Fisheries in 1997 (described in O’Reagain et al. 2011). Each paddock contained three habitat types: box in the northeast, ironbark in the southwest ends of the paddocks, with Bendee across the center. A total of eight sampling sites, four in each habitat type (1 ha each) were selected in the box and ironbark habitats, which covered more area than the habitat dominated by Bendees.

Arboreal cover board surveys

Arboreal cover boards consisted of two materials: card-board (50 x 50 x 0.6 cm; length, width, thickness) and closed-cell foam (50 x 50 x 1.0 cm; PolyTuf, Mayo Hardware Ltd., Moorebank, NSW, Australia). At each site, 8–10 arboreal cover boards (half cardboard and half closed- cell foam) were strapped to the main trunks of trees with two elastic straps 1.5 m above ground level (Figure 2.1). Every arboreal cover board was removed from the tree daily (between 0800 and 1200 h) to check for sheltering animals. All reptiles found under the boards were captured by hand, if possible, for processing. Morphological data (e.g., body mass [± 0.01 g], snout–vent length [± 0.1 cm], tail length [± 0.1 cm], and sex) were recorded for all captured individuals (Table 2.1). All lizards were marked for individual recognition using visible implant elastomer by injecting inert colored plastic pigment under the skin; no individual received more than one colored injection per limb. After processing, each animal was released under the arboreal cover board at the site of capture; if cover boards were being relocated, processed animals were placed back on the tree near flaking bark or near natural shelters where possible. Arboreal cover boards remained strapped to the same trees for three consecutive days before they were moved to different trees. By frequently moving cover boards to different trees, we hoped to avoid attracting animals to trees by providing enhanced shelter sites.

Visual encounter surveys

We conducted VES during the late morning and early afternoon for diurnal species, and just after sunset for nocturnal species. During diurnal VES, two observers systematically searched the study site (1 ha) for arboreal skinks (*Cryptoblepharus australis*) on the trunks of trees, branches, and snags. The same techniques were used during nocturnal spotlight surveys for geckos (*Gehyra dubia*, and several other rarer species [e.g., *Oedura castelnaui* and *Strophurus williamsi*]) with two observers searching tree trunks, branches, and stumps for eye-shine and movement. When possible, lizards were captured by hand; otherwise individuals were identified and recorded according to species.

Data analysis

To compare the capture rates across all survey methods for each species, we divided the total number of captures per species in each survey by the total effort (hours) spent surveying. This gave us a rate of capture for each survey method (arboreal cover boards and active searches) for the two species we captured most often (*C. australis* and *G. dubia*). We calculated capture success (%) for each survey method by dividing the total number of captured animals from each species for each method by the total number of observed animals (captured and non-captured). We compared the capture success of the two different materials used for artificial bark (cardboard versus closed-cell foam) by calculating the total number of individuals observed under each material and then compared them using a chi-square goodness-of-fit test. We used the total number of observations rather than total number of captures when comparing methods to negate any differences in capture skill between observers. Then, we converted the total number of observations to observations per hour to account for differences in survey effort.

Each artificial bark survey required 20 min to complete, in which 10 arboreal cover boards could be checked and replaced; approximately 30 boards could be checked in 1 h. We used a Student's t-test to compare the mean snout–vent length of captured lizards (*C. australis* and *G. dubia*) from both arboreal cover boards and VES to compare the distribution of body sizes from each trapping method. We also calculated sex ratios (female:male) and age class ratios (adult:juvenile) from captured individuals as a function of trapping method. All analyses were performed using SPSS (v19.0, SPSS Inc., Chicago, IL, USA) with an α 0.05.

RESULTS

Arboreal cover board surveys

A total of 3276 arboreal cover boards (996 cardboard and 2280 closed-cell foam) were checked over six separate trapping sessions from May 2014–February 2015, a total of 113.3 h. The two most common lizard species captured under arboreal cover boards were inland snake-eyed skinks (*C. australis*, 179 captures) and Australian native house geckos (*G. dubia*, 162 captures; Table 2.1). There were no differences between the number of *C. australis* ($\chi^2 = 0.03$, df = 1, $P = 0.86$) or *G. dubia* ($\chi^2 = 0.01$, df = 1, $P = 0.92$) occurring under cardboard or closed-cell foam. We captured 1.4 *G. dubia*/h and 1.6 *C. australis*/h under arboreal cover boards. We captured about half of all *C. australis* (49.6%) and a majority of *G. dubia* (83.5%) observed under arboreal cover boards.

Visual encounter surveys

We conducted 20 h of VES for diurnal *C. australis*, with 82 observations and a 17.1% capture success rate. Although we achieved similar numbers of observations per hour in VES (4.1/h) and arboreal cover board surveys (3.2/h), the capture success during VES for *C. australis* was lower than the capture success when using arboreal cover boards (Table 2.2). During VES, *Cryptoblepharus* skinks could easily avoid capture by fleeing up the tree before the observer could get close enough to attempt to catch it.

We conducted 69.3 h of nocturnal active searches (spotlight surveys) for *G. dubia* resulting in 476 observations and 214 captures (capture rate 44.9%). We observed 6.8 geckos/h during spotlight surveys, but only captured 3.1 geckos/h because geckos could not be captured if located at heights >2 m. Although we observed more geckos during spotlight surveys than arboreal cover board surveys, the capture success during spotlight surveys (44.9%) was less than that of the artificial bark surveys (83.5%). Furthermore, we captured geckos from all size and age classes in arboreal cover board surveys, whereas we captured mostly adult geckos during spotlight surveys (Figure 2.2). Nocturnal spotlight surveys were useful for identifying other species of arboreal reptiles, including rarer species such as northern velvet geckos (*Oedura castelnaui*), eastern spiny-tailed geckos (*Strophurus williamsi*), and pale-headed snakes (*Hoplocephalus bitorquatus*; Table 2.3).

Population structure

We found that spotlight surveys were biased towards the capture of adult geckos ($t = 13.0$, df = 213, $P < 0.001$). Spotlight surveys resulted in a 22.8:1 adult:juvenile ratio and a 0.7:1 female:male ratio. Arboreal cover board surveys produced a 1.6:1 adult:juvenile ratio and a more even distribution of female and male geckos (0.9:1). We found that both survey methods for diurnal skinks resulted in similar capture patterns between adults and juvenile skinks ($t = 1.6$, df = 15, $P = 0.14$) and sex ratios (VES adults:juveniles = 6:1; VES females:males = 1:1; arboreal cover board adults:juveniles = 6.5:1; arboreal cover board females:males = 1:1).

DISCUSSION

Capture success

We found that visual searches were a successful means of observing lizards, both for diurnal and nocturnal species, although more so for nocturnal species. Capture success, however, was appreciably enhanced for both diurnal and nocturnal species when we used arboreal cover boards. Overall, we observed and captured fewer diurnal lizards in VES compared to our use of arboreal cover boards. We observed more geckos during spotlighting surveys than under cover boards, but our capture success for geckos was much higher when using cover boards.

Although *Cryptoblepharus* skinks were diurnally active, the arboreal cover boards could be used as shelters from predators and direct solar radiation, and as microhabitats for thermoregulation and foraging. One reason that *C. australis* were more easily captured when sheltering under cover boards than during VES was because all boards were placed 1.5 m above ground level; therefore, all individuals sheltering under cover boards were within a catchable height. In addition, our rate of capture success benefitted from the element of surprise when removing the cover boards. In contrast, during VES, skinks were often either too high to catch, or quickly fled out of reach as the observer approached.

Active searches for nocturnal geckos (via spotlight surveys) resulted in a large number of observations (6.8/h) and a relatively high capture success (3.1/h; 44.9%). Although arboreal cover boards were not as productive as spotlight surveys in terms of number of observations (1.7/h), the capture success rate for *G. dubia* under arboreal cover boards was much higher (83.5%). We again attribute this to the element of surprise when removing the cover boards, and the fact that all the animals are at catchable height when encountered. Another major benefit of using arboreal cover boards to sample *G. dubia* was a more even sex ratio and greater distribution of body sizes for captured individuals compared to spotlight surveys. This might be a result of a more standardized search area (the area under the cover board) that does not rely on an observer detecting individuals throughout a large study area. Geckos captured during spotlight surveys tended to be large adult individuals, whereas arboreal cover boards produced geckos from all age classes (hatchlings, juveniles, and adults). We speculate that adult male geckos might have larger home ranges and move more frequently (e.g., mate searching or defending territory) than females, which leads to a higher detectability by an observer during spotlight surveys. Spotlight surveys might be sufficient if data are needed to quantify abundance, presence/absence, or distribution within the habitat, but if the researcher requires information on growth rates or population structure, using arboreal cover boards (or a combination of active searches and arboreal cover boards) should produce more biologically meaningful data.

Time and material

While trapping can be costly and time consuming (e.g., setting up, monitoring, and removing traps) arboreal cover boards are comparatively cheap and require little effort to maintain. They can be made from a variety of materials (e.g., cardboard, closed-cell foam, fabric, metal sheeting) depending on target species and budget restrictions. For the cheapest option, cardboard can be obtained or purchased from many businesses, and attached to trees using elastic straps for easy removal. One downfall of using cardboard is that it breaks down and tears rapidly in wet or humid conditions (EJN, personal observation). For longer-lasting cover boards, closed-cell foam mats can be purchased from most building-supply or hardware stores. Closed-cell foam is more resistant to harsh environmental conditions and does not break down when wet. We used the same foam cover boards for six sampling trips—each board withstanding a total of 45 d strapped to trees—without replacing or repairing them. For long-term monitoring, arboreal cover boards can be left in place without requiring constant monitoring because animals can freely use the shelters without getting trapped.

Multi-species use and habitat restoration potential

Arboreal cover boards can be used to sample a variety of organisms (Table 2.3). Although we used them to target arboreal lizards, we observed (and captured) other taxa as well. This technique may be especially useful for monitoring arboreal invertebrates that typically shelter under loose bark or in cracks and fissures (Hodge et al. 2007; Bell 2009). Other studies have had success in using artificial arboreal shelters to monitor populations of invertebrates, such as New Zealand’s rare Tree Wetas

(*Hemideina ricta*; Bowie et al. 2014), Red Katipo Spiders (*Latrodectus katipo*; Lettink and Patrick 2006), and spider communities (Hodge et al. 2007).

Although we have described this technique as a useful sampling method, artificial cover has also been used for habitat restoration (Webb and Shine 2000; Wilson et al. 2007; Croak et al. 2010; Bowie et al. 2014). For many species, habitat degradation is a leading cause of population decline. By placing artificial cover objects into degraded environments that resemble natural refugia, we can begin to artificially restore habitats (Webb and Shine 2000; Croak et al. 2010; Bowie et al. 2014). After 40 wks of their placement within degraded habitats, 100% of artificial rock formations were colonized by fauna (Croak et al. 2010), including endangered broad-headed snakes (*Hoplocephalus bungaroides*). These artificial rock formations not only resembled appropriate shelter sites, but they also mimicked the thermal properties of natural rock crevices, and can be equally, if not more, important for recolonization. Adding refugia to degraded habitats can greatly impact vulnerable species. By adding artificial burrows to the landscape, Souter et al. (2004) were able to increase the density of endangered pygmy bluetongue skinks (*Tiliqua adelaidensis*).

The placement of artificial refugia is a relatively inexpensive and easy way to monitor populations or increase habitat value in disturbed areas. Long-term placement of arboreal shelters might increase microhabitats available for shelter, thermoregulation, or oviposition for threatened or rare arboreal species, and might be useful for ecological restoration and management practices.

TABLES

TABLE 2.1. The total number of observations, captures, and capture success rates for three survey methods—visual encounter surveys (VES), arboreal cover boards (ACB), and spotlight surveys (SS)—to sample arboreal skinks (*Cryptoblepharus australis*) and arboreal geckos (*Gehyra dubia*).

Species	Survey method	Survey time (h)	Total observations	Total captures	Unique captures (recaptures)	Captures (per/h)	Capture success (%)
Cryptoblepharus australis	VES	20.0	82	14	14 (0)	0.7	17.1%
	ACB	113.3	361	179	175 (4)	1.6	49.6%
Gehyra dubia	SS	69.3	476	214	176 (38)	3.1	44.9%
	ACB	113.3	194	162	137 (25)	1.4	83.5%

TABLE 2.2. Population structure and morphological data of captured arboreal lizards (*Cryptoblepharus australis* and *Gehyra dubia*) from visual encounter surveys (VES), spotlight surveys (SS), and arboreal cover board surveys (ACB). Population structure ratios are listed as F:M = females to males, and A:J = adults to juveniles.

					Ratios		Mean ± SE		
Species	Survey type	Age class	Sex	*n*	F:M	A:J	SVL (mm)	Mass (g)	TL (mm)
Cryptobelpharus australis	VES	Adult	Female	6	1:1	6:1	37.7 ± 1.7	0.9 ± 0.09	45.7 ± 6.5
		Adult	Male	6			40.0 ± 0.7	1.0 ± 0.07	29.0 ± 8.2
		Juvenile	—	2			29.8 ± 1.8	0.4 ± 0.03	17.3 ± 2.3
	ACB	Adult	Female	79	1:1	6.5:1	40.9 ± 0.3	1.1 ± 0.03	28.3 ± 2.3
		Adult	Male	76			40.7 ± 0.3	1.1 ± 0.02	28.7 ± 2.3
		Juvenile	—	24			30.8 ± 0.6	0.4 ± 0.03	13.5 ± 1.3
Gehyra dubia	SS	Adult	Female	82	0.7:1	22.8:1	56.8 ± 0.7	4.6 ± 0.16	49.4 ± 1.6
		Adult	Male	123			56.3 ± 0.5	4.2 ± 0.10	51.4 ± 1.0
		Juvenile	—	9			35.8 ± 1.5	1.0 ± 0.13	25.1 ± 4.8
	ACB	Adult	Female	46	0.9:1	1.6:1	50.1 ± 1.1	3.1 ± 0.20	44.2 ± 1.9
		Adult	Male	53			50.9 ± 0.9	1.4 ± 0.19	50.5 ± 1.7
		Juvenile	—	63			31.4 ± 0.5	0.7 ± 0.03	28.2 ± 1.1

TABLE 2.3. The number and species composition of animals observed using three arboreal survey methods: arboreal cover boards (ACB), visual encounter surveys (VES), and spotlight surveys (SS). Numbers represent the number of individuals observed in each survey method.

Taxon	ACB	VES	SS
Invertebrates			
Ants (Formicidae)	88†	—	—
Beetles (Coleoptera)	83	—	3
Caterpillars (Lepidoptera)	6	—	1
Centipedes (Chelopoda)	24	—	1
Cockroaches (Blattodea)	118	—	13
Crickets (Gryllidae)	26	—	9
Grasshoppers (Caelifera)	23	—	3
Huntsman Spiders (Sparassidae)	57	—	246
Praying Mantis (Mantodae)	6	—	—
Red-back Spiders (*Latrodectus hasseltii*)	6	—	—
Scorpions (Scorpiones)	28	—	—
Spiders (Araneae)	38	—	23
Termites (Isoptera)	24†	—	—
Amphibians and Reptiles			
Green Tree Frogs (*Litoria caerulea*)	—	—	9
Inland Snake-eyed Skinks (*Cryptoblepharus australis*)	361	82	—
Australian Native House Gecko (*Gehyra dubia*)	194	—	476
Northern Velvet Geckos (*Oedura castelnaui*)	—	—	7
Spiny-tailed Geckos (*Strophurus williamsii*)	—	—	3
Bynoe’s Geckos (*Heteronotia binoei*)	5	—	5
Pale-headed Snakes (*Hoplocephalus bitorquatus*)	2	—	12
Ornamental Snakes (*Denisonia maculata*)	—	—	1

†Represents the total number of cover boards under which ants and termites were found, not number of individuals.

FIGURES

Figure 2.1. Arboreal cover boards (cardboard, left panel; closed-cell foam, right panel) that were strapped to the trunks of trees using elastic straps 1.5 m above ground level. The elastic straps could be removed to detach the cover board from the tree and capture animals taking shelter under them.

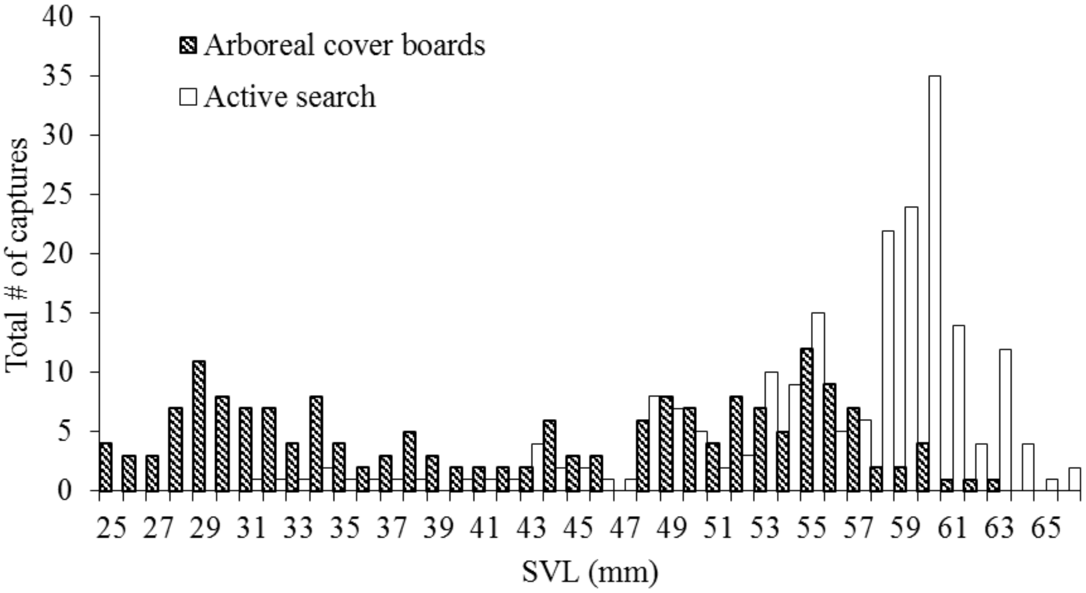

Figure 2.2. The numbers of individuals representing a range of snout–vent lengths (SVL) for *Gehyra dubia* captured during arboreal cover board (hatched bars) and visual encounter surveys (open bars).

Chapter 3 – Arboreality Increases Reptile Community Resistance to Disturbance from Livestock Grazing

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ABSTRACT

1. Domestic livestock grazing directly alters ground-level habitat but its effects on arboreal habitat are poorly known. Similarly, the response to grazing of ground-dwelling fauna has been examined, but there are few studies of arboreal fauna. Globally, grazing has been implicated in the decline of vertebrate fauna species, but some species appear resistant to the effects of grazing, either benefiting from the structural changes at ground level or avoiding them, as may be the case with arboreal species. Here, we examine arboreal and terrestrial habitat responses and reptile community responses to grazing, to determine whether arboreal reptile species are more resistant than terrestrial reptile species.
2. We conducted arboreal and terrestrial reptile surveys on four different grazing treatments, at a 19-year experimental grazing trial in northern Australia. To compare the grazing response of arboreal and terrestrial reptile assemblages, we used community, functional group and individual species-level analyses. Species responses were modelled in relation to landscape-scale and microhabitat variables.
3. Arboreal reptile species were resistant to the impact of grazing, whereas terrestrial reptiles were negatively affected by heavy grazing. Terrestrial reptiles were positively associated with complex ground structures, which were greatly reduced in heavily grazed areas. Arboreal lizards responded positively to microhabitat features such as tree hollows.

4. *Synthesis and applications*. Arboreal and terrestrial reptiles have different responses to the impact of livestock grazing. This has implications for rangeland management, particularly if management objectives include goals relating to conserving certain species or functional groups. Arboreal reptiles showed resistance in a landscape that is grazed, but where trees have not been cleared. We highlight the importance of retaining trees in rangelands for both terrestrial and arboreal microhabitats.

KEYWORDS

Agriculture, Arboreal, Cattle Grazing, Habitat Fragmentation, Herpetofauna, Off-Reserve Conservation, Rangelands, Reptiles, Response Mechanisms

INTRODUCTION

Grazing by domestic livestock occurs across 25% of the Earth's land surface (Asner, Elmore, Olander, Martin, & Harris, 2004) and is implicated as a contributing factor in the decline of vertebrate species' richness and abundance (Donald, Green, & Heath, 2001). The extent of grazing impact will depend on how much that species relies on the niches that are affected by grazing (Milchunas, Sala, & Lauenroth, 1988). Grazing alters ground-level habitat structures such as vegetation, woody debris and leaf litter (Brown, Dorrough, & Ramsey, 2011; Eldridge, Val, & James, 2011). It is, however, unclear exactly how grazing affects arboreal habitat. Alterations in habitat structure affect the vertebrate fauna that live in grazed environments, potentially impacting on their ability to access food, avoid predation and thermoregulate (Neilly, Vanderwal, & Schwarzkopf, 2016). Grazing impacts can have a positive effect on species, causing them to increase in abundance ("increasers"), have a negative effect ("decreasers") or have no effect.

Within a fauna community, the presence of increaser species, or a lack of decreaser species, suggests a degree of resistance to grazing. Here, "resistance" means the ability to tolerate (i.e. not be negatively impacted by) livestock grazing (Carpenter, Walker, Anderies, & Abel, 2001). Resistance may be represented by an increase in abundance, or no detectable response to grazing. In arid Australia and North America, some reptiles show no response to grazing, due to their preference for the open habitats and higher ground temperatures promoted by heavy grazing (Germano, Rathbun, & Saslaw, 2012; Read, 2002; Read & Cunningham, 2010). Likewise, bird communities can remain unaffected by grazing or even show an increase in diversity, provided trees are not cleared (Lusk & Koper, 2013; Martin & McIntyre, 2007). At a functional group or species level, heavy grazing may facilitate predation (Curry & Hacker, 1990; Kutt et al., 2013; Piana & Marsden, 2014) or affect predator avoidance strategies (Bylo, Koper, & Molloy, 2014; Pettigrew & Bull, 2014). Overall, those species resistant to grazing either benefit directly or indirectly from the structural changes at ground level, or avoid these areas by using other habitat strata, for example arboreal niches.

The degree to which "arboreality" influences a species' response to grazing impacts, has been explored for birds, where bird foraging height has been used to predict species response to grazing (Kutt & Martin, 2010; Martin & Possingham, 2005), but has yet to be explicitly addressed in reptiles. Arboreal reptiles are abundant in disturbed areas, including areas grazed by domestic livestock (Knox, Cree, & Seddon, 2012; Woinarski & Ash, 2002) and generally use upper-strata microhabitats such as tree hollows, cracks and fissures in dead branches, and loose bark (Gibbons & Lindenmayer, 2002). Therefore, they may be unaffected by ground-level disturbances because they spend little time in the altered habitat layer. They may also benefit where other species have declined due to reduced competition for food and other resources.

The effect of grazing on arboreal habitat has received less attention compared to the obvious, ground-based impacts. However, livestock may indirectly affect trees through soil compaction (Fleischner, 1994), consuming or trampling saplings (Pitt, Newman, Youwe, Wikeem, & Quinton, 1998), breaking low branches or consuming palatable shrubs (Jones, 1981). Furthermore, soil compaction leads to excess run-off, erosion, and ultimately a decrease in water infiltration to root systems (Castellano & Valone, 2007). Bare ground, created by a lack of herbaceous foliage, grasses, or even leaf litter, can lead to increased soil temperatures, resulting in high evaporative water loss (Yates, Norton, & Hobbs, 2000). A decrease in water and nutrient absorption begins to change the vegetation community and structure, including trees, leading to desertification (Belsky & Blumenthal, 1997; Fleischner, 1994). Arboreal species may also respond to grazing-related land management techniques, such as tree clearing. Tree clearing is used in conjunction with livestock grazing to promote grass growth, directly impacting arboreal fauna by removing habitat (Gibbons & Lindenmayer, 2002; Martin & McIntyre, 2007).

Here, we investigate the response of arboreal and terrestrial reptile communities to four different cattle grazing strategies at a long-running, experimental grazing trial in a northern Australian, tropical savanna woodland. The reptile community at this location is diverse and abundant and, importantly, operates at scales appropriate to the size of this grazing trial, as opposed to more vagile avian and mammalian fauna. We measured the effect of different grazing treatments on ground and arboreal habitat, hypothesizing that ground-level habitat would be more impacted than arboreal habitat. We aimed to identify how arboreal and terrestrial reptiles responded to the grazing treatments as a community, as functional groups and individual species. We predicted that those species that relied on ground-level heterogeneity (e.g. ground-dwelling litter skinks) would likely respond negatively to higher levels of grazing. Conversely, we predicted that arboreal reptile species may be more likely to exhibit resistance to the effects of grazing.

METHODS

Wambiana grazing trial

This study was conducted at the Wambiana Grazing Trial (WGT), located on a commercial cattle station near Charters Towers, Queensland, Australia. The trial is 1040 ha and surrounded by extensive cattle grazing. Average annual rainfall at the study site is 643 mm, with a summer wet season and winter dry season. The WGT was established in 1997 by the Queensland Department of Agriculture and Fisheries to determine the effect of several grazing strategies on cattle production, profitability and land condition (O’Reagain, Bushell, Holloway, & Reid, 2009; O’Reagain, Bushell, &

Holmes, 2011). The WGT consists of two dominant vegetation types: Reid River Box (*Eucalyptus brownii*) and Silver-leaf Ironbark (*Eucalyptus melanophloia*; see Kutt, Vanderduys, & O'Reagain, 2012 for vegetation community descriptions). Each vegetation community has an understory of grass species and patchily distributed Currant Bush (*Carissa ovata*). Eight paddocks were randomly assigned one of four grazing treatments, therefore each treatment paddock was replicated twice (Table 3.1).

Reptile surveys

Twenty-four 1-ha sites were established, with six sites located in each of the four grazing treatments. Additionally, sites were located in different vegetation types; 16 in Reid River Box and eight in Silver-leaf Ironbark. The different number of sites in the vegetation communities reflects their relative area within each paddock. The sites were located at least 100 m from vegetation boundaries and 200 m from cattle watering points. Within a treatment and vegetation type, adjacent sites were at least 400 m apart. Species detectability was assumed to be equal as standardized survey methods were used at each site and our primary aim was to compare among treatments.

Terrestrial reptile survey

Four surveys were conducted to assess the terrestrial reptile community. These occurred in 2014 and 2015, in April (end of the wet season) and October (end of the dry season). At each site, a trap array was set-up and comprised: 4 × 30 cm diameter pitfall buckets at 10 m intervals in a "T" configuration, intersected by drift fence (one 20 m length and one 10 m length); and 6 × funnel traps (18 × 18 × 79 cm), two placed either side of the drift fence at each of the three ends of the fence. Pitfall and funnel traps were opened for 10 nights and checked twice daily. Captured animals were removed from traps, identified, weighed, measured and then released at the site of capture.

Arboreal reptile survey

Timed nocturnal spotlighting was conducted at each site, twice per trapping session, where observers searched the ground, bushes and trees for arboreal reptiles.

We conducted 16 spotlight surveys (5.3 man-hours) per site between 2014 and 2015. In addition, 24 arboreal cover boards (ACBs; Nordberg & Schwarzkopf, 2015) were used to monitor populations of both diurnal and nocturnal arboreal lizards in April and October of 2015 only (total of 2,304 trap nights). ACBs were set-up a day prior to the surveys, allowing animals time to utilize the shelters and then checked each morning (07.00–11.00 hr). Due to variation in trapping methods and survey dates, capture data of *Cryptoblepharus australis,* were excluded from community analysis, but were used for individual species analyses.

Microhabitat surveys

Structural complexity of microhabitat features was measured during each of the four reptile surveys. At each site*,* 3 × 100 m parallel transects, 50 m apart, were established. Terrestrial features such as ground cover (e.g. bare ground, leaf litter, grass cover, etc.) were categorized along each transect (Table 3.2). All trees within 1 m on either side of each transect were identified and their height and diameter at breast height (DBH) was measured. Arboreal habitat characteristics were measured in overstory trees throughout the site, including canopy cover, number of dead trees and hollows (Table 3.2).

Data analysis

We used a range of complementary univariate and multivariate analyses in R (R Core Team, 2016). Where relevant, optimal models were determined by comparing models based on the Akaike information criterion (AICc) using the *dredge* function in *MuMIn* (Barton, 2015), pairwise comparisons were made of the terms in the optimal model using the Tukey test in *lsmeans* (Lenth, 2016) and the final models were validated by examining the deviance residuals.

Habitat characteristics

Structural habitat features were analysed using two-way analysis of variance to investigate the effects of vegetation type and grazing treatment on the mean cover of structural variables in the lower strata (ground level) as well as mean values for arboreal habitat characteristics. Pairwise comparisons were made using Tukey’s tests.

Reptile abundance and richness

Abundance and species richness were collated for a trapping session (n = 96) for arboreal and terrestrial species. Generalized linear mixed models (GLMM) with a negative binomial distribution (accounting for overdispersion) were used to examine abundance and species richness in relation to grazing treatments and vegetation type (fixed effects), with year and season as random effects (*lme4*; Bates, Maechler, Bolker, & Walker, 2015). Variables were explored for collinearity before including them in the model.

Reptile community composition

Arboreal and terrestrial community compositional differences were explored using a multivariate extension of a generalized linear model (GLM), using the function *manyglm* in *mvabund* (Wang, Naumann, Wright, & Warton, 2012). This analysis is an alternative to distance-based multivariate analyses. Multiple GLMs are fitted to many variables simultaneously and an *anova.manyglm* function can be used for hypothesis testing. Univariate test statistics and *p* values were calculated for each species in the model to indicate their relative contribution to the overall variance among the communities. We constructed a site-by-species table populated by the abundance of species that were present in at least five sites. This function does not allow for mixed effects models and so each year was analysed separately. Multivariate GLMs with a negative binomial distribution were applied, with grazing treatment, vegetation type, season and year (and their interactions) as the explanatory variables. Arboreal and terrestrial reptile communities were modelled separately. To visualize the overall community response to grazing, we plotted the standardized model coefficients from a GLM with LASOO penalties to create a “heat-map” (Brown et al., 2014). Reptile species taxonomy followed Wilson (2015).

Individual species and functional group responses

Generalized linear models, with a negative binomial distribution, were used to analyse the responses of the most abundant arboreal and terrestrial species, and functional groups, to the relevant arboreal and terrestrial microhabitat variables (Table 3.2). We analysed two terrestrial functional groups: diurnal litter skinks and terrestrial geckos, and one arboreal functional group: arboreal geckos. Their responses to grazing treatment and vegetation type (landscape-scale variables) were analysed with GLMMs using year and season as random effects (*lme4*; Bates et al., 2015). A poisson or negative binomial distribution was applied where appropriate.

RESULTS

Microhabitat characteristics

Grazing treatment had a major effect on the structural complexity available to terrestrial reptiles. Six of eight terrestrial habitat features were significantly affected by grazing treatment (Figure 3.1). Grass cover, grass height, leaf litter and coarse woody debris were all greatly reduced in areas with high stocking rates. In H, the consumption of grasses and leaf litter by cattle lead to large areas with bare ground and low structural complexity. Conversely, only two of 10 arboreal habitat characteristics (% Canopy connectivity and no. of trees >30 cm DBH) were significantly different among the grazing treatments (Figure 3.2, Appendix 3.S1, Table 3.1).

Reptile abundance and species richness

Over 3,840 pitfall and 5,760 funnel trap nights, 684 terrestrial reptiles of 18 species were observed. Over 57.6 hr of spotlighting and 2304 ACB trap nights, 624 arboreal reptiles of eight species were observed. The optimal GLMM for terrestrial reptile abundance included grazing treatment and vegetation type (Table 3.3, Figure 3.3a). M, R and V all had significantly higher terrestrial reptile abundance than in H, but were not different from each other. Overall, the H sites in Ironbark had significantly lower terrestrial reptile abundance than all the other grazing treatment and vegetation type combinations. The Box vegetation type had higher terrestrial reptile abundance than the Ironbark.

Arboreal reptile abundance was also significantly affected by grazing treatment and vegetation type, however, in this case, H and V supported higher abundances (Table 3.3, Figure 3.3b). Furthermore, reptile abundance was higher in Ironbark than in Box. The interaction of these two variables, although included in the second best model, was not statistically significant. The optimal model for terrestrial reptile richness included vegetation, although it was not statistically distinguishable from the null model (ΔAICc = 0.12). The best arboreal reptile richness model was the null model. Model coefficients for the optimal abundance models are included in Appendix 3.S2 (Tables 3.1 and 3.2).

Reptile community

Eight species were included in the terrestrial community analysis: three small, litter-dwelling, diurnal skinks (*Carlia munda, Menetia greyii* and *Morethia taeniopleura*), a larger, surface active, diurnal striped skink (*Ctenotus robustus*), a diurnal dragon (*Diporiphora nobbi*), and a group of nocturnal, ground-dwelling geckos, including the fat-tailed gecko (*Diplodactylus platyurus*), Bynoe's gecko (*Heternotia binoei*), and the box-patterned gecko (*Lucasium steindachneri*). Overall, the response of the terrestrial reptile community to grazing was more negative than the response of the arboreal reptile community (Figure 3.4). In 2014 and 2015, terrestrial reptile community composition was explained by season and an interaction between grazing and vegetation (Table 3.4). The seasonal responses were driven by the same individual species (*C. munda*, *M. greyii*, *C. robustus, M. taeniopleura*), however the individual species driving the interaction of grazing and vegetation changed from 2014 to 2015. Only *H. binoei* consistently influenced this interaction term. The H Ironbark community was most different from the other communities, with a lower abundance of all species, except at the end of the dry season in 2015. During this trapping session, abundance of all species was much lower than at any other time in any other year, so detecting differences among treatments was difficult (Appendix 3.S3, Figure 3.1).

Four arboreal species were included in the community analysis: Australian native house geckos (*Gehyra dubia*), pale-headed snakes (*Hoplocephalus bitorquatus*), northern velvet geckos (*Oedura castelnaui)* and eastern spiny-tailed geckos (*Strophurus williamsi*). *Gehyra dubia* was the most abundant species in this community subset. In the arboreal reptile community, there was a significant effect of season in 2014 and of vegetation type in 2015, strongly driven by *G. dubia* (Table 3.4). Fitted value plots for *H. bitorquatus*, *O. castelnaui and S. williamsi* could not be drawn due to their relatively low abundance. Due to the overwhelming influence of *G. dubia*, individual species analysis may be more appropriate than community analysis.

Cryptoblepharus australis was not included in the arboreal community analysis due to a difference in trapping method and effort (ACBs), as well as the limitation that surveys were only conducted in 2015, however this species is examined individually.

Individual species and functional group responses

The five most abundant terrestrial species and the terrestrial functional groups (see Appendix 3.S4) were analysed separately (Table 3.5). There was a significant effect of grazing on four of the five species, and in the litter-skink and terrestrial gecko functional groups (Table 3.5, Figure 3.5a–g). *Carlia munda* (Figure 3.5a) and *M. taeniopleura* (Figure 3.5c) both had highest abundance in M and were lowest in H. The interaction between grazing and vegetation is evident for *H. binoei* (Figure 3.5b), where abundance was higher in Box in H, M and R but not in V. Overall, litter skinks were less abundant in H, whereas terrestrial geckos typically showed different responses to grazing in different vegetation types. Individual species responded to various microhabitat features (Table 3.5). Litter skinks were negatively associated with bare ground and positively associated with grass cover, whereas terrestrial gecko abundance was influenced by fine-woody debris and *C. ovata* cover.

Only two arboreal species could be analysed separately (Table 3.5, Figure 3.6a–c). *Gehyra dubia* responded to grazing and vegetation (Figure 3.6a), and were least abundant in M and R and most abundant in H and V. There was no significant effect of grazing on *C. australis*. Both species were more abundant in Ironbark. *Gehyra dubia* was negatively associated with small trees (trees 5–10 cm DBH) whereas *C. australis* was negatively associated with trees 10–20 cm DBH and positively associated with the Bark Index (they were more common on trees with more complex bark). Arboreal geckos responded negatively to small trees (5–10 cm DBH) and positively to the number of trees with hollows and cavities.

DISCUSSION

While habitat features at ground level were significantly modified by grazing treatment, the arboreal habitat was not affected. In H, ground-level microhabitat was significantly altered, and vegetation structural complexity was reduced. Diverse structural habitat is of great importance to ground-dwelling reptile communities as they create a mosaic of thermal and other conditions (Dorrough et al., 2012). The simplified ground habitat found in H had major implications for the ground-dwelling herpetofauna in this study.

Conversely, the only differences we found in arboreal habitat features among the grazing treatments were in terms of canopy connectivity and number of Trees >30 cm DBH. R had significantly lower canopy connectivity than H, and V had more large, overstory trees. In both cases, if grazing were the driving mechanism, then we would have expected to see the largest differences among the highest contrast treatments (i.e. H vs M). Further, younger size classes of trees were not different among the grazing treatments, suggesting no difference in recruitment. It is possible that changes to arboreal habitat will be identified in the future, as a result of long-term soil compaction, decreased water infiltration, and increased soil temperature (Castellano & Valone, 2007; Yates et al., 2000). Trees may take a long time to respond to grazing disturbance, but after 19 years of the WGT, the impact on overstory trees and arboreal habitat features is minimal.

Arboreal reptile response to grazing

Arboreal reptiles were not only resistant to the impacts of heavy livestock grazing, but had an apparent preference for H and V. However, while there was a diverse assemblage of arboreal reptiles at our sites, overall abundance patterns were driven by *G. dubia*. Most arboreal reptile species were much less abundant than *G. dubia*, so our community analysis was limited to four species. While community composition was not strongly affected by grazing treatment, the abundance of individual species (namely *G. dubia*) was affected (positively) by grazing. The most abundant arboreal reptiles, *G. dubia* and *C. australis*, flourished in all of the grazing treatments, including the heavily stocked paddocks, where many ground-dwelling reptiles suffered. *Cryptoblepharus australis* did not respond to grazing, and was, therefore resistant to the effects of heavy grazing, whereas *G. dubia* showed an increaser pattern, increasing in abundance with increasing stocking rate. Both species were apparently buffered from the direct negative impacts of grazing, such as microhabitat loss. This supports a similar study, where several arboreal lizard species were more abundant in communal rangelands (high disturbance area) compared to adjacent protected rangeland (low disturbance) (Smart, Whiting, & Twine, 2005). Here, the arboreal community was not negatively impacted by heavy grazing, but this may not be the case elsewhere, depending on the extent of tree clearing, fire, and other indirect impacts on arboreal habitats. Tree clearing, often associated with grazing, is a major threat to arboreal fauna (Gibbons & Lindenmayer, 2002; Parsons, Kutt, Vanderduys, Perry, & Schwarzkopf, 2017). Indirectly, long-term soil compaction, may suppress new tree growth (Fischer, Lindenmayer, & Cowling, 2004) and grazing can interact with browsing by large native herbivores, resulting in changes to arboreal structure (Ogada, Gadd, Ostfeld, Young, & Keesing, 2008; Pringle, 2008). Fischer et al. (2009) suggest that current grazing management styles are leading to major tree declines. As keystone structures, loss of trees will have major impacts on the distribution and biodiversity across vast regions of the world (Manning, Fischer, & Lindenmayer, 2006). Both dead and living trees, and the accumulation of course woody debris, are prime habitat for diverse animal communities (Whiles & Grubaugh, 1996). Even damaged trees increase structural complexity, and can increase occupancy of arboreal lizards (Pringle, 2008). Unlike other areas used for livestock grazing, the WGT has not been cleared within the last 100 years and therefore has many old, overstory trees. Additionally, fire is not regularly used to suppress woody growth at this location. While open-canopy woodlands such as the WGT have naturally sparse tree cover, the trees that are present support a wide variety of wildlife, especially old trees with hollows and flaking bark (Bryant, Dundas, & Fleming, 2012; Gibbons & Lindenmayer, 2002).

We could only model *G. dubia* and *C. australis* individually, but made observations of other arboreal reptiles on the WGT. For example, *O. castelnaui* and *H. bitorquatus* were found in every grazing treatment and were not linked to vegetation type. Both *O. castelnaui* and *H. bitorquatus* use loose bark and hollows as diurnal refugia and forage on branches and the trunks of trees at night (Fitzgerald, Lazell, & Shine, 2010; Gibbons & Lindenmayer, 2002). Both species appear resistant to the effects of grazing. *Strophurus williamsi* were generally found in the lower strata (on small trees and shrubs) and were not present in either H or V. By using the lower strata, *S. williamsi* may be less tolerant to the impacts of grazing than other arboreal reptiles. In our analyses, we have applied a binary notion of arboreality (either arboreal or terrestrial), but in reality, arboreal species use vertical habitat strata to different extents. In a more diverse arboreal community, it may be beneficial to classify species along an "arboreality gradient" and use this as a predictor of resistance to disturbance. This has been used effectively to predict bird response to livestock grazing (Martin & Possingham, 2005) and the resilience of frogs and lizards to extreme climatic events (Scheffers, Edwards, Diesmos, Williams, & Evans, 2014).

Terrestrial reptile response to grazing

Unlike arboreal reptiles, terrestrial reptiles generally had a negative association with increasing grazing pressure. This relationship was clearly seen in overall abundance, most individual species responses, and at a functional group level. The community compositional differences were complex and subtle, making interpretation of these results difficult on their own. The community analysis is greatly complemented by the assessment of individual species using GLMMs, where we had the benefit of treating year and season as random effects.

As a group, litter skinks performed as typical decreaser species, supporting the results from other Australian grazing studies with similar terrestrial reptile assemblages (James, 2003; Kutt & Woinarski, 2007; Woinarski & Ash, 2002). The litter skinks that were analysed separately mostly showed the same negative response to increased grazing. *Carlia munda* and *M. taeniopleura* were both least abundant in the heavily stocked sites. *Ctenotus robustus* also responded negatively to heavy grazing, in accordance with the response of *Ctenotus* sp. in other grazed locations, and likely due to a reduction of thermal refuges at ground level in heavily grazed areas (Abom & Schwarzkopf, 2016; Hacking, Abom, & Schwarzkopf, 2014).

The response of terrestrial geckos is clearly influenced by the most abundant terrestrial gecko *H. binoei*. While seemingly unaffected by grazing in the Box vegetation type, *H. binoei* was significantly less abundant in H Ironbark. In other vegetation types, *H. binoei* is more abundant in areas of heavy grazing (Woinarski & Ash, 2002), further suggesting this species' response to grazing is greatly influenced by the surrounding vegetation community. Ground-dwelling reptiles often respond to habitat characteristics such as woody debris, leaf litter and fallen logs, which are actually a function of arboreal habitat structure (Fischer et al., 2004). The importance of tree-provided structure to ground features further supports the importance of retaining trees in grazed environments, for both the arboreal and terrestrial fauna.

The terrestrial reptile assemblage at this location was dominated by abundant diurnal skinks susceptible to grazing. At other locations, particularly more arid areas, the terrestrial reptile assemblage often has a higher proportion of increaser species, that prefer more open, less complex ground environments (Germano et al., 2012; Read, 2002; Read & Cunningham, 2010). One agamid species found during the study, *D. nobbi*, would likely prefer open habitats and higher ground temperatures, however, due to low capture numbers we could not detect differences in its abundance among grazing treatments.

Our interpretation of reptile responses to grazing is limited by our knowledge of species' habitat requirements, for thermoregulation, predator avoidance and food. Here, we suggest the negative response of many species to grazing is driven by a loss of microhabitat complexity, but we have not determined the mechanism allowing arboreal groups or species to be resistant. It is likely there are complex indirect mechanisms driving arboreal reptile abundance and it would be beneficial to test these. Reptiles can be affected by changed predator–prey dynamics in grazed environments (e.g. Curry & Hacker, 1990; Knox et al., 2012; Pafilis, Anastasiou, Sagonas, & Valakos, 2013; Pettigrew & Bull, 2014). Most grazing response mechanisms are suggested or assumed, and very few have been experimentally tested or examined in detail (but see Rosi et al., 2009; Villar, Lambin, Evans, Pakeman, & Redpath, 2013). A better understanding of the mechanisms behind individual species' responses may make it possible to predict species responses to grazing. Our results illustrate the importance of examining arboreal and terrestrial community composition separately, and individual species in more detail, rather than focusing on just overall biodiversity measures such as abundance and richness. Species and functional groups often respond to disturbances in different (even opposite) ways (Neilly et al., 2016), thus we highlight the importance of analysing community response data appropriately.

Management implications

Measures of plant and animal resistance and resilience have been successfully used to build risk-based frameworks to guide rangeland management (Chambers et al., 2017). An understanding of the attributes that influence resistance, such as arboreality, can help when devising grazing management strategies. In this case, the recommended grazing strategy for conserving arboreal geckos would be different compared to a grazing strategy aimed at conserving diurnal litter skinks. The varied response of vertebrates to different grazing strategies calls for a nuanced approach to management recommendations (Neilly et al., 2016).

Across the globe, a diversity of biomes support livestock grazing systems and these systems vary in their extent of vertical strata (Asner et al., 2004). Therefore, our findings will be more relevant to rangelands from similar biomes. Diverse arboreal reptile communities may be unique to Australian rangelands, however arboreal reptiles, mammals and birds, are found in rangelands globally (Neilly et al., 2016). Furthermore, trees not only harbor extensive microhabitats for arboreal species, but indirectly provide habitat for terrestrial species (Fischer et al., 2004). It is widely accepted that the retention of trees increases biodiversity and landscape-scale species richness (Benton, Vickery, & Wilson, 2003; Manning et al., 2006). Therefore, one universal management practice to increase or retain arboreal and terrestrial fauna may be to retain standing trees and woody debris. Unlike more intense agricultural land uses (e.g. cropping), rangelands where trees are retained and stocking rates are moderate, are potentially areas where animal production and biodiversity conservation can coexist.

TABLES

Table 3.1. The grazing treatments of the Wambiana Grazing Trial.

Grazing treatment	**Description**	**Reasoning**
Moderate (M)	Stocking rate at the long term carrying capacity (LTCC); 8-10 ha per animal equivalent (AE)	Minimize the risk of over-grazing, maintains land condition
Rotational wet-season spelling (R)	Stocking at 50% above the LTCC and ⅓ of the paddock spelled (no grazing) on a rotation basis during the wet season; 7-10 ha per AE	Spelling can buffer against rainfall variability
Variable (V)	Stocking rate adjusted annually at the end of the wet season in accordance with remaining feed availability; 3-12 ha per AE	Stocking rate to match feed availability, which minimize the risk of over-grazing during dry years, but allows heavier stocking rates during wet years
Heavy (H)	Stocking at twice the LTCC; 4-6 ha per AE	Potentially high profitability, especially during wet years

Table 3.2. Measured micro-habitat characteristics with a description of methodology.

Habitat characteristics	Description
Terrestrial	
Ground cover	A tape measure was laid on the ground along the 100m transect. The amount of bare ground (BG), rock, leaf litter (LL) and leaf litter depth (mm), fine woody debris (<10cm diameter) (FWD), coarse woody debris (>10cm diameter) (CWD) was recorded and converted into a percentage.
Vegetative cover	Along the 100m transect, the amount of grass (and grass height), shrub and other vegetative cover was recorded and converted into a percentage.
Other features	Other ground features were noted along the 100m transect including termite mounds, and burrows.
Arboreal	
Trees	Any tree that fell 1-m either side of the 100m transect was identified and measured for diameter at breast height (DBH) (cm) and height category (m)
Canopy Cover (%)	Estimated canopy cover via spherical densitometer.
Distance to nearest tree (m)	Distance (m) between adjacent trees >2 m tall.
Bark Index (1-3)	An index of bark roughness/flakiness ranging from 1-3; 1 representing little or no flaking bark, and often little no known refuge options for sheltering lizards; 3 represents very flaky and loose bark with ample refuge microhabitats available for sheltering lizards.
Canopy connectivity (%)	The percentage of overstory trees sampled that had overlapping canopy or branches.
Tree hollows (%)	The percentage of overstory trees sampled that had hollows or cavities visible from the ground.

Table 3.3. The relationship between reptile abundance and species richness and grazing treatment and vegetation type (fixed effects) and season and year (random effects) as described by a generalized linear mixed model (GLMM) with negative binomial distribution. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (p<0.05) are reported.

Response Variable	Model	df	Log Likelihood	AIC	ΔAICc	AICc weight	Post hoc test
Terrestrial Reptile Abundance	Grazing + Vegetation	8	-262.837	543.3	0.00	0.521	<u>Grazing</u> Moderate > Heavy Rotational > Heavy Variable > Heavy <u>Vegetation</u> Box > Ironbark
	Grazing*Vegetation	11	-259.424	544.0	0.66	0.374	<u>Grazing * Vegetation</u> Moderate Box > Heavy Box Moderate Box > Heavy Ironbark Rotational Box > Heavy Ironbark Variable Box > Heavy Ironbark Moderate Ironbark > Heavy Ironbark Rotational Ironbark > Heavy Ironbark
	Grazing	7	-265.634	546.5	3.21	0.105	As above
Terrestrial Reptile Richness	~Vegetation	5	-168.561	347.8	0.00	0.252	Not significant
	~1 (null model)	4	-169.737	347.9	0.12	0.237	
	Grazing	7	-166.359	348.0	0.20	0.228	
Arboreal Reptile Abundance	Grazing + Vegetation	8	-214.477	446.6	0.00	0.856	<u>Grazing</u> Heavy > Moderate Variable > Moderate <u>Vegetation</u>

							Ironbark > Box
	Vegetation	5	-220.585	451.8	5.23	0.063	As above
	Grazing * Vegetation	11	-213.398	451.9	5.33	0.060	Not significant
Arboreal Reptile Richness	~1 (null model)	4	-100.222	208.9	0.00	0.669	Not significant
	Vegetation	5	-100.042	210.8	1.87	0.263	
	Grazing	7	-99.406	214.1	5.20	0.050	

Table 3.4. The ManyGLM analysis showing the relationship between reptile assemblages (arboreal and terrestrial) and grazing treatment, vegetation type and season (and their interactions) for 2014 and 2015. The p-values of the variables in the optimal model are given, first for the multivariate community analysis, and then broken down by individual species contribution. *C. mund = Carlia munda; M. grey = Menetia greyii; M. taen = Morethia taeniopleura; C. robu = Ctenotus robustus; D. nobb = Diporiphora nobbi; H. bino = Heteronotia binoei; L. stein = Lucasium steindachneri; D. platy = Diplodactylus platyurus; G. dubi = Gehyra dubia; S. will = Strophurus williamsi; O. cast = Oedura castelnaui; H. bito = Hoplocephalus bitorquatus.*

Terrestrial Reptile Community			Individual Species Contributions (P value)							
	Optimal Model	Community (P value)	*C. mund*	*M. grey*	*M. taen*	*C. robu*	*D. nobb*	*H. bino*	*L. stein*	*D. plat*
2014	Grazing *Vegetation	<0.01	0.38	0.05	0.54	0.01	0.05	0.07	0.79	0.52
	Season	<0.01	0.06	0.06	0.06	<0.01	0.06	0.14	0.14	0.31
2015	Grazing *Vegetation	0.02	0.31	0.65	0.6	0.24	0.27	<0.01	0.15	0.91
	Season	<0.01	<0.01	0.01	<0.01	0.04	0.34	0.19	0.25	0.58

Arboreal Reptile Community			Individual Species contribution (P value)			
	Optimal Model	Community (P value)	*G. dubi*	*S. will*	*O. cast*	*H. bito*
2014	Season	<0.01	0.01	1.00	1.00	0.11
2015	Vegetation	<0.01	<0.01	0.23	0.68	1.00

Table 3.5. The response of reptile species and functional groups to habitat variables using generalised linear mixed models (GLMM) and generalised linear models (GLM). '+' indicates a positive association and '-', a negative association. GLMM distributions are indicated (P = poisson, NB = negative binomial). All GLM models use a negative binomial distribution. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (P<0.05) are reported.

	Landscape Scale Full Model: GLMM				**Microhabitat Scale** Full Model: GLM	
Terrestrial Species	Grazing * Vegetation + (1|Year) + (1|Season)				Grass + Grass height + FWD + CWD + Carissa ovata + LL<5mm + LL>5mm + TM + BG + CanopyCover	
	Terms in optimal model	**Distribution**	**P value**	**Post Hoc**	**Terms in optimal model**	**P value**
Carlia munda	Grazing	NB	0.03	M>H	Carissa ovata (-)	0.02
				V>H	BG (-)	<0.01
Heternotia binoei	Grazing * Vegetation	P	<0.01	MB>HI MB>MI RB>HI VI>HI VI>MI	FWD (+) Carissa ovata (+)	<0.01 <0.01
Morethia taeniopleura	Grazing	NB	0.02	M>H	Carissa ovata (+)	<0.01
	Vegetation		<0.01	B>I	BG (-) Grass (+)	0.02 <0.01
Ctenotus robustus	Grazing * Vegetation	P	0.01	VB>HB	Grass (+)	<0.01

Menetia greyii	Vegetation	P	0.08	Not significant	TM (+)	0.11
Litter skinks	Grazing	NB	<0.01	M>H V>H	BG (-) Grass (+)	<0.01 <0.01
Terrestrial Geckos	Grazing * Vegetation	NB	<0.01	MB>HI RB>HI VI>HI	FWD (+) Carissa ovata (+)	<0.01 <0.01
	Landscape Scale Full Model: GLMM				**Microhabitat Scale** Full Model: GLM	
Arboreal Species	Grazing * Vegetation + (1|Year) + (1|Season)				MeanDist.NearTree + Mean Bark Index + Hollows + Canopy Connectivity + Trees dead + Trees <5cm DBH + Trees 5-10 cm DBH + Trees 10-20cm DBH + Trees 20-30cm DBH + Trees >30cm DBH + Canopy Cover	
Gehyra dubia	Grazing	NB	<0.01	H>M V>M	Trees 5-10cm DBH (-)	0.01
	Vegetation		<0.01	I>B		
Cryptoblepharus australis	Vegetation	NB	<0.01	I>B	Trees 10-20cm DBH (-) Mean bark index (+)	<0.01 0.05
Arboreal geckos	Grazing	NB	<0.01	H>M V>M	Trees 5-10cm DBH (-)	0.02
	Vegetation		<0.01	I>B	Hollows (+)	0.06

FIGURES

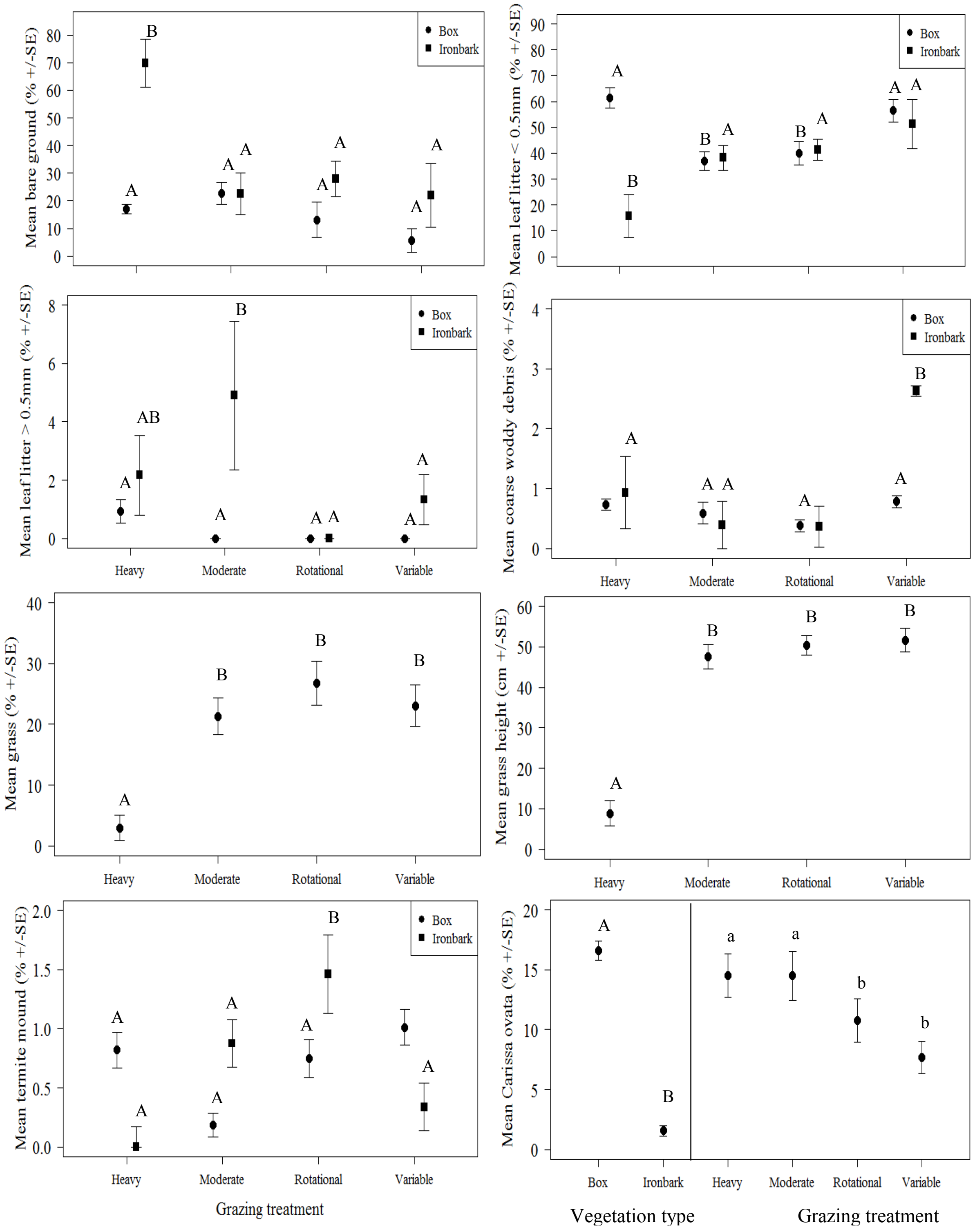

Figure 3.1. Mean ± SE measures of terrestrial habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; α = 0.05).

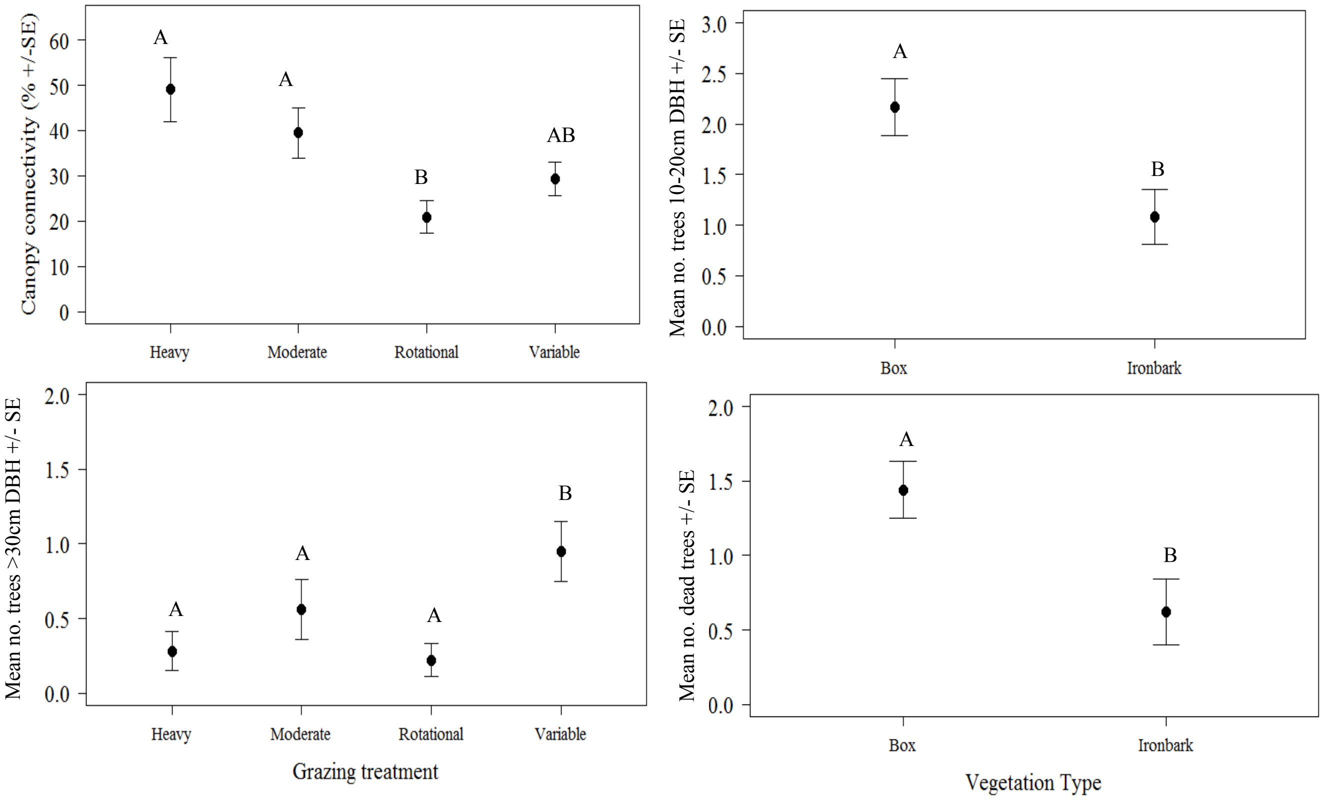

Figure 3.2. Mean ± SE measures of arboreal habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; α = 0.05).

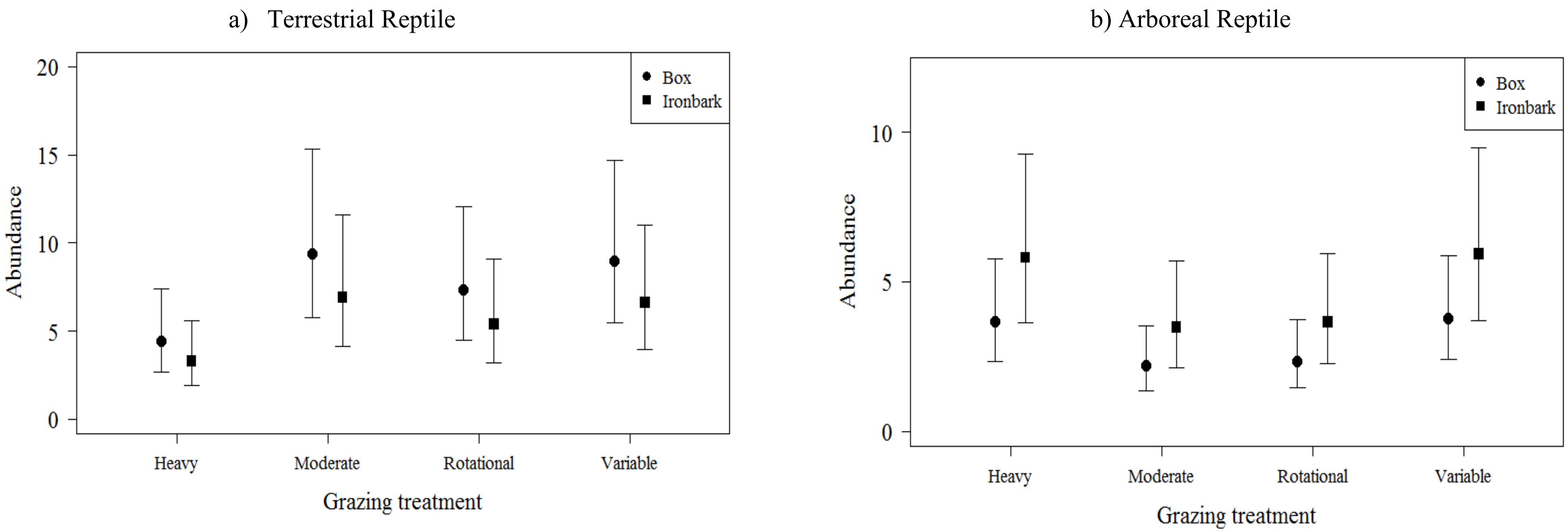

Figure 3.3. The mean fitted values with 95% confidence intervals of the negative binomial GLMMs for: a) Terrestrial Reptile Abundance ~ Grazing + Vegetation, and b) Arboreal Reptile Abundance ~ Grazing + Vegetation.

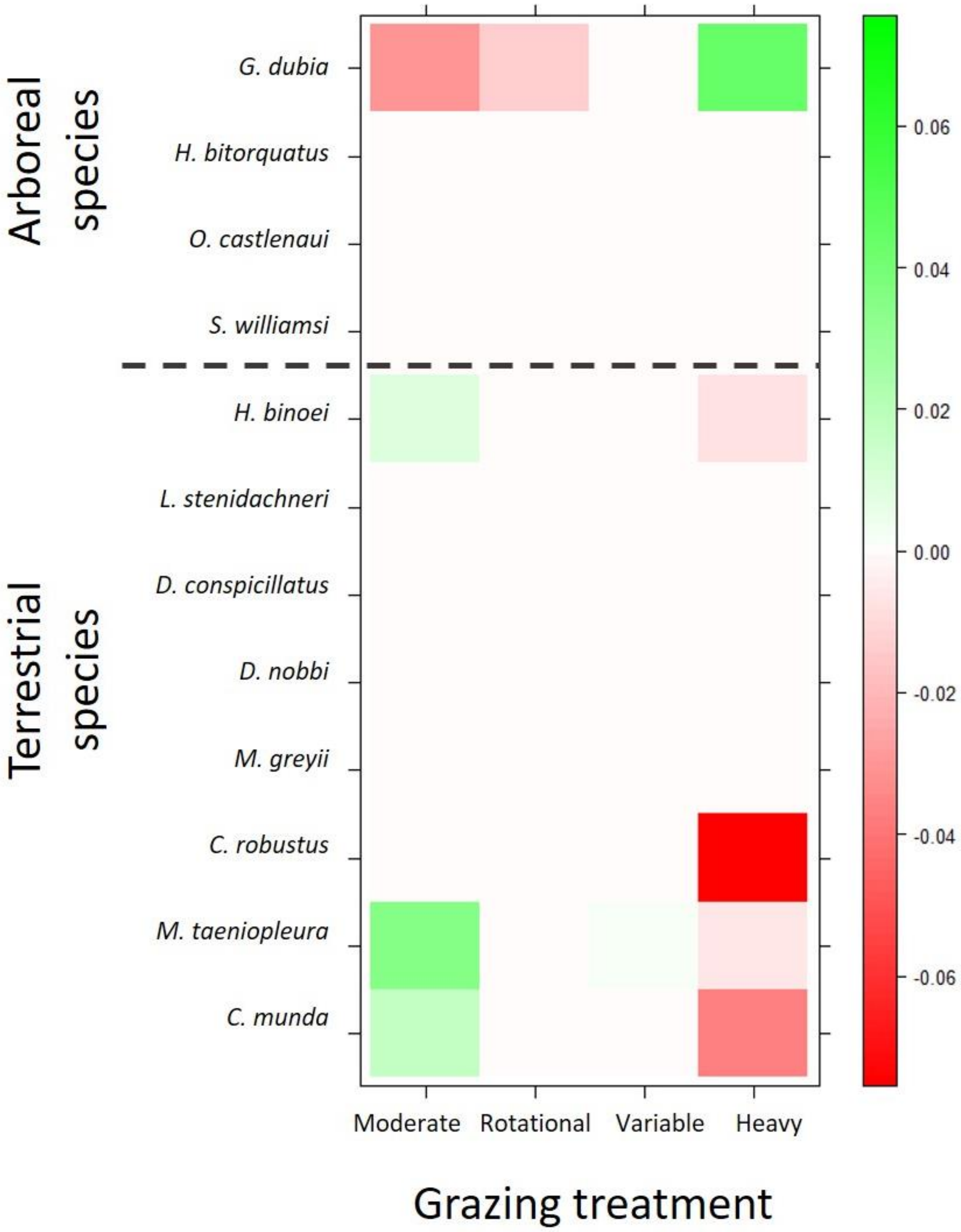

Figure 3.4. The response of arboreal and terrestrial reptile communities to grazing, as visualised using the standardised model coefficients from a generalised linear model-LASOO model. Terms which do not explain any variation in species response are set to zero. The stronger the association, the brighter the square, positive associations are in green and negative associations are in red.

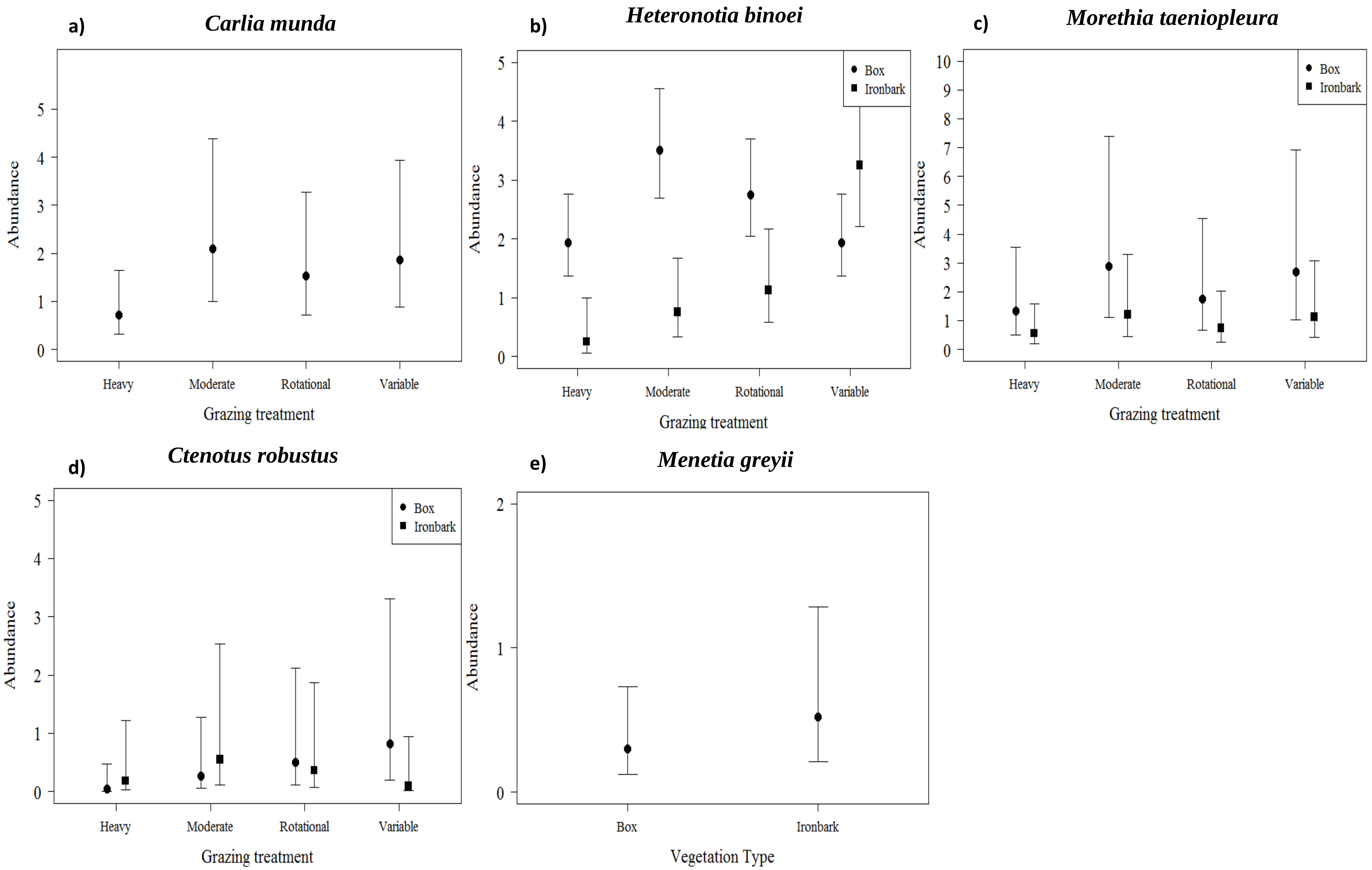

Figure 3.5. Fitted values with 95% confidence intervals for the optimal terrestrial reptile species and functional group models.

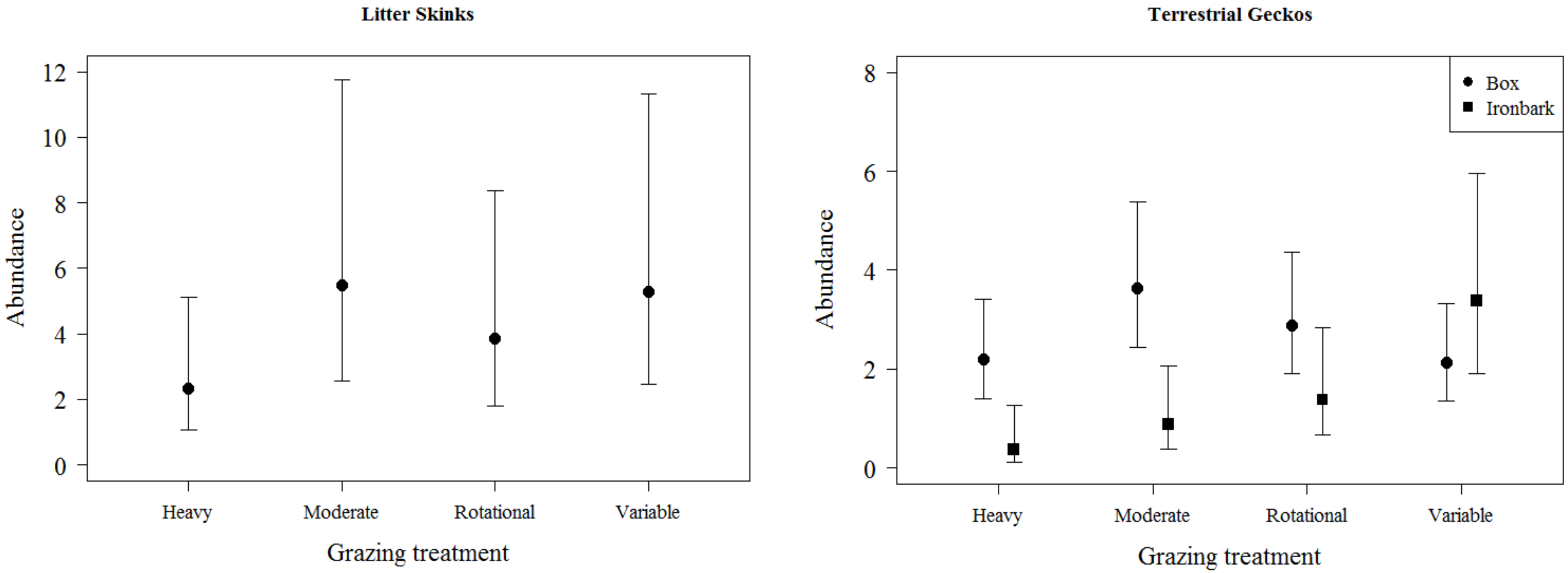

Figure 3.5 (continued). Fitted values with 95% confidence intervals for the optimal terrestrial reptile species and functional group models.

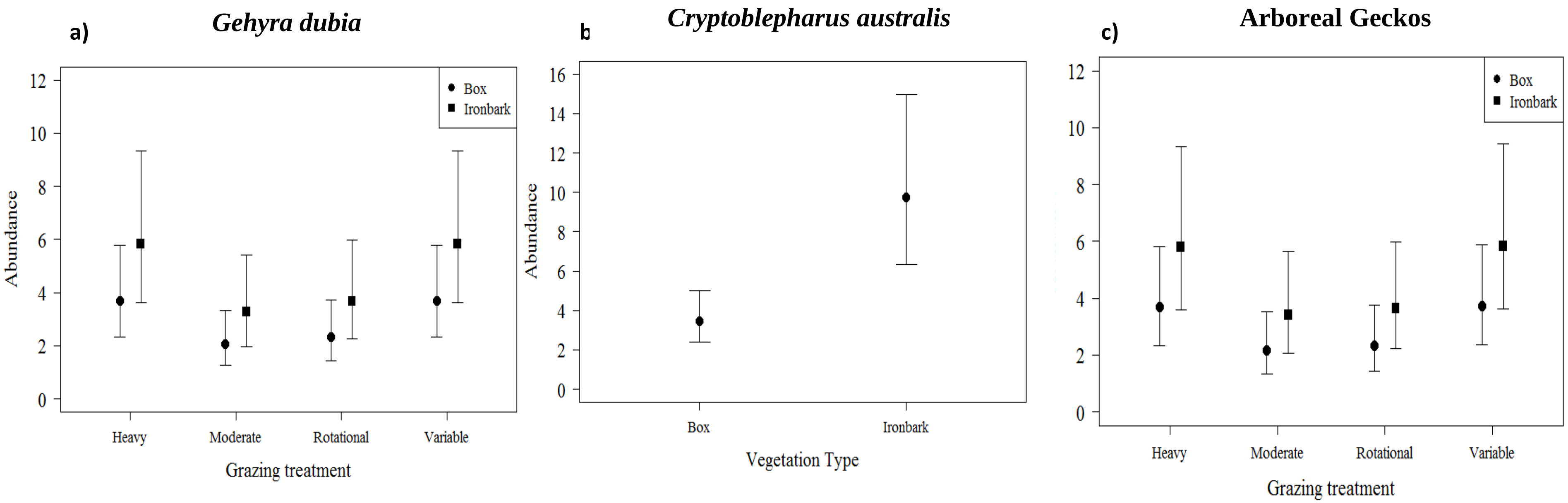

Figure 3.6. Fitted values with 95% confidence intervals for the optimal arboreal reptile species and functional group models.

Chapter 4 – Abundance, Diet, and Prey Selection of Arboreal Lizards in a Grazed Tropical Woodland

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ABSTRACT

The diet of predators is a critical determinant of their ecological effects. Small vertebrate predators of invertebrates are often characterized as diet generalists based on diet descriptions, but few studies examine prey availability to determine whether prey choice occurs. We studied the prey availability in relation to the diet of two common and abundant, but understudied small vertebrates: *Gehyra dubia*, an arboreal nocturnal gecko, and *Cryptoblepharus australis*, an arboreal diurnal skink. We sampled lizards in two major woodland habitat types, Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*) and among four cattle grazing regimes (ranging from moderate – heavy stocking). *Cryptoblepharus australis* were more abundant in the Silver-leaf ironbark habitat, but there was no effect of grazing regime on their abundance. In contrast, *G. dubia* did not differ significantly in abundance in relation to habitat type, but were more abundant in paddocks with heavier stocking rates. We quantified invertebrate prey available to lizards in these habitats using defined area searches and light trapping. Invertebrate community composition did not differ significantly between the habitat types or among the four grazing regimes. Although *G. dubia* and *C. australis* both occupied the same microhabitats, they were temporally segregated based on their activity times. While both species are apparently habitat generalists, we found that *G. dubia* and *C. australis* are selective in their diets. Only half of the invertebrate groups available in the environment occurred in the diets of either lizard species. Both species positively selected Coleoptera (beetles), Araneae (spiders), and Scorpiones (scorpions), and they exhibited high dietary niche overlap (O = 0.97). We suggest the increased availability of the top three preferred prey groups (beetles, spiders, and scorpions) may contribute to the high abundances of *G. dubia* in heavily grazed areas.

KEYWORDS

Arthropods, Australia, electivity, feeding ecology, reptiles.

INTRODUCTION

Knowing the diet, foraging mode, and prey choice of predators are fundamental to understanding their effects on the ecology, behaviour, and distributions of prey among ecosystems (Johnson 1980; Dayton 2003). For example, generalist predators may stabilise ecosystem dynamics, whereas specialists may drive prey cycles or cause extinction of their prey (e.g., Turchin 2003). However, the nature of predation by many small vertebrate predators is often poorly known (Manicom 2010), even though the biomass of such species may be high, and their ecological effects are likely large.

Lizards are excellent model organisms with which to quantify the nature of predation by small vertebrates, as they are important predators of a wide variety of invertebrates. Insectivorous lizards make interesting model organisms to study prey selection because in many environments, invertebrate abundance and richness are high, providing an opportunity for selective foraging (Stamps & Tanaka 1981; Manicom & Schwarzkopf 2011). Although many studies describe diet (Bustard 1968; Floyd & Jenssen 1983; Sales & Freire 2015), few estimate prey availability as well (Dubas & Bull 1991; Griffiths & Christian 1995; Manicom & Schwarzkopf 2011; Lisboa *et al.* 2012). To estimate prey selectivity, a description of the diet must be compared with some measure of prey availability (Diaz & Carrascal 1990).

The majority of studies of the diet and feeding strategies of Australian lizards describe terrestrial or leaf litter species (e.g. Pianka 1969, Crome 1981; Brown 1986, 1988; James 1991; Abensperg-Traun & Steven 1997; Manicom & Schwarzkopf 2011). Although the diversity of Australian arboreal lizards is high, few studies have examined diet with the exception of some varanid lizards (Pianka 1971, 1982, 1994; Shine 1986; Weavers 1989; Thompson *et al*. 1999) and frill-neck lizards (*Chlamydosaurus kingii*, Shine & Lambeck 1989; Griffiths & Christian 1995). Australia’s native house gecko (*Gehyra dubia*), belonging to a group of geckos called “dtellas”, and the inland snake-eyed skink (*Cryptoblepharus australis*) are wide-spread lizard species that occur in eastern Australia (Cogger 2014; Wilson 2015; Figure 4.1). Both are small arboreal lizards commonly found in open eucalypt woodlands, on the trunks of trees, on logs, and in hollows. Surprisingly little is known about either species’ diet although they are abundant and common throughout their range. In fact, little is known about their ecology and natural history altogether. A few natural history studies of the related tree dtella (*Gehyra variegata*) describe their general ecology, including growth, reproduction, and activity cycles (Bustard 1967, 1968), population ecology (Bustard 1969), and movement patterns (Gruber & Henle 2004, 2008) but do not estimate food availability or describe diet and prey selection (but see Henle 1990). These remain some of the only ecological studies on dtella geckos. Further, while only few genera of skinks in Australia contain more species than *Cryptoblepharus*, little is known about their natural history, ecology, and behaviour. To our knowledge, there are no diet studies of *Cryptoblepharus australis* or other *Cryptoblepharus* species.

The primary objective of this study was to test for dietary niche overlap of two co-occurring arboreal lizards (*Cryptoblepharus australis* and *Gehyra dubia*) in relation to the arboreal invertebrate communities available as prey in a grazed tropical woodland. We quantified the diet of two arboreal, ecologically similar lizards, to test for differences in prey availability, diet, prey selectivity, prey diversity in the diet, and niche overlap among various factors including habitat type, grazing regime, age class, and sex.

METHODS

Study site

This study was conducted on the Wambiana Grazing Trial (WGT), a subset of the Wambiana Cattle Station, approximately 70 kms southwest of Charters Towers, Queensland, Australia. Since 1997, it has been the location of a large-scale experiment examining the effects of grazing regimes on cattle production and vegetation. This study used eight 100 ha paddocks on the WGT with four replicated grazing regimes (2 replicates of each): Heavy Stocking Rate (HSR), Moderate Stocking Rate (MSR), Rotational Stocking Rate (ROT), and Variable Stocking Rate (VAR) (Appendix 4.S1, Table 4.S1; O'Reagain *et al*. 2011). Each paddock contains equal proportions of two major habitat types: two thirds is dominated by Reid River box woodland (*Eucalyptus brownii*) and the remaining third is dominated by Silver-leaf ironbark woodland (*Eucalyptus melanophloia*). Each paddock (1 replicate of a grazing treatment) contained three sampling sites, two sites in the Reid River box habitat, and one in the Silver-leaf ironbark habitat; a total of 24 sites, six per grazing treatment. We sampled arboreal lizards and invertebrate communities within both habitat types in four grazing treatments over the course of seven days in February 2015.

Lizard sampling

The two lizard species were sampled using arboreal cover board surveys (50 x 50 x 1.0 cm; PolyTuf expanded foam boards, Mayo Hardware Ltd., Moorebank, NSW, Australia) and visual encounter surveys via spotlighting (for details on methodology see Nordberg & Schwarzkopf 2015). Arboreal cover boards were strapped to the main trunks of trees to provide artificial bark shelter retreats for diurnal skinks (*Cryptoblepharus australis*) and nocturnal geckos (*Gehyra dubia)* (Nordberg & Schwarzkopf 2015). All captured lizards were individually marked using coloured injectable elastomer tags prior to release at their capture sites for an ongoing mark-recapture study (Nordberg unpublished data).

Invertebrate sampling

Invertebrates were sampled using several techniques: manual collection using an aspirator or forceps, and attraction and collection using a light trap. We sampled a total of 30 trees per grazing treatment, once during the day to collect diurnal invertebrates, and once at night to collect nocturnal invertebrates. Aspirator and manual searches targeted 10 randomly selected trees at each site at which we conducted a defined-area search. During visual searches we collected invertebrates on the outside of the tree bark from 0 – 2 m from ground level. To sample invertebrates that may use microhabitats under bark or within cracks or fissures, we removed the 'artificial bark' cover boards and collected invertebrates using the aspirator or forceps. We used a light trap lure stationed at the centre of each site to sample flying invertebrates. We constructed a light trap lure by placing plain white paper on the lid of a plastic storage bin (65 x 42 cm [L x W]) and hanging it vertically on a post with a torch shining in the centre of the paper. As flying invertebrates were attracted to the light lure, we used an aspirator to collect small flying invertebrates and forceps to collect larger flying invertebrates (e.g., moths). All captured invertebrates were placed in 80% ethanol to be sorted in the lab for identification. We identified invertebrates by placing them into groups of the lowest taxonomic level possible.

Lizard diet

As part of an on-going mark-recapture study, lizard faecal samples were collected from G*ehyra dubia* and *Cryptoblepharus australis* captured by hand (Nordberg unpublished data). All faecal samples were placed in 2 ml vials and preserved with 80% ethanol. They were later examined under a dissecting microscope to identify the remains of food items. Invertebrate remains were identified to the lowest possible taxonomic level.

Invertebrate availability and lizard diet

To ensure that we did not include invertebrates too large to be considered 'available' prey items, we only included invertebrates with total body length or width less than or equal to the maximum jaw width of each lizard species (*G. dubia* = 19 mm and *C. australis* = 7 mm). Prey items we included if at least one dimension (length or width) was less than or equal to maximum jaw width for each lizard species because lizards are capable of swallowing large prey (e.g., long but narrow), but are often limited by head size or jaw width (Vitt & Pianka 2007). To describe invertebrate communities, we first combined taxonomic groups by the lowest common taxonomic group into which all the invertebrates could be identified (i.e., Order). We describe prey species richness overall, as well as broken down by habitat types and among the four grazing regimes. Prey availability was calculated for each lizard species separately due to variation in the appropriate size of prey items, as well as differences in the available prey assemblages during the day (for *C. australis*) and night (for *G. dubia*).

We calculated the niche breadth (Eq. 1; Levins 1978), niche overlap (Eq. 2; Pianka 1973), and species diversity in the diet (Eq. 3; Shannon & Weaver 1949) for both *C. australis* and *G. dubia* as a measure of resource use and similarity between species.

Niche breadth (*B*; Eq. 1) is a measure or range of resources an organism uses, often used to indicate the specialization of a species in a given environment (Levins 1968). A large niche breadth (*B*) indicates a generalist feeder that uses a wide variety of the available resources, whereas a small niche breadth indicates a species specializing on a small subset of resources. Niche breadth is calculated from the proportion (*P*) of individuals utilizing the resource (*i*). An adjusted *B* value (B_{adj}) is often used, created by standardizing the niche breadth to a value from 0 – 1 (Hurlbert 1978).

Pianka's measure of niche overlap (*O*; Eq. 2) indicates the amount of overlap or similarity in resources used between species (Pianka 1973). This measure is calculated using the proportion that resource *i* is of the total resource used by species *j* (P_{ij}), and the proportion that resource *i* is of the total resource used by species *k* (P_{ik}). This value can range from 0 – 1, where 0 indicates no resources in common and 1 indicates a total overlap of resources.

We used the Shannon's Diversity Index to represent the species diversity found in the environment (food availability) as well as species diversity in the diet of both *G. dubia* and *C. australis*. This gave us an additional indication as to the diet selectivity of these lizards. Shannon's Diversity Index (H'; Eq. 3) accounts for both abundance and evenness of all species, where *S* is the total number of species encountered and p_i is the proportion of species *i* compared to the total number of species (Shannon & Weaver 1949). Higher values of H' indicate a more diverse community.

Prey selection

We used the Jacobs' Selectivity Index to identify any resource selection preferences, in our case, food or dietary preference (Eq. 4; Jacobs 1974). The Jacobs' selectivity index (*D*) compares the frequency of a resource (i.e., a group of invertebrates found in the diet) and the frequency of that resource available in the environment; where *r* = the proportion of prey items from a specific taxon found in the faecal samples, and *p* = the proportion of prey items from the same taxon found in the environment (Jacobs, 1974). The *D* index ranges from -1 to +1, where -1 indicates complete avoidance; 0 indicates that selection is random; and +1 indicates an extreme preference. This index allowed us to compare patterns in prey selection as ranks, in which negative values indicate prey items that are generally not eaten or avoided, values near 0 represent prey items that are consumed with the same frequency as their availability in the environment, and positive values represent high preference prey items.

Data analysis

We tested for differences in invertebrate prey composition among grazing treatments and between habitat types for invertebrate prey in the environment (prey availability) as well as in the diet of lizards. We used permutational multivariate analysis of variance (PERMANOVA; 'vegan' package in R; Oksanen *et al*. 2017) to test for differences in the composition of invertebrate prey using the proportion of invertebrates in each taxon as the response vector, grazing treatment, habitat type, and their interaction as fixed effects, and site as a stratum, to account for the fact that both habitats occurred within each grazing treatment plot. We compared the mean number of taxa as well as mean number of prey items present in the diet among the four grazing treatments (Kruskal-Wallis test), age classes (*G. dubia*: male, female, and juvenile, Kruskal-Wallis test; *C. australis*: male and female only, Wilcoxon-Mann-Whitney U-test), and two habitat types (WMW U-test). Lizard abundance was compared using a nested two-factor ANOVA with habitat type nested within grazing treatment, and both as fixed effects. All analyses were completed in the statistical program R (R Core team 2016).

RESULTS

Lizard sampling

We captured 103 *Cryptoblepharus australis* and 203 *Gehyra dubia* from 48 person-hours of spotlighting and flipping 1152 arboreal cover boards (Table 4.1). The abundance of *Cryptoblepharus australis* did not differ significantly among the grazing regimes ($F_{3,19} = 0.439$, $P = 0.727$) but they were significantly more abundant in the ironbark habitat ($F_{1,19}$ = 8.402, P = 0.009; Figure 4.2). *Gehyra dubia* were significantly more abundant in the HSR and VAR paddocks, areas with higher stocking rates, ($F_{3,19}$ = 7.158, P = 0.002) while there were no significant effects of habitat type on *Gehyra* abundance ($F_{1,19}$ = 1.364, P = 0.257; Figure 4.2).

Invertebrate prey availability

We sampled 240 trees and identified 1029 invertebrates from 17 orders (Table 4.2). We found no significant differences in the composition of the invertebrate prey community between the box and ironbark habitat types (*C. australis*: $F_{1,15}$ = 0.642, P = 0.632; *G. dubia*: $F_{1,15}$ = 0.795, P = 0.617), or among the four grazing regimes (*C. australis*: $F_{3,15}$ = 0.999, P = 0.625; *G. dubia*: $F_{3,15}$ = 1.197, P = 0.562) for either lizard species. Furthermore, principal component analysis also indicated minimal separation among the habitats and grazing regimes for available prey groups of both *C. australis* and *G. dubia* (Appendix 4.S1, Figure 4.S1). We encountered high numbers of flying Isopterans (termite swarm during emergence) on one night of our invertebrate sampling in the ROT grazing regime in Silver-leaf ironbark habitat. This termite emergence event was short and lasted two hours. This undoubtedly biased our estimated invertebrate composition in towards isopterans in that grazing regime and habitat type, and inflated the variance of invertebrate assemblage compositions among habitat types, as we did not experience a termite flight event at any other site. However, the composition of invertebrate assemblages did not differ significantly among the grazing treatments and habitat types even when we removed these data.

Diet and prey preference of Cryptoblepharus australis

We examined the diet of *C. australis* by collecting faecal samples (n = 40) from captured lizards. We found nine of the 18 available orders of invertebrates in the faecal samples. The adjusted diet breadth of *C. australis* was fairly narrow (B_{adj} = 0.39), with only three orders making up approximately 80% of the invertebrates in the diet (Coleoptera = 41.9%; Hymenoptera = 19.4%; Hemiptera = 16.1%). Coleopterans (D = 0.8) followed by Scorpiones (D = 0.5), and Aranidae (D = 0.3) were the most highly preferred prey groups for *C. australis*.

Prey preference was similar between male and female *C. australis*, with high niche overlap (*O* = 0.94). Males showed a preference for Lepidoptera (*D* = 0.2), which were not preferred by females, while females showed a preference for Diptera (*D* = 0.4). Males and females had similar prey diversity in their diet ($H'_{♂}$ = 1.54, $H'_{♀}$ = 1.42; Table 4.3).

In the box habitat, *C. australis* preferred Coleoptera (*D* = 0.8) and Araneae (*D* = 0.2), and had lower prey diversity in their diet (*H′* = 1.25). However, in the ironbark habitat, skinks preferred a more diverse group of prey items (*H′* = 2.06) including Coleoptera (*D* = 0.8), Scorpiones (*D* = 0.7), Aranea (*D* = 0.2), Lepidoptera (*D* = 0.2), and Diptera (*D* = 0.1). We found no difference between the habitat type, among grazing regimes, or between male and female skinks in the mean number of taxonomic groups or number of prey items consumed, (Table 4.4). The diets of *C. australis* in the box habitat overlapped strongly (*O* = 0.93) with those in the ironbark habitat. Overall, the proportions of invertebrates in the diet did not differ significantly among habitat types ($F_{1,15}$ = 2.031, *P* = 0.257) or grazing regimes ($F_{3,15}$ = 1.491, *P* = 0.125). Among the grazing treatments, *C. australis* always showed a high preference for Coleoptera while all its preferences for other groups fluctuated among grazing regimes (Figure 4.3).

Diet and prey preference of Gehyra dubia

We examined the diet of *Gehyra dubia* by examining faecal samples (n = 59) from captured lizards. We found nine of the 18 invertebrate orders available in the environment in faecal samples from *G. dubia*. Similar to *C. australis*, approximately 80% of the food items came from four families (Colepotera = 31.4%; Hymenoptera = 27.6%; Lepidoptera = 11.4%; and Araneae = 10.5%). *Gehyra dubia* showed a positive prey preference for Aranea (*D* = 0.6), Coleoptera (*D* = 0.6), Scorpiones (*D* = 0.4), and Lepidoptera (*D* = 0.2).

Male and female *G. dubia* showed similar prey preferences (with high niche overlap; *O* = 0.92) and diversities ($H'_{♂}$ = 1.73, $H'_{♀}$ = 1.73; Table 4.3); female *G. dubia* also showed a preference for Scorpiones (*D* = 0.7) not shown by males. Juvenile geckos, like adults, preferred Coleoptera (*D* = 0.5) and Aranea (*D* = 0.5), but also preferred Hymenoptera (*D* = 0.4). There was less prey diversity in the diet of juveniles

(H' = 1.50) and lower niche overlap between juveniles and adult males (O = 0.87) and juveniles and adult females (O = 0.71) that there was between the sexes of adults.

In the box habitat, *G. dubia* selected Coleoptera (D = 0.5), Aranea (D = 0.4), and Lepidoptera (D = 0.3). *Gehyra dubia* in the ironbark habitat selected a variety of taxa including Coleoptera (D = 0.9), Aranea (D = 0.8), Hymenoptera (D = 0.3), Lepidoptera (D =0.3), Hemiptera (D = 0.2), Orthoptera (D = 0.2), and Diptera (D = 0.1). While prey preferences differed between the two habitat types, invertebrate diversity in the diet was similar (H'_{box} = 1.65; H'_{ironbark} = 1.70). Overall, the diets of *G. dubia* in the box and ironbark habitats overlapped strongly (O = 0.92). We found no differences between the habitat types, among grazing regimes, or among the age/sex classes in the number of prey taxonomic groups or number of prey items in the diet (Table 4.3). The proportions of invertebrates in the diet did not differ significantly among habitat types ($F_{1,15}$ = 1.594, P = 0.273) or grazing regimes ($F_{3,15}$ = 0.857, P = 0.625). *Gehyra dubia* always showed high selective preference for Araneae and Coleoptera in all grazing treatments, while their preferences for other taxonomic groups differed (Figure 4.3).

DISCUSSION

Many small lizards are considered diet generalists, thought to consume prey items at the frequency of occurrence (e.g., Pianka & Pianka 1976), although some species are specialists, selecting one or a small group of prey (Pianka & Parker 1975; Pianka & Pianka 1970). The generalization that most small lizards are generalist feeders is likely due to relatively small number of dietary studies completed on small lizards compared to their diversity (but see Bustard 1968; Pianka & Pianka 1970; Pianka & Parker 1975; Pianka & Pianka 1976; Henle 1990; Brown 1991).

To identify the diet of an organism, dissection of stomach contents (Shine 1977), stomach flushing (Legler & Sullivan 1979) or faecal dissection (McKnight *et al.* 2015) are relatively instant and inexpensive methods for determining diet. However, each technique has pros and cons: examining stomach contents generally require sacrificed animals or museum specimens; stomach flushing can be harmful to the animal if not done properly; and faecal dissection results can be bias towards organisms with durable exoskeletons, bones, and body parts that remain intact after digestion (Rabinowitz & Tuttle 1982). We note a lack of soft-bodied invertebrates that appeared in the diets of both our lizard species. This may be due to both lizard species not eating many soft-bodied invertebrates, but more likely because soft-bodied prey items would likely be fully (or near fully) digested and broken down during digestion (Floyd & Jenssen 1983). We acknowledge that by quantifying diet via faecal dissection, our results may be biased towards hard-bodied invertebrate prey items. Although faecal dissection may have its limitations detecting particular prey items, it is much less intrusive than stomach flushing or sacrificing the animal to look at stomach contents from dissection, and most invertebrates leave some hard parts if faecal dissection is thorough (e.g., caterpillars have legs, moths have wing scales, etc). New alternatives continue to be developed, including genetic techniques such as next generation sequencing of genetic material found in faecal samples (Pompanon *et al*. 2012; Vesterinen *et al*. 2013; Sint *et al*. 2015). However, even genetic analyses have their drawbacks. DNA extraction provides mostly presence-absence information, and while it may be able to identify prey items of soft-bodied prey that break down throughout digestion, it relies on previous identification of DNA sequences in databases, and it, at present, cannot identify counts or quantities of prey items found in faecal samples, unlike manual sorting.

Our study indicates that both *G. dubia* and *C. australis*, rather than being generalist predators of invertebrates, prefer specific prey. Both species have moderately narrow diet breadths and show specific preferences for certain taxonomic groups of prey, which they select while avoiding others available in the environment. We found striking similarities in prey preference and diet composition between *C. australis* and *G. dubia*; both select Coleoptera, Araneae, and Scorpiones over many other possible prey. Beetles, ants, whip scorpions and spiders were selected by both species, but skinks most preferred beetles whereas geckos mostly preferred spiders. There were few effects of grazing treatment or habitat type on available prey or on prey choice. Sex and life stage also had few effects on diet, with diets of different groups typically overlapping strongly in both skinks and geckos.

While *C. australis* and *G. dubia* share remarkably similar diets and prey selectivity, their activity patterns rarely overlap, due to temporal differences in their activity times. *Cryptoblepharus australis* is an arboreal diurnal skink, active throughout the day, while *G. dubia* is a nocturnal arboreal gecko actively foraging at night (Cogger 2014). Although these species use the same habitat, separated by time, we have observed *G. dubia* basking in early morning sunlight, adjacent to diurnal refugia; and similarly, *C. australis* foraging (presumably) at night (EN pers. obs). While these observations were rare, *G. dubia* and *C. australis* may directly compete for food or shelter. Similar in size, habitat use, and geographic distribution, both lizards show selectivity in their prey choice and represent a feeding strategy closer to specialist or selective forager than generalists.

Although *Gehyra dubia* is a common and widespread gecko, to our knowledge there are no other studies on their diet or feeding ecology. While this makes comparisons with different localities or from other research groups difficult, a few studies exist on the closely related species *G. variegata* from New South Wales (Bustard 1968; Henle 1990) and Western Australia (Pianka & Pianka 1976), as well as on other medium-sized arboreal geckos (Pianka & Pianka 1976). Interestingly, the diet of *G. variegata* from Western Australia appears more broad (prey items from 16 prey groups; Pianka & Pianka 1976) than in populations in New South Wales (prey from seven prey groups; Bustard 1968). These differences could stem from differences in sample sizes and collection duration or timing. For example, Bustard (1968) in New South Wales presents data from 105 individuals from June 1963 – March 1965, whereas Pianka & Pianka (1976) in Western Australia present data from 287 individuals from October 1966 – January 1968. We found *G. dubia* have narrow prey preference (9 of 18 available groups, from 59 individuals) in northeast Queensland, and showed high prey selectivity for beetles and spiders, similar to *G. variegata* (Bustard 1968; Henle 1990). Prey preference likely changes geographically and throughout the year when there are boom and bust periods of particular prey groups. Termites play an important role in the diets of many species, not only termite-specialists such as *Diplodactylus conspicillatus*, *D. pulcher*, or *Rhynchoedura ornata* (Pianka & Pianka 1976), but also other insectivores, because termite abundance dominates the landscape during emergence flights. We found no termites in the diet of *G. dubia*, even though there were termite swarms on one night of our sampling.

Possibly, the digestion and passage time of termites was longer than our study period (our study concluded two days after the termite swarms).

The diet breadth of both *C. australis* and *G. dubia* only encompassed about half of the invertebrate orders that are available in the environment. True generalist species would have consumed prey items at their available frequency. This is not the case with either *C. australis* or *G. dubia*. While each species did consume a few prey groups apparently at random (*C. australis*: Dipetera and Lepidoptera; *G. dubia*: Diptera and Hymenoptera), both species had strong preferences for and avoidance of particular prey types. Moreover, their prey preference was similar among the grazing treatments and habitat types, with only minor variation in the magnitude of prey preferences, not preferred prey categories, again suggesting strong preferences.

Some authors have suggested that a greater availability of prey in disturbed areas may drive higher abundance of arboreal lizards (e.g., Pringle 2008). In our study, the HSR and VAR stocking regimes had the highest average stocking rates (O'Reagain *et al*. 2011), and supported the highest abundance of arboreal lizards (Neilly *et al*. 2017). We therefore suspected that the greater abundance of lizards in high stocking rate paddocks may be due to differences in prey availability, although we found no significant differences in the taxonomic composition of the available invertebrate community among the grazing regimes. However, the heavy stocking regime, which had the largest populations of geckos, supported the highest proportion of Araneae, Coleoptera, and Scorpiones, which are the top three most preferred prey items for *G. dubia*. Thus, while we did not find statistically significant differences in the availability of preferred food items among the grazing treatments, high abundance of preferred prey items may contribute to high abundance of these lizards in disturbed areas.

Conclusions

We quantified the diets, in relation to prey availability, of two widespread lizard species. While it is difficult to definitively classify groups or species as "generalist" or "specialist" foragers because there is no numerical value or indicator that ensures their place in that category, both *C. australis* and *G. dubia* had strong prey preferences for a narrow group of invertebrate prey groups, including beetles and spiders, suggesting they more closely resemble specialist foragers than generalists. In terms of abundance, *Gehyra dubia* respond positively to grazing pressure, while *C. australis* are not significantly affected by grazing. We found no statistically significant differences in the composition of the invertebrate community among the various grazing regimes or habitat types, although there was a trend for highly stocked paddocks to contain higher proportions of preferred prey groups for both lizard species: Coleoptera, Araneae, and Scorpiones. We suggest this increase in availability of the top three preferred prey groups may contribute to the high abundances of *G. dubia* in heavily grazed areas.

EQUATIONS

Eq. 4.1:

$$Levins\ Niche\ Bredth:\quad B = \frac{1}{\sum P_i^2}\quad ;\quad B_{adj} = \frac{B-1}{n-1}$$

Eq. 4.2:

$$Pianka's\ Niche\ Overlap:\quad O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum {P_{ij}}^2 {P_{ik}}^2}}$$

Eq. 4.3:

$$Shannon\ Diversity\ index:\quad H' = \sum_{i=1}^{S} -(pi * \ln pi)$$

Eq. 4.4:

$$Jacobs\ Selectivity\ Index:\quad D = \frac{r-p}{r+p-2rp}$$

TABLES

Table 4.1. Descriptive statistics (mean ± SE [range]) from captured lizards.

		Measurements†		
Species	n	SVL (mm)	TL (mm)	Mass (g)
Cryptoblepharus australis	103	39.6 ± 0.38	84.8 ± 2.34	1.1 ± 0.03
		[30 – 47]	[51 – 107]	[0.43 – 1.55]
Gehyra dubia	203	47.3 ± 1.17	91.1 ± 2.33	3.0 ± 0.19
		[24 – 65]	[37 – 130]	[0.26 – 6.90]

† SVL = snout-vent-length; TL = total length.

Table 4.2. Invertebrate community composition, diet, and prey selection among all sites, Wambiana Grazing Trial, Queensland, Australia.

		Gehyra dubia†						*Cryptoblepharus australis*†				
Prey items	Count #	RA %	Diet % n=59	Occur %	Jacobs Index‡	Pref. Rank	Count #	RA %	Diet % n=40	Occur %	Jacobs Index‡	Pref. Rank
Araneae (spiders)	36	3.5	10.5	18.6	0.6	1	36	3.7	6.5	10.0	0.3	3
Blattodea (cockroaches)	56	5.9	1.9	3.4	-0.5	7	41	4.3	1.6	2.5	-0.5	7
Coleoptera (beetles)	96	9.4	31.4	45.8	0.6	1	84	8.7	41.9	65.0	0.8	1
Diptera (flies)	36	3.5	2.9	5.1	0.0	4	36	3.7	4.8	7.5	0.1	4
Embioptera (web spinners)	10	1.0	0.0	0.0	-1.0	8	10	1.0	0.0	0.0	-1.0	8
Hemiptera (leaf hoppers)	214	21.0	9.5	13.6	-0.5	7	196	20.3	16.1	22.5	-0.1	5
Hymenoptera (ants/wasps)	316	30.7	27.6	39.0	-0.1	5	316	32.8	19.4	30.0	-0.3	6
Isoptera (termites)	28	2.8	0.0	0.0	-1.0	8	28	2.9	0.0	0.0	-1.0	8
Ixodida (ticks)	1	0.1	0.0	0.0	-1.0	8	1	0.1	0.0	0.0	-1.0	8
Lepidoptera (moths/butterflies)	99	9.6	11.4	20.3	0.2	3	99	10.3	8.1	12.5	-0.1	5
Mantodea (mantids)	13	1.3	0.0	0.0	-1.0	8	13	1.3	0.0	0.0	-1.0	8
Neuroptera (antlions)	4	0.4	0.0	0.0	-1.0	8	4	0.4	0.0	0.0	-1.0	8
Orthoptera (grasshoppers/locusts)	77	7.5	3.8	6.8	-0.3	6	68	7.1	3.8	0.0	-0.3	6
Phasmatodea (stick insects)	14	1.4	0.0	0.0	-1.0	8	14	1.5	0.0	0.0	-1.0	8
Pseudoscorpionida (pseudoscorpions)	1	0.1	0.0	0.0	-1.0	8	1	0.1	0.0	0.0	-1.0	8
Scolopendromorpha (centipedes)	4	0.4	0.0	0.0	-1.0	8	3	0.3	0.0	0.0	-1.0	8
Scorpiones (scorpions)	5	0.5	1.0	1.7	0.4	2	5	0.5	1.6	2.5	0.5	2
Zygentoma (silverfish)	9	0.9	0.0	0.0	-1.0	8	9	0.9	0.0	0.0	-1.0	8

† Abundance (Count #), relative abundance available in the environment (RA %), relative abundance found in the diet (Diet), occurrence in the diet (Occur %), Jacobs' selectivity index (Jacobs Index), and dietary preference rank (Pref. Rank) are indicated for each invertebrate prey order.

‡ Jacobs' selectivity index represents the dietary preference, where values approaching +1 indicate a positive selection, values near 0 indicate random selection, and values approaching -1 indicate avoidance.

Table 4.3. Species richness, diversity, and niche breadth of invertebrates available in the environment (Available) and in the diet (Diet) of two arboreal lizards, *Gehyra dubia* and *Cryptoblepharus australis*. Habitat types include Reid River box (Box; *Eucalyptus brownii*) and Silver-leaf ironbark (Ironbark; *Eucalyptus melanophloia*).

			Available		Diet		
			Species Richness	Shannon Diversity	Species Richness	Shannon Diversity	Niche Breadth
Gehyra dubia	Total		18	2.12	9	1.82	0.46
	Sex/Age Class	Male	--	--	8	1.73	0.51
		Female	--	--	8	1.76	0.53
		Juvenile	--	--	7	1.51	0.39
	Habitat	Box	16	2.09	8	1.66	0.44
		Ironbark	16	1.34	8	1.70	0.50
	Grazing Regime†	HSR	16	2.01	7	1.58	0.45
		VAR	16	2.00	7	1.82	0.49
		ROT	16	2.41	8	1.59	0.60
		MSR	12	2.05	5	1.41	0.66
Cryptoblepharus australis	Total		18	2.06	9	1.76	0.39
	Sex/Age Class	Male	--	--	7	1.55	0.45
		Female	--	--	6	1.42	0.48
		Juvenile	--	--	1	--	--
	Habitat	Box	16	2.05	6	1.26	0.36
		Ironbark	16	1.97	8	1.69	0.49
	Grazing Regime†	HSR	16	1.96	6	1.56	0.57
		VAR	16	1.84	6	1.42	0.40
		ROT	15	2.09	6	1.25	0.75
		MSR	12	1.95	2	0.64	0.60

† Grazing regimes include heavy stocking rate (HSR), variable stocking rate (VAR), rotational stocking rate (ROT), and moderate stocking rate (MOD).

Table 4.4. A comparison of the mean number of prey taxa and mean number of prey items found in faecal samples of *Gehyra dubia* (n = 59) and *Cryptoblepharus australis* (n = 40). The two major habitat types are Reid River box (Box; *Eucalyptus brownii*) and Silver-leaf ironbark (Ironbark; *Eucalyptus melanophloia*).

			n	Mean # of Prey Taxa	SE	Significance	Mean # of Prey Items	SE	Significance
Gehyra dubia	Habitat	Box	28	1.57	0.15	$P = 0.710^{‡}$	1.75	0.20	$P = 0.746^{‡}$
		Ironbark	31	1.48	0.15		1.77	0.18	
	Sex	Male	20	1.70	0.16	$P = 0.273^{§}$	2.05	0.18	$P = 0.077^{§}$
		Female	23	1.43	0.19		1.57	0.23	
		Juvenile	16	1.44	0.18		1.69	0.30	
	Grazing Regime†	HSR	14	1.29	0.13	$P = 0.740^{§}$	1.57	0.20	$P = 0.960^{§}$
		MSR	9	1.67	0.33		1.78	0.32	
		ROT	15	1.67	0.27		1.87	0.34	
		VAR	21	1.52	0.15		1.81	0.24	
Cryptoblepharus australis	Habitat	Box	18	1.56	0.18	$P = 0.673^{‡}$	1.94	0.25	$P = 0.867^{‡}$
		Ironbark	22	1.50	0.16		2.05	0.34	
	Sex	Male	22	1.45	0.16	$P = 0.400^{‡}$	1.77	0.21	$P = 0.474^{‡}$
		Female	17	1.65	0.19		2.29	0.44	
		Juvenile	1	1.00	--		2.00	--	
	Grazing Regime†	HSR	12	1.50	0.19	$P = 0.380^{§}$	2.00	0.35	$P = 0.929^{§}$
		MSR	4	1.00	0.00		1.50	0.29	
		ROT	12	1.67	0.22		2.33	0.58	
		VAR	12	1.58	0.26		1.83	0.27	

† Grazing regimes: HSR = heavy stocking rate; MSR = moderate stocking rate; ROT = rotational stocking rate; VAR = variable stocking rate

‡ Wilcoxon test; § Kruskal-Wallis test

FIGURES

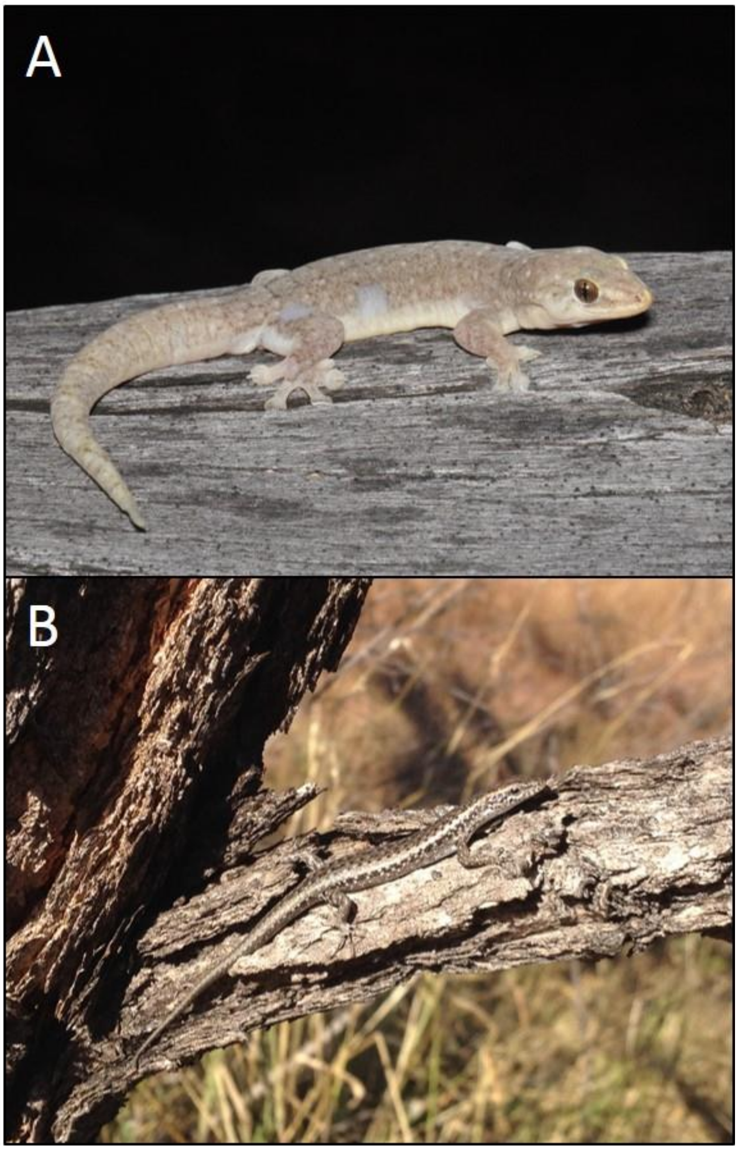


Figure 4.1. *Gehyra dubia* (A) and *Cryptoblepharus australis* (B) photographed at Wambiana Cattle Station, northeast Queensland, Australia. Photographed by E. Nordberg.

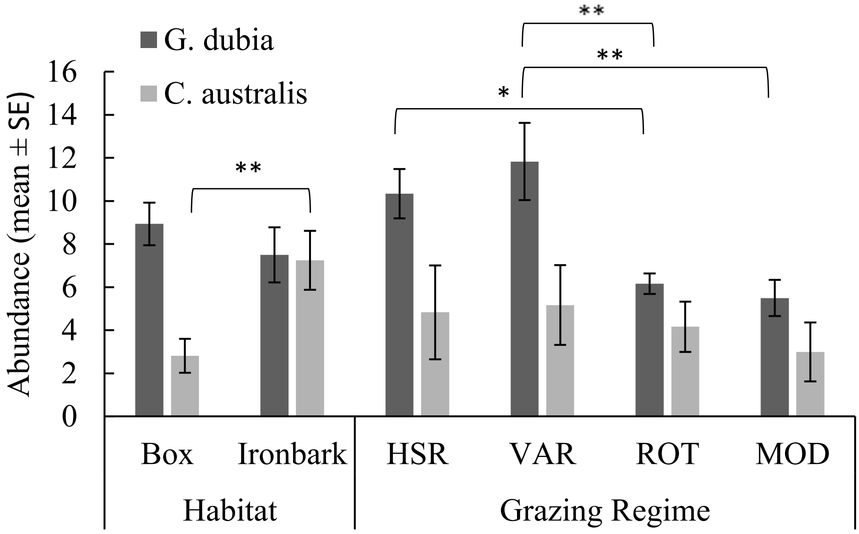


Figure 4.2. Mean number of lizards found between the Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*), and among four grazing regimes: heavy stocking rate (HSR), variable stocking rate (VAR), rotational stocking rate (ROT), and moderate stocking rate (MSR). * indicates significance of $P < 0.05$; ** indicates significance $P < 0.01$.

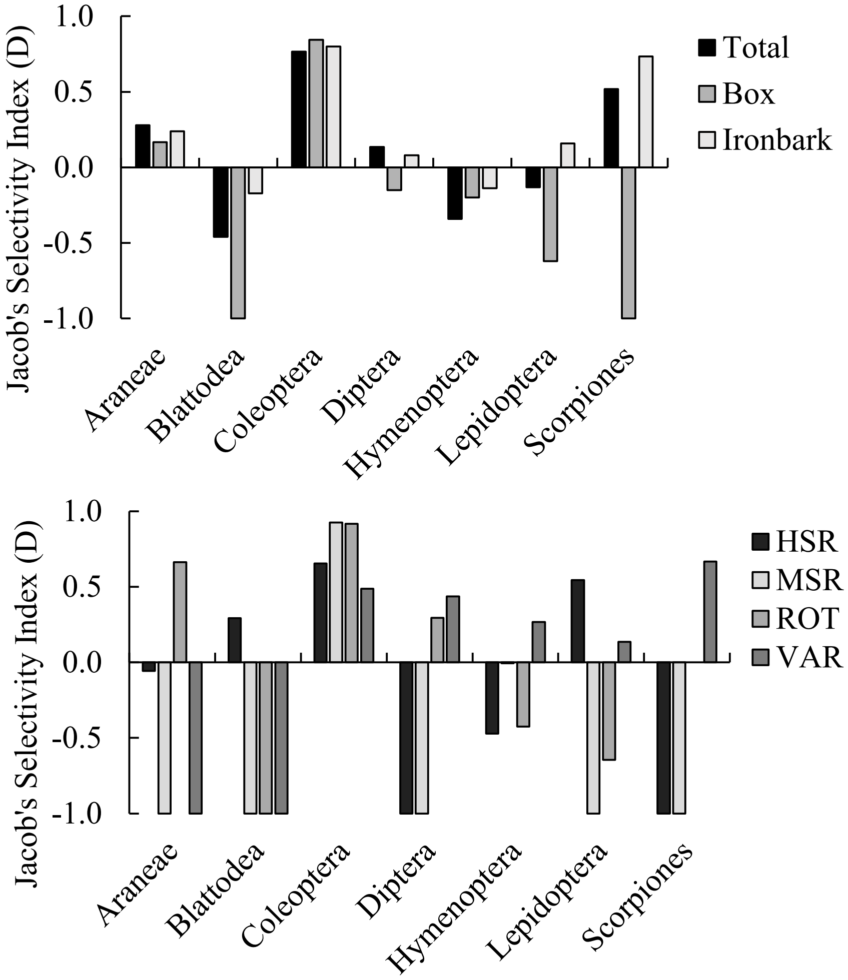


Figure 4.3. Prey selectivity for *Cryptoblepharus australis* between the two habitat types (top; Reid River box and Silver-leaf ironbark), and among four grazing regimes (bottom; HSR = heavy stocking regime, MSR = moderate stocking regime, ROT = rotational stocking regime, and VAR = variable stocking regime). Values approaching +1 indicate a positive selection, values near 0 indicate random selection, and values approaching -1 indicate a negative selection or avoidance.

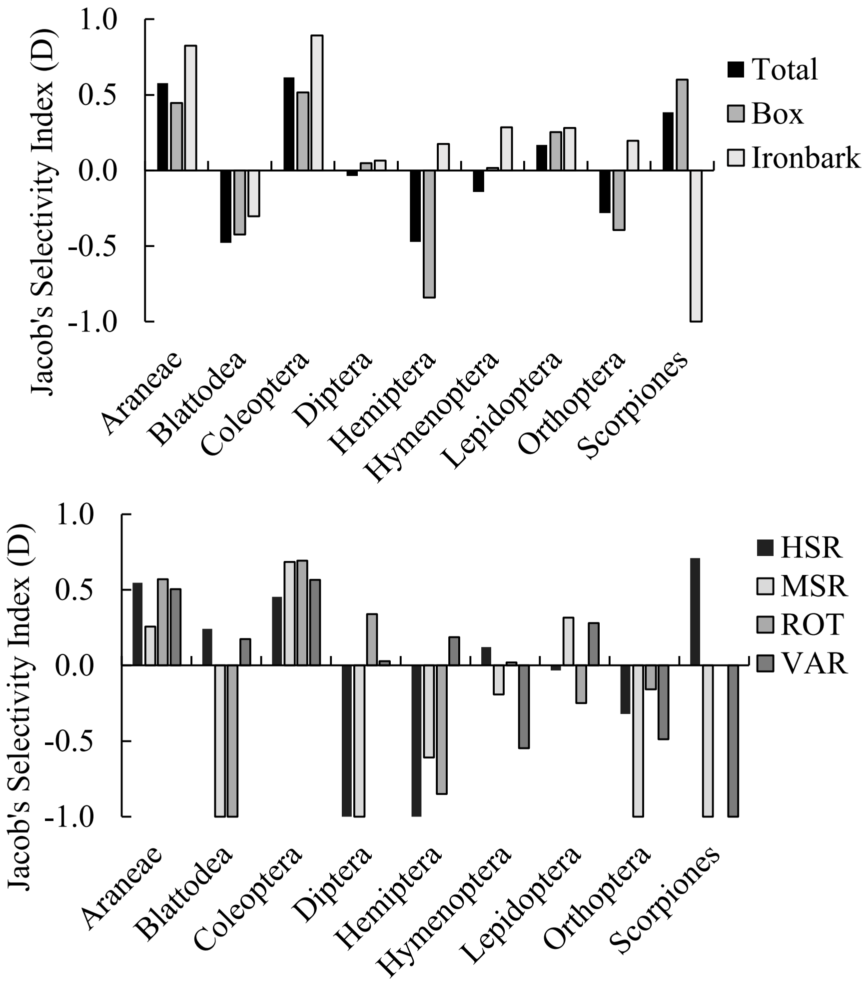


Figure 4.4. Prey selectivity for *Gehyra dubia* between the two habitat types (top; Reid River box and Silver-leaf ironbark), and among four grazing regimes (bottom; HSR = heavy stocking regime, MSR = moderate stocking regime, ROT = rotational stocking regime, and VAR = variable stocking regime). Values approaching +1 indicate a positive selection, values near 0 indicate random selection, and values approaching -1 indicate a negative selection or avoidance.

Chapter 5 – Alternative Prey Availability, Not Predator Abundance, Determines Predation Risk

Under Review as: Nordberg, E.J., and L. Schwarzkopf. Under review. Alternative prey availability, not predator abundance, determines predation risk. Functional Ecology.

ABSTRACT

1. Predator–prey interactions play a critical role in shaping community assemblages and population structure. Traditionally, predation is viewed from the point of view of predators (e.g., functional and numerical responses) or prey (e.g., non-consumptive effects), but few studies have examined predation risk in relation to both predator and prey populations.
2. We estimated predation risk on lizards, and tested two competing hypotheses: i) predation risk is predator-density dependent (more predators cause increased predation risk); and ii) predation risk follows the alternative prey hypothesis (predation risk is dependent on alternative prey availability). We assessed seasonal changes in predator–prey relationships and predation risk to small lizards by quantifying the abundance of lizards, potential predators, and alternative prey (invertebrates). We used physical models (n = 800) and real lizard survival to determine predation risk.
3. Bird strikes were responsible for the majority of attacks on model lizards (84.6%). Predatory bird abundance was greater in the wet season, although lizard models were attacked more frequently in the dry season (18.9%) than the wet season (11.6%) despite fewer predators. Similarly, real lizard weekly survival was highest in the wet season (wet season = 0.98; dry season = 0.94).
4. Predatory birds, although more abundant, attacked fewer lizards when invertebrate prey were abundant, then switched to lizard prey when invertebrate abundance dropped, and lizard abundance was greatest.
5. Predation risk did not follow a predator density-dependent response: predation risk was greatest when predator abundance was lowest. Instead,

predation risk to small lizards was inversely related to the abundance of invertebrate (alternative) prey, supporting the alternative prey hypothesis.

KEYWORDS

Alternative prey hypothesis, birds, diet shift, lizards, predator–prey dynamics, prey-switching

INTRODUCTION

Predator–prey relationships are often complex and highly temporally and spatially variable (Holling 1959; Murdoch & Oaten 1975). The interactions between predators and their prey have been of major interest to many ecologists as they have tried to disentangle these complicated relationships. Ecologists have been modelling predator–prey dynamics with mathematical formulas for close to a century (Lotka 1925; Volterra 1926) from relatively simple Lotka-Volterra models to complex non-linear relationships that incorporate predator and prey density, foraging success, and reproductive rates, among other factors (Holling 1959; Rosenzweig & MacArthur 1963, Pech et al. 1995). While it is often easier to conceptualize predator–prey systems with one predator and one prey species, such simple interactions rarely exist in nature.

Predator–prey dynamics are capable of altering the structure and composition of both predator and prey communities (Carpenter et al. 1985, Hoopes et al. 2005; Terborgh et al. 2010). These trends are generally non-linear and highly variable, resulting in cycles of oscillation in both predator and prey densities (Huffaker 1958; Rosenzweig & MacArthur 1963). Predator–prey dynamics are often visualised as comprising two major components: the functional response, which represents the attack rate or predation rate per predator as a function of prey density; and the numeric response, which represents the increase in predator population size as prey densities rise (Holling 1959). There are three classic types of functional responses: Type 1 describes a linear relationship between predation rate and prey density, Type 2 describes a decelerating predation rate and assumes that predation rate is limited by a predator’s food handling time, and Type 3 (represented as a sigmoidal curve, or “S” shape), describes a scenario in which predation rate is low at low prey densities, increases rapidly at intermediate prey densities, and decreases and levels off at high densities. Type 3 functional responses are often assumed to occur with prey-switching, in which prey species are consumed proportionally more at high prey densities, and proportionally less at low prey densities (Murdoch 1969).

In cases such as in specialist predators, a predator's prey preference remains unchanged over time, irrespective of prey densities, resulting in a linear (Type 1) functional response (e.g., Batzli et al. 1981). This means predators consume the same proportion of prey irrespective to changes in alternative prey availability. In some, more generalist foraging predators, prey preference may change seasonally or in relation to changes in prey availability (Latham et al. 2013), causing Type 3 response, a scenario is often referred to as the alternative prey hypothesis (Lack 1954; Anglestam et al. 1984). Predators that change their prey preference, or exhibit prey-switching, consume prey items disproportionally to their availability (Murdoch 1969). A prey-switching predator will consume *prey species A* while it is more commonly encountered, until the density or encounter rate of *prey species A* drops below that of *prey species B*, in which case the predator switches prey species and consumes *prey species B* while it is more commonly encountered. Prey-switching predators often switch due to prey availability (e.g., search time to locate prey may be less for a more commonly encountered prey species) or due to dietary requirements (e.g., changes in nutritional requirements, for example in relation to breeding; e.g., Morrissey et al. 2010). Prey-switching due to frequency-dependent selection (Ayala & Campbell 1974; Allen 1988) can be beneficial to the predator, ensuring maximum food intake per unit effort (Cornell 1976; Hughes & Cory 1993). Prey-switching behavior is beneficial to predators because predators can alter their diet to maximize foraging efficiency (Stephens & Krebs 1986), and to prey because when prey populations fall below that of alternative prey sources, predation pressure reduces, allowing reduced prey populations to recover, and to the community because it promotes prey species diversity and coexistence (Abrams & Matsuda 2003).

Predation risk is a major outcome of predator–prey dynamics. Abrams (1993) suggests that predator–prey relationships are non-linear in nature, and that predation rates should increase at a decreasing rate as predator density increases. At high predator densities, prey species should elicit antipredator behaviors, become more vigilant, and reduce their exposure to predators, therefore decreasing the rate of predation (Abrams 1993; Orrock & Fletcher 2014). Many studies on the indirect impacts (non-consumptive effects) of predation have shown behavioral changes in prey activity in the presence of predators, especially regarding habitat use and foraging behavior (Werner et al. 1983; Lima & Dill 1990; Cowlishaw 1997; Schmitz et al. 1997; Heithaus & Dill 2002; Valeix et al. 2009). Yet, little research has been done on the relationship between predator abundance or density and the associated risk of mortality to prey. It seems intuitive that there should be a positive relationship between predator abundance and predation risk: i.e., an increase in predator abundance should lead to an increase in predation risk, but this idea has not been well documented, and surprisingly few studies exist on predator-density dependent predation risk (but see Essington & Hansson 2004; Schmitt & Holbrook 2007; White 2007; White & Samhouri 2011).

Predation risk is not solely dependent on the presence, abundance, or density of predators; the relative abundance of alternative prey populations are important factors determining risk in multiple-prey systems (Norrdahl & Korpimaki 2000; Reif et al. 2001; Iles et al. 2013). Population oscillations of prey species are often classified into two major categories or hypotheses: the shared predation hypothesis, which states that all prey groups are at high risk when predator populations are high, synchronizing prey population cycles (Holt & Lawton 1994; Norrdahl & Kopimaki 2000); or the alternative prey hypothesis, which states that predators selectively switch prey groups after prey densities drop below the density of alternative prey, producing asynchronous prey population cycles (Lack 1954; Hornfeldt 1978). Prey-switching can be beneficial for prey groups because as a primary prey group becomes depleted, predators switch to alternative prey sources, allowing depleted primary prey populations to recover (Abrams & Matsuda 1996).

The aim of this study was to assess the relationship between predator abundance and predation risk to prey, in a natural, field-based experiment. We tested two hypotheses regarding predation risk: i) is predation risk dependent on predator density, i.e., does predation risk increase with an increase in predator abundance; and, ii) is predation risk inversely dependent on the abundance of alternative prey (the alternative prey hypothesis). In this study, we used physical (Blu-Tack™) models of small arboreal geckos, Australian native house geckos, *Gehyra dubia*, and survival estimates from telemetry data, in combination with data on predator abundance, to examine predation risk to arboreal lizards. Plasticine and clay models of small vertebrates, especially herpetofauna, have been widely used to assess predation rates across various habitat types (Shepard 2007; Steffen 2009), morphological traits such as color pattern (Castilla et al. 1999; Stuart-Fox et al. 2003; Saporito et al. 2007), and body sizes (Bittner 2003; Mitrovich & Cotroneo 2006). We quantified the abundance of predators at the time of our lizard model deployment to test if predation risk is proportional to predator abundance. Herein, we describe the abundance, predation risk, and survival of lizards in relation to the abundance of their potential predators in two habitat and microhabitat types in both the wet and dry season in the dry tropics of Australia.

METHODS

Study system and site

This study was conducted on at Wambiana Station, a cattle grazing property southwest of Charters Towers, Queensland, Australia (-20.542790, 146.132204, datum = WGS84). The study area, a tropical savanna woodland, contains two major open eucalyptus forest types: Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*). A total of eight sites (1 ha. each) were distributed across both habitat types, four in each. Sites were 1.52 ± 0.12 km (mean ± SE) apart and were not spatially autocorrelated (Mantel permutation test; $r = -0.134$, $P = 0.735$). We sampled all sites for one week in the dry season (August 2015) and the wet season (January 2016).

In this study, we chose small lizards as our model system to test our hypotheses regarding predator–prey dynamics due to their high abundance as potential food for a variety of predators. We selected a locally abundant lizard, the

Australian native house gecko (*Gehyra dubia*) as our model organism. Native house geckos are small arboreal, insectivorous geckos found throughout eastern Australia (Wilson 2015; Nordberg et al. 2017). While *G. dubia* is primarily nocturnal, they have been known to thermoregulate and bask in the late evening and early morning sun (Nordberg, unpublished data), making them susceptible to predation by many crepuscular predators.

Lizard model construction

We constructed life-size lizard models to simulate attack rates and predation attempts on lizards. Lizard models (Figure 5.1) were formed with Blu-Tack™ putty (Blu-Tack™, Bostik Australia Pty Ltd., Thomastown, VIC, Australia) and were shaped by hand to form lizards with similar dimensions (snout-vent length = 40 – 60 mm; mass = 4 – 6 g) as *Gehyra dubia* (snout-vent length = 47.8 ± 0.65 mm; mass = 3.0 ± 0.10 g; mean ± SE). Prior to shaping lizard models, small amounts of graphite powder (Pressol Graphite, Hordern and Company Pty Ltd, Artarmon, NSW, Australia) were added and worked into the Blu-Tack™ by hand to make models more life-like in coloration. We compared spectral reflectance of lizard models and the skin of *G. dubia* using a spectrophotometer to verify that our models produced similar reflectance as actual lizards (Nordberg & Schwarzkopf, unpublished data). We used a graphite pencil to created darker dorsal patterns commonly found in our population of geckos to make lizard models more realistic in appearance. Once the lizard models were formed, we placed each model on a transparent plastic sheet cut into lizard shapes (Lowell™ Laminating Pouches, Officeworks Ltd, Bentleigh, VIC, Australia) with an exposed tab for attaching it to a substrate. A small 20 mm tack was used to secure the model to different microhabitats (e.g., trunks of trees, or the ground).

Due to the pliable nature of Blu-Tack™, predation attempts left indentations on the lizard models (Figure 5.1). We identified attacking predators by inspecting indentations on the models, and classified predators into categories (e.g., bird, reptile, invertebrate, etc.). The indentations from birds left a deep “V” shape in the model, which could be distinguished from large invertebrates which left two fang or pincer punctures. We validated the indentations created by birds from visual observations of attacks on models. We presented models to large huntsman spiders (Sparassidae) and coerced them to bite a lizard model to validate the bite mark indentations from large predatory invertebrates.

Lizard model placement

In the dry season (August 2015) we placed 400 lizard models among our eight sites. We placed models in two microhabitats used by lizards, on the trunks of trees and on the ground. At each site, 50 lizard models were placed on the trunks of trees approximately 2 m from the ground and 50 lizard models were placed on the ground on various substrata (e.g. bare ground, leaf litter, under *Carissa ovata* bushes, or on woody debris). Models were collected after six days and scored as “not attacked” or “attacked”. Models were only scored as “attacked” if they had bite mark indentations from a potential lethal predator; bite marks from ants and other small invertebrates were not scored as a potentially lethal attack. Attacked lizard models were categorized by predator type. In the wet season (January 2016) we implemented the same procedure for model placement but with the addition of 400 control models (patternless Blu-Tack™ rolled by hand into spheres) to test if predators could distinguish foreign objects from lizard-shaped models. We hypothesized that if control models were attacked at the same rate as lizard models, then attack rates were likely a result from inspecting novel objects and may not accurately depict predation. We also checked the fate of models twice daily, just after dawn to check for nocturnal attacks, and just before sunset to check for diurnal attacks.

Invertebrate prey abundance

Invertebrate predator and prey abundance was monitored using arboreal cover boards (see Nordberg & Schwarzkopf 2015 for methodological details). Closed-cell foam cover boards (50 x 50 x 1 cm) were strapped to the main trunks of trees using elastic bungee cords approximately 1.5 m from the ground. Cover boards were removed during morning surveys (between 0800 – 1000 hrs) to quantify the invertebrate community. Cover boards remained on a particular tree for two days before being moved and replaced on different trees throughout each site. Twenty-four trees were sampled at each site, for a total of 192 trees or 384 trap-nights. This method has been used to monitor small invertebrate prey groups, such as beetles, ants, crickets, and spiders, as well as large invertebrate predators such as centipedes and huntsman spiders (Nordberg and Schwarzkopf 2015; Nordberg et al. 2017).

Nocturnal surveys: gecko and predator abundance

Gecko abundances were monitored via timed spotlight surveys and the use of arboreal cover boards (see description above). Nocturnal surveys consisted of time-constrained spotlight surveys for geckos and nocturnal predators (i.e., birds, snakes, invertebrates). Each spotlight survey consisted of two researchers searching all trees, logs, and the forest floor for 20 min in a "U" shaped transect (to avoid overlap in search area) around each 1 ha. site. All spotlight surveys were completed within the first 3 hours after sunset.

Diurnal surveys: predatory bird abundance

Diurnal predators (mainly omnivorous or insectivorous birds) were monitored using timed point-count dawn bird surveys at the center of each site. Each survey was conducted by two researchers for 10 min between 05:30 – 07:00. We recorded all birds seen or heard during the survey, and later removed the non-predatory birds (birds not known to consume small lizards; Barker & Vestjens, 1989, 1990) from the data.

Gecko survival

We calculated the survival of real geckos (not lizard models) based on radio telemetry relocation data using the methods of Trent and Rongstad (1974), which estimates the daily survival of individuals based on the daily fate of telemetered animals (Equation 5.1). This method used radio-gecko days (e.g. 15 geckos with transmitters monitored for 10 days = 150 "radio-gecko days") and the fate of each animal (dead or alive at the end of each day) to calculate a daily survival estimate. Survival (S) can be calculated for any number of days (n) using the total number of mortalities (y), and the total number of radio-gecko days (x). By adjusting the value of n, estimates can be extrapolated to weekly, monthly, or any other number of days. We tracked 15 geckos in the dry season (female = 4, SVL = 57.67 ± 1.56 mm, mass = 6.25 ± 0.44 g; male = 11, SVL = 57.41 ± 0.77 mm, mass = 5.63 ± 0.21 g; total relocations = 430) and 24 in the wet season (female = 14, SVL = 56.0 ± 1.3 mm, mass = 5.8 ± 0.3 g; male =

10, SVL = 58.9 ± 0.5 mm, mass = 5.7 ± 0.1 g; total relocations = 319) equipped with small radio transmitter belts (LB-2XT model, 8 x 4 x 2.8 mm (L x W x H), 0.25 g, Holohil Systems, Ontario, Canada). Radio transmitters were attached externally around the waist of each gecko using thin rubber dialysis tubing and tied with cotton thread. Different geckos were tracked in both seasons. All geckos were located six times daily (e.g. every four hours throughout the day and night) for a total of 7 days. Geckos were recaptured at the end of the tracking period to remove the transmitter belts. We calculated daily survival (based on the fate of the gecko) and extrapolated to weekly survival (length of lizard model study).

Data analysis

We used generalized linear mixed-models (GLMMs; R package *lme4*, Bates et al. 2015) and model selection to identify the best predictor variables for a series of response variables: predation/attack rate, predator abundance, predatory invertebrate abundance, invertebrate prey abundance, and lizard abundance. We constructed a correlation matrix to identify and remove any variables that showed collinearity. Two sets of models were used, "environmental models" used *season*, *habitat type*, and *microhabitat* as predictor variables to our response variables listed above, while our "biological models" used the abundance of other organisms as predictor variables (predatory bird abundance, predatory invertebrate abundance, lizard abundance, and invertebrate prey abundance; Table 5.1). We used TukeyHSD post-hoc tests for each categorical factor in the top environmental model, and identified whether the response variable had a positive or negative response to the factors in the top model for the biological models. All models included *site* as a random factor. We used a Student's *t*-test to test differences in attack frequencies between lizard shape and control (sphere) shaped models. Attack frequencies on lizard models were analyzed using a binomial distribution due to the nature of the response variable (model fate: attacked or not attacked). In all other models dealing with count data, we used a Poission distribution to account for overdispersion. We conducted model selection with the function 'dredge' in the R package *MuMIn* (Barton 2016) using the Akaike Information Criterion to identify optimal models (with a ΔAICc

< 2). Model averaging was used when no optimal model could be identified (i.e., there were multiple top models with ΔAICc < 2).

RESULTS

Lizard abundance and survival

The top models (ΔAICc < 2) indicated that *invertebrate prey abundance* and *season* were the best predictor of gecko abundance (Table 5.1). Lizards were more abundant in the dry season than the wet season, a trend opposite to invertebrate prey abundance (Figure 5.2). Average weekly wet season survival (0.98 [0.88 – 1.00 95% CI]) was higher than the dry season (0.94 [0.86 – 0.99]) based on radio telemetry data. While my survival estimates were similar (not significantly different from each other based on confidence interval overlap), we compare the trends from the survival data (radio telemetry) to the fate of lizard models (Blu-Tack) for comparison.

Lizard model predation

We feel the lizard shape models resembled real lizards because predators attacked the lizard-shaped models significantly more (10.8% of models) than the control models (4.8%) during the wet season when both control and lizard models were present (t = -3.394, df = 13, P = 0.004; Figure 5.3). The top biological model included *invertebrate abundance* as fixed effects and *site* as a random effect (Table 5.1; Appendix 5.S1), thus invertebrate prey abundance was the best predictor of model attack rates. There were more attacks on lizard models when invertebrate prey abundance was low, and vice–versa. The top environmental model included *season*, *habitat type*, and *microhabitat* as a fixed factors; lizard models were attacked nearly twice as frequently in the dry season when invertebrate prey abundance was low than in the wet season (dry = 18.9%, wet = 11.6%; P = 0.005). There was no significant effect of microhabitat (models placed on trees vs. ground; P = 0.541) or habitat type (Reid River box vs. Silver-leaf ironbark; P = 0.260; Table 5.1). The attack rates on model lizards likely represent a conservative estimate because all models that were stepped on (by cattle or humans; n = 2) or were missing (n = 39) were removed from analysis because the fate of the model could not be determined.

Predatory birds were responsible for a majority of overall model attacks (84.6%), followed by large invertebrates (12.8%), and other (unidentifiable) predators (2.6%). While some of the unidentifiable attacks or missing models could have come from small predatory mammals, this study system has remarkably low numbers of small mammals. Neilly and Schwarzkopf (unpublished data) reports low capture rates of small mammals at this site, with only 39 captures from 20,160 trap nights over 3 years. This trend is similar to other dry savanna woodlands across northeast Queensland (Kutt and Gordon 2012). We suspect that most of the bird attacks on lizard models came from large predatory birds abundant at our site, including grey butcherbirds (*Cracticus torquatus*), pied butcherbirds (*Cracticus nigrogularis*), Australian magpies (*Cracticus tibicen*), blue-winged kookaburras (*Dacelo leachii*), laughing kookaburra (*Dacelo novaeguineae*), Torresian crow (*Corvus orru*), and Australian ravens (*Corvus coronoides*). We found no significant difference in the rate of attacks on lizard models during the day or night ($t = 0.289$, df = 13, $P = 0.776$; Figure 5.3). Invertebrate predators were likely huntsman spiders (Sparassidae) and centipedes (Scolopendromorpha) based on fang indentations left on lizard models and the high abundance of these invertebrates throughout the study area. Most of the attacks by invertebrates occurred at night (90%). We did not detect any attacks on lizard models from snakes or other reptiles. Predation rate was not correlated to the abundance of either predator group (birds: *rho* = -0.017, $P = 0.949$; invertebrates: *rho* = 0.049, $P = 0.854$).

Predator abundance

We conducted 13.3 hrs of dawn surveys for diurnal predatory birds, and 13.3 hrs of nocturnal spotlight surveys for nocturnal predators, including large invertebrates, nocturnal birds, and snakes. We identified 14 species of predatory birds, two groups of predatory invertebrates, and one species of snake (see Appendix 5.S2, Table 5.1). Magpies, butcherbirds, and corvids made up 71.8% of all the predatory bird abundance. Pale-headed snakes (*Hoplocephalus bitorquatus*) were the only snakes we encountered, but are nocturnal, arboreal, and a likely a predator of small lizards (Wilson 2015). Huntsman spiders were the most abundant invertebrate predator and made up 73.7% of the invertebrate predator abundance.

Predatory bird abundance

The top environmental model included a *season* by *habitat* interaction and was the best predictor of predatory bird abundance based on AICc values (Table 5.1). Predatory birds were more abundant in the wet season than the dry season, and in the ironbark than the box habitat (Figure 5.2). The top biological model included only *gecko abundance*, but was not significant (*P* = 0.150).

Snake and invertebrate predators

Snake abundances were too low throughout the duration of this study to adequately produce models using snake abundance, although they are likely potential predators (see Appendix 5.S2). We only found two snakes, both *Hoplocephalus bitorquatus* in box habitat in the wet season. While invertebrates (predominantly huntsman spiders) were responsible for only 6.8 – 23.3% (dry season and wet season respectively) of attacks on lizard models, they may be important predators of small vertebrates, such as lizards, even though invertebrates are often overlooked in this capacity (Nordberg et al. in review; see Appendix 5.S2). The top environmental models included a *season* by *habitat* interaction as the best predictor of predatory invertebrate abundance (Table 5.1). There was a trend for the ironbark habitat to support higher abundances of predatory invertebrates than the box habitat in both the dry and wet season (see Figure 5.S2). The top biological model included *gecko abundance* and *invertebrate prey abundance* as the best predictors of predatory invertebrate abundance, but both were not significant (gecko abundance: *P* = 0.121; invertebrate prey abundance: *P* = 0.202).

Invertebrate prey

The top environmental model included only *season* as a fixed effect and *site* as a random factor (Table 5.1). Invertebrate prey abundance was highest in the wet season and lowest in the dry season (Figure 5.2). The top biological model included only *gecko abundance* as a fixed effect and *site* as a random factor. Invertebrate prey were significantly negatively related to gecko abundance (*P* = 0.002).

DISCUSSION

We had the unique opportunity to examine the predator–prey relationships of predatory birds with small lizards and invertebrate prey. Predation risk on lizards from predators (predominantly birds) was not proportional to the abundance of predatory birds, lending no support to the hypothesis that predator density drives predation risk. Instead we found an inverse relationship, with higher predation when few birds were present, and vice versa. We found the abundance of alternative prey (invertebrates), were also inversely related to lizard predation risk; when the abundance of alternative prey was low, predation risk was greater for lizards, lending strong support to the alternative prey hypothesis. Predation rate on small lizards oscillated over time in opposition to the rise and fall of invertebrate prey populations, consistent with the alternative prey hypothesis, and not consistent with the predator density hypothesis.

Few studies present data on predator abundances and densities when discussing predator–prey interactions, although predator abundance and density may be major contributing factors for both consumptive and non-consumptive effects on prey populations. Liebezeit & Zack (2008) monitored nests of ground-dwelling birds in the Arctic using remote cameras, and identified potential nest predators from timed point-count surveys. There were more avian predators in the environment (80%), yet Arctic foxes were responsible for over 80% of the predation events captured on remote cameras. Although a high density of avian predators were present, there was not a strong association between risk and avian predation pressure for nests (Liebezeit & Zack 2008). Similarly, high density of predators does not necessarily mean they are responsible for increased predation. For example, DeGregorio et al. (2014) found high predation of passerine bird nests near powerlines and at habitat edges where raptors were abundant, yet video surveillance of nests indicated that snakes were responsible for the majority of nest predation events. Predator groups can often be misrepresented without confirmation of predation attempts from remote cameras (Liebezeit & Zack 2008; DeGregorio et al. 2014), artificial models (e.g. teeth indentations; Stuart-Fox et al. 2003; Webb & Whiting 2005), or visual confirmation. Without confirmation of predation events, abundant ‘potential’ predators may be erroneously classified as important predators in an ecosystem simply due to their abundance (DeGregorio et al. 2014).

Birds are often the most common predators of small herpetofauna in many ecosystems (frogs: Poulin et al. 2001; Stuart-Fox et al. 2003; Saporito et al. 2007; lizards: Poulin et al. 2001; Steffen 2009; snakes: Webb & Whiting 2005; Wilgers & Horne 2007). We identified predator groups from indentations left on lizard models after predation attempts, enabling us to conclude predatory birds were responsible for a majority of attacks on lizard models (84.6%). Both grey (*Cracticus torquatus*) and pied butcherbirds (*Cracticus nigrogularis*) were common in our study (21.2% of total bird abundance) and often forage around and under loose or peeling bark (Barker & Vestjens 1989). Butcherbirds consume *G. dubia* (Nordberg, unpublished data), which are vulnerable while thermoregulating in early morning and late afternoon, but may also be dislodged from diurnal refugia under loose or peeling bark. Despite having little overlap in activity and foraging time with our nocturnal model species (*G. dubia*), diurnal birds were a major contributor to the predation on our models, especially at dawn and dusk, when many birds were foraging and lizards theromoregulating.

Many of our predatory bird species were generalists and opportunistic feeders (Barker & Vestjens 1989, 1990). In regions where food availability fluctuates seasonally, it is advantageous to eat abundant and easy-to-obtain resources. We suspect that birds in our study changed their diet and foraging strategy to take advantage of the most available food sources. Our results indicate a strong seasonal shift in the attack rate (predation risk) on lizards. In the dry season, lizard abundances were the highest, and predation risk was greatest, indicating predation risk was the greatest when lizard abundances were highest. The survival of lizards (radio telemetry data) was lowest in the dry season, suggesting the fate of our lizard models and the fate of real lizards were similar. These trends were reversed in the wet season: lizard abundance was lowest, predation risk (determined from models) was lower, and survival (from radio telemetry data) was highest in the wet season.

The presence of alternative prey (invertebrates) help explain the fluctuation in predation risk on lizards. When examining the trends in an alternative food source (invertebrates) for predatory birds, we find that they follow the opposite pattern from lizard abundance; invertebrates had highest abundance in the wet season, and lowest in the dry season. The pattern in predator and alternative prey abundances can best be explained by the alternative prey hypothesis, in which predation risk is reduced on lizards when the population of alternative prey (invertebrates) increases. We suggest predators were taking advantage of the most abundant prey source, and switching to an alternative prey when lizard prey populations were depleted. Our estimations of predation risk (highest in the dry season and lowest in the wet season) and lizard survival (lowest in the dry season and highest in the wet season) are consistent with this hypothesis. Other studies have found greater frequency of vertebrates (lizards and frogs) in the diet of birds during the dry season (e.g., Poulin et al. 2001) and reduced invertebrate abundances during the direst parts of the year (James 1991; Griffiths & Christian 1996; Recher et al. 1996; Taylor 2008), although none have compared them in this way.

Many bird species exhibit seasonal shifts in prey preference (Cooper 1988; Korpimaki et al. 1990; Reif et al. 2001). American dippers (*Cinclus mexicanus*) exhibit a seasonal diet shift with a greater proportion of fish in their diet than aquatic invertebrates prior to egg laying (Morrissey et al. 2010). A diet of fish has more calories, lipid, and protein, essential for eggshell formation (Morrissey et al. 2010). The major predatory birds in our study all breed and lay eggs in the dry season (Beruldsen 2003). Whereas we found the predatory birds switched prey from invertebrate to lizard prey based on their relative abundance, we also suggest birds may switch from primarily invertebrate prey to a larger proportion of vertebrates (lizards) during the dry season to acquire additional nutrients prior to breeding and egg laying, although this should be experimentally tested.

While we did not find a difference in the attack rates on lizard models in relation to microhabitat, Steffen (2009) found that lizard models in the canopy were attacked with a higher frequency than those on the trunk-ground level. We did not test height differences to the same scale as Steffen (2009); 10 m = canopy vs. 0.5 m = trunk/ground; whereas our height differences were 0 m = ground vs. 2 m = trunk. A majority of the predatory birds in our study forage on or near the ground (Barker &

Vestjens 1989, 1990), which may explain why we didn't see a difference in the attack rates among the microhabitat types.

Conclusions

Predator–prey dynamics are among the more complicated ecological processes studied by ecologists. We demonstrated that abundances of both predators and prey varied between seasons, and predation risk on lizards was greatest in the dry season, at the time we observed the lowest abundances of predatory birds. Our results indicate that the relationship of small lizards and their predators is not a function of abundance or density of predators; more predators did not indicate higher predation risk. In fact, predation risk was lowest when predatory birds were most abundant. Thus, although predation risk is often thought to be driven by the number of predators, our results indicate that the relationship among prey types may be more important. Predation risk and survival of small lizards varied seasonally, probably as predatory birds shifted their diet in response to the abundance of alternative (invertebrate) prey, and potentially in relation to nutritional requirements prior to egg laying. Our study suggests it is important to directly determine predation risk, rather than assuming it varies in relation to predator abundance.

EQUATIONS

Eq. 5.1:

$$Survival\ (Trent\ and\ Rongstad\ 1974):\quad S_n = \left(\frac{x-y}{x}\right)^n$$

TABLES

Table 5.1. Results from generalized linear mixed-effects models (GLMM) indicating the terms present in the top model as the best predictor for each response variable. Response variables represent attacks on lizard models (Attacks), abundance of predatory birds (Predatory Birds), abundance of predatory invertebrates (Predatory Invertebrates), abundance of lizards (Lizards), and abundance of alternative (invertebrate) prey (Invertebrate Prey). Responses indicate Tukey post-hoc tests for each categorical factor in the top model for the environmental models, and whether the response variable had a positive (+) or negative (-) response to the factors in the top model for the biological models.

	Response Variable	Terms in top model	Distribution	*P*-value	Response
	Global model GLMM: ~ Season + Habitat Type + Microhabitat + (1|Site)				
Environmental Models	Attacks	Season	Binomial	**0.005**	Wet < Dry
		Habitat Type		0.260	Box > Ironbark
		Microhabitat		0.541	Ground < Tree
	Predatory Birds	Season*Habitat Type	Poisson	**<0.001**	Dry.Box < Wet.Box
				<0.001	Dry.Box < Dry.Ironbark
				<0.001	Dry.Box < Wet.Ironbark
	Predatory Invertebrates	Season*Habitat Type	Poisson	0.135	Not significant
	Lizards	Season	Poisson	**0.017**	Dry > Wet
	Invertebrate Prey	Season	Poisson	**0.023**	Dry < Wet
	Global model GLMM: ~ Pred.Birds + Pred.Inverts + Lizards + Invert.Prey + (1|Site)				
Biological Models	Attacks	Invert.Prey	Binomial	**0.048**	(-)
	Predatory Birds	Lizards	Poisson	0.150	(-)
	Predatory Invertebrates	Lizards	Poisson	0.161	(-)

		Invert.Prey		0.202	(+)
	Lizards	Invert.Prey	Poisson	**<0.001**	(-)
	Invertebrate Prey	Lizards	Poisson	**0.002**	(-)

Significant *P*-values are marked in bold.

FIGURES

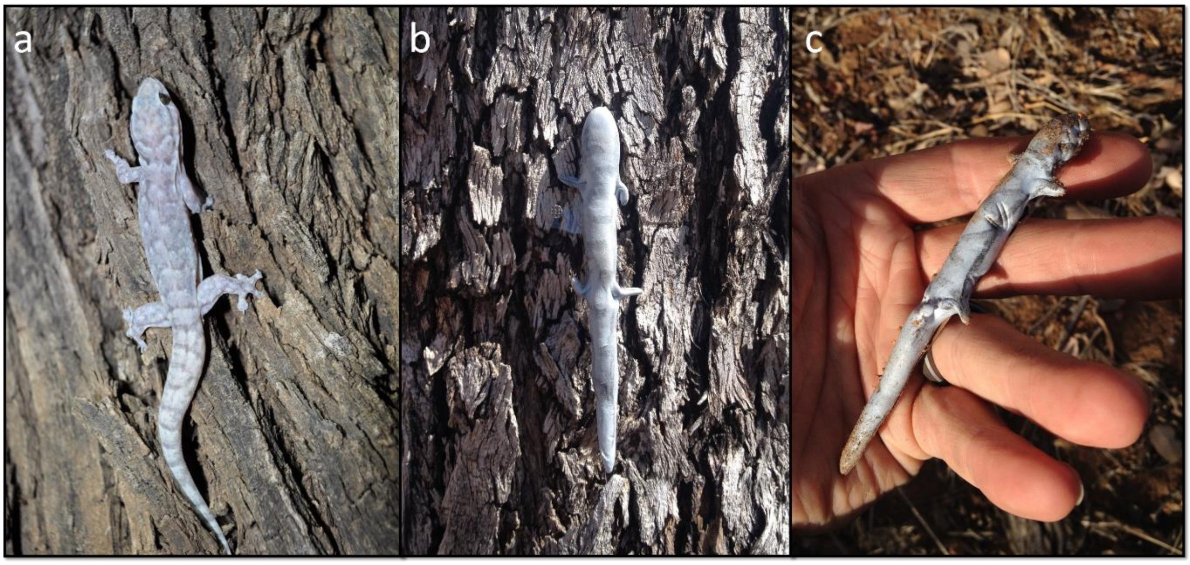


Figure 5.1. The Australian native house gecko, *Gehyra dubia* (a), is an arboreal, nocturnal gecko found throughout northeast Australia. We used Blu-Tack™ to make physical models of *G. dubia* for deployment in various macro- and microhabitats to test predation risk in lizards (b and c). Due to its pliable nature, attacks on models can be inferred from indentations remaining after predation events (c; indentations from a bird beak).

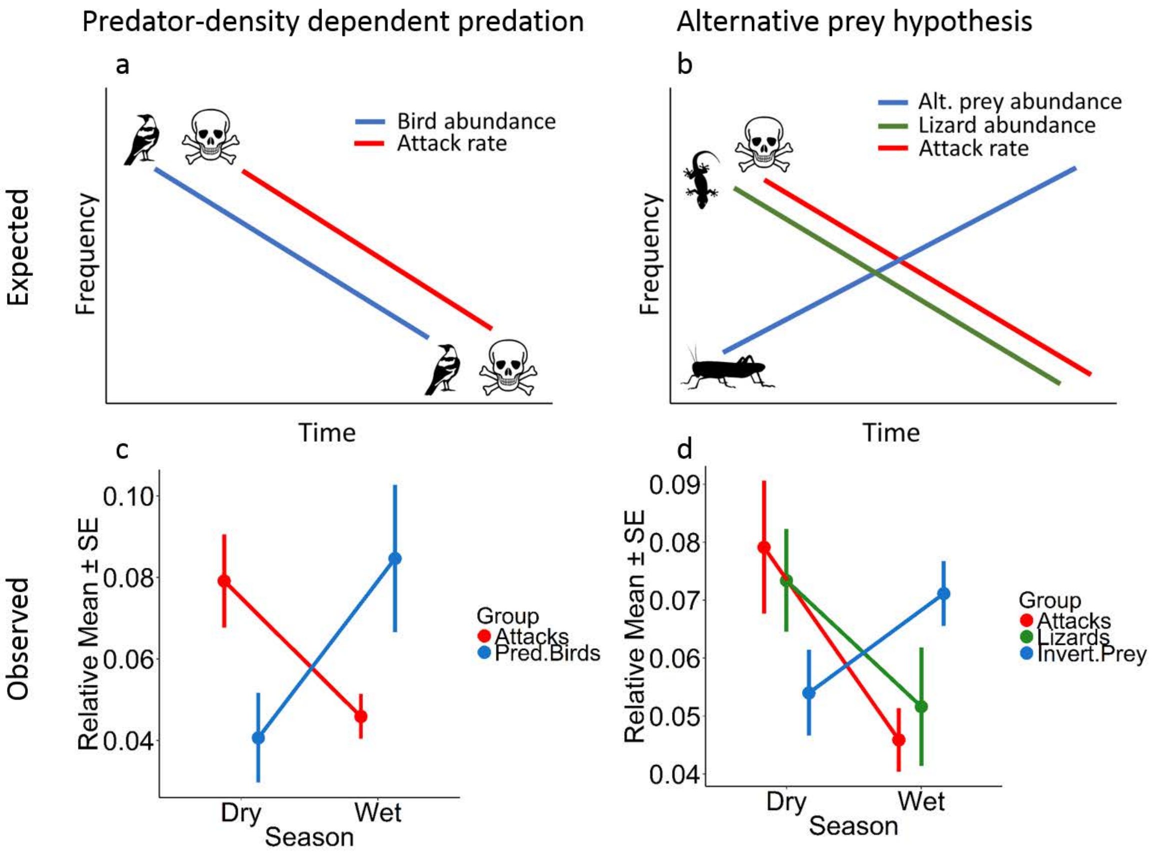


Figure 5.2. Expected and observed results of our two hypotheses: i) that predation risk (skull and crossbones) is predator density-dependent, i.e., predation risk increase with an increase in predator abundance (a); or, ii) is predation risk is inversely dependent on the abundance of alternative prey, i.e, the alternative prey hypothesis (b). The observed values for the predator-density dependent predation risk (c) indicate that predation risk was not predator-density dependent, as the mean number of attacks (Attacks; red) and the mean abundance of predatory birds (Pred.Birds; blue) show an inverse relationship to each other. Alternatively, the observed values for the alternative prey hypothesis (d) indicate that predation risk on lizards (Attacks; red) was inversely related to the mean abundance of invertebrate (alternative) prey (Invert.Prey; blue), showing support for the alternative prey hypothesis.

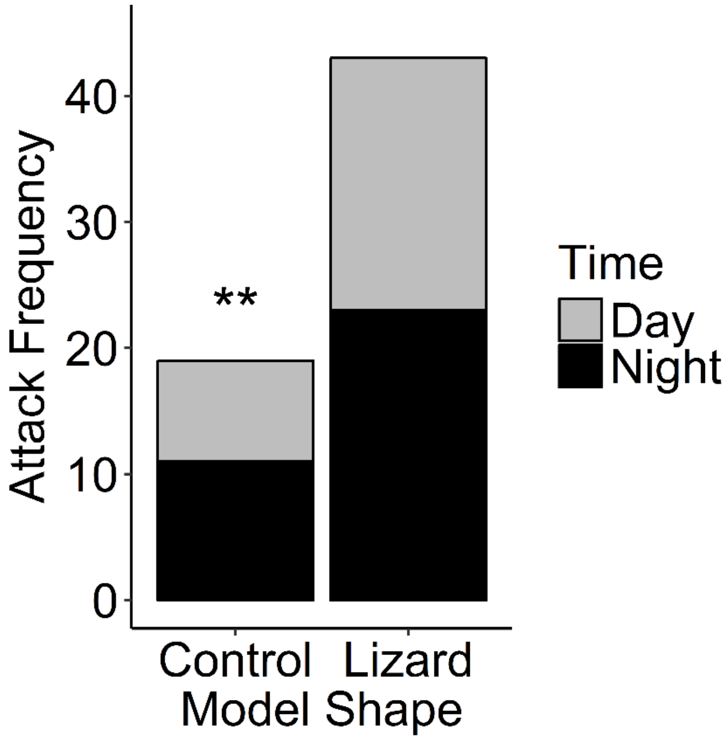


Figure 5.3. Attack frequencies on Blu-Tack™ model lizards vs. control models (patternless spheres). Predators attacked lizard shaped models significantly more often than control models (*t* = -3.394, df = 13, *P* = 0.004), yet there was no difference in the attack frequency during the day vs. night (*t* = 0.289, df = 13, *P* = 0.776).

Chapter 6 – Terrestrial Invertebrates: An Underestimated Predator Guild for Small Vertebrate Groups

Under Review as: Nordberg, E.J., L. Edwards, and L. Schwarzkopf. Under review. Terrestrial invertebrates: an underestimated predator guild for small vertebrate groups. Food Webs.

ABSTRACT

A fundamental goal of ecology is to describe how organisms co-exist in environments, including predator-prey interactions. However, one challenge for this field of study is that predation events can be rare and relatively difficult to observe, thus they are seldom quantified in nature. Vertebrates are the top predators in many systems, but large invertebrates such as spiders, mantids, and centipedes may be important predators of small vertebrate groups. We used several approaches to determine the relative frequency of predation by invertebrate and vertebrate predators in terrestrial systems. We conducted 500 hours of visual surveys and compiled observations of *in situ* predation events from 2014 – 2016 in north Queensland, Australia. Predation events were rarely observed: in 500 hours of visual searches, we observed 9 instances of predation (vertebrates consuming another vertebrate, $n = 4$; invertebrates consuming a vertebrate, $n = 5$). In addition to spotlight surveys, we deployed 800 lizard-shape models to quantify attack frequencies on small lizards. While vertebrate predators were responsible for the most attacks on lizard models (76.7% and 93.3%, wet and dry season respectively), invertebrate predators were responsible for 23.3% and 6.8% of attacks. While predation events (of any kind) were rarely observed, we suggest that predation by invertebrate predators on vertebrate prey should not be overlooked in terrestrial systems. Invertebrate predators may play an important predatory role in shaping populations of small vertebrates, similar to more “typical” predators such as snakes, birds, and mammals.

KEYWORDS

Australia; Diet; Herpetofauna; Predation; Predator–prey; Spiders

INTRODUCTION

Predator–prey interactions are important factors determining community assemblage and population dynamics, and have been well documented in a variety of taxa: vertebrates as predators of vertebrates, invertebrates as predators of invertebrates, and vertebrates as predators of invertebrates (e.g., McCormick and Polis, 1982; Sih et al., 1985; Sidorovich, 2011). Invertebrate predators of vertebrates have been well documented in aquatic systems, in which carnivorous insects (e.g., Odonata; dragonflies; Coleoptera; water beetles) are known to be major predators of amphibian larvae (Brodie and Formanowicz, 1983; McCollum and Leimberger, 1997; Van Buskirk et al., 2004; Kopp et al., 2006; Ohba, 2008), juvenile fish (e.g., Gertsch, 1979, Smith 1980; McCormick and Polis, 1982), and even reptiles (Mori and Ohba, 2004; Ohba, 2011). In terrestrial environments, however, there are far fewer examples for which invertebrates are well documented as important predators of vertebrate prey (but see Toledo, 2005; Nyffeler and Knornschild, 2013, Nyffeler et al., 2017). In particular, few studies have examined predation under natural conditions, likely because observing un-manipulated predation events in nature are rare.

Literature reviews on vertebrate predation by invertebrates (e.g., McCormick and Polis, 1982; Toledo, 2005) highlight that a majority of observations of invertebrates preying on vertebrates come from anecdotal observations or natural history descriptions appearing in the literature as natural history notes (e.g., Mitchell, 1990; Raven, 1990; Bastos et al., 1994; Owen and Johnson, 1997; Blackburn et al., 2002). Although these data are important observations and highlight rarely observed predation events, the broader context surrounding these behaviors are difficult to interpret on a population level. Unlike aquatic systems, for example, where studies have experimentally quantified the predation of tadpoles by water beetles (Brodie and Formanowicz, 1983; Toledo, 2003), we lack similar studies in terrestrial systems.

Australia is home to large variety of predatory invertebrates that occupy similar niches as many small vertebrates. For example, there are many large spiders that occupy tree hollows, loose and peeling bark, and woody debris, all of which are commonly co-occupied by small vertebrates, especially small herpetofauna (Gibbons and Lindenmayer, 2000). We predict that large spiders and other predatory invertebrates may play a significant role in the predation of small vertebrate communities such as frogs and lizards, yet this remains largely un-tested. Few studies have documented such interactions in great detail (but see McCormick and Polis, 1982; Bauer, 1990; Menin et al., 2005; Toledo, 2005; Brooks, 2012), other than anecdotal or opportunistic descriptive observations (e.g., Maffei et al., 2010; Borges et al., 2016).

Here, we quantitatively compared the predator–prey interactions between vertebrate–vertebrate and invertebrate–vertebrate predation events. In systems with large predatory invertebrate communities and abundant small vertebrate communities, such as frogs and lizards, we hypothesize that predation rates by invertebrates are likely similar to those of vertebrate predators.

METHODS

Study sites and surveys

We used two methods to quantify the frequency of predation by both vertebrate and invertebrate predators on small vertebrate groups at two locations in northeast Australia. We conducted nocturnal spotlight surveys (500 hours total) at the Wambiana Grazing Trial (WGT; 70km southwest of Charters Towers, Queensland, Australia) and at the Town Common Conservation Park (TCCP; Townsville, Queensland, Australia) from 2014 – 2016. Surveys were conducted throughout the wet and dry seasons at both sites. Both savanna woodlands contain similar predator and prey communities (Nordberg, unpublished data). During spotlight surveys, two observers searched the ground, logs, bushes, trunks of trees, and branches for predator–prey interactions. We documented all predation events of vertebrates consuming another vertebrate (vertebrate–vertebrate) and invertebrates consuming a vertebrate (invertebrate–vertebrate).

Lizard models

In August 2015 and January 2016, a total of 800 lizard-shaped Blu-Tack™ models (Blu-Tack™, Bostik Australia Pty Ltd., Thomastown, VIC, Australia) were deployed across eight sites at the WGT to estimate the predation risk to small lizards. Lizard-shaped models were created by hand using pliable Blu-Tack™ (Figure 6.1; lizard model "snout-vent-length and mass" = 40 – 60 mm and 4 – 6 g). Lizard models were designed to resemble Australian native house geckos (*Gehyra dubia*; Figure 6.1). We placed a total of 800 lizard models (400 in August 2015 and 400 in January 2016) throughout the environment in microhabitats commonly used by lizards (Nordberg, unpublished data). Clay or plasticine models have successfully been used to measure attack frequencies and predation pressure for a variety of groups including but not limited to frogs (Saporito et al., 2007), lizards (Steffen, 2009), snakes (Brodie, 1993), and birds (Hollander et al., 2015). In January 2016, we also deployed 400 control models (patternless sphere models) to test if there was a difference in attack rates between lizard and control shaped models. This was done to test if attacks on models were predominantly from predators inspecting foreign objects and therefore not a true representation of predation. We compared the attacks on lizard and control models using a Student's *t*-test.

Lizard model fate scoring

Lizard models were deployed for seven days and were scored as "attacked" or "not attacked" upon collection. We identified predators from unique indentations from their mouthparts left on the lizard models. We verified invertebrate attack indentations by placing a lizard model in a small container with a potential predator (e.g., huntsman spider and centipede), and coercing it to bite the model. In cases when lizard models disappeared and could not be recovered, the data were removed and not included in the analysis. We acknowledge that some missing models may have been indeed removed by birds or other real predators, but because we occasionally found models trampled or chewed by cattle, we did not want to assume all displaced models represented actual predation events on lizards. Therefore, we acknowledge our predation rates, especially for vertebrate predators, are conservative estimates.

RESULTS

Spotlight surveys

We observed predation of frogs and geckos by snakes, birds, lizards, centipedes, spiders, and mantids, during our nocturnal surveys. In total, we observed four instances of vertebrate–vertebrate predation events and five invertebrate–vertebrate predation events (Table 6.1 and Figure 6.2). We emphasize that visual observations of predation events *in situ* were rare for both predator groups (vertebrate–vertebrate: 1 for every 125 surveys hours; invertebrate–vertebrate: 1 for every 100 survey hours).

Lizard models

Predators attack lizard shape models more frequently than control shapes models (t = -3.394, df = 13, P = 0.004) indicating that predators were able to distinguish the difference in model shape. Therefore, we feel confident that our estimates of predation on lizards are not a matter of predators exploring foreign objects. Predation on lizard models were also fairly rare (117 of 759 models attacked over seven days [after missing models were removed from the data; n = 41]). Only 15.4% of lizard models showed signs of predation attempts. The two most common predator groups were birds and invertebrates (Table 6.2). The predation on lizard models varied between the two sample periods (seasons) with more attacks on lizard models in the dry season (74 attacks; 18.9%) than the wet season (43 attacks; 11.6%). While birds remained the largest contributor of attacks in both the dry and wet season (91.9% and 72.1% respectively) invertebrate predation fluctuated between 6.8% in the dry season and 23.3% in the wet.

DISCUSSION

We have shown that predation events are rarely observed *in situ* in nature by researchers, yet these interactions must be common in natural populations. Most ecologists accept that just because predator–prey interactions are rarely observed, it does not mean they are not common or ecologically irrelevant. For example, vertebrate–vertebrate predation events are rarely observed, yet we accept that these interactions must occur quite frequently to sustain animal populations. We found, however that invertebrate–vertebrate predation events were approximately as common, in these systems, as vertebrate–vertebrate predation events.

Our visual observations indicated that invertebrate–vertebrate interactions were slightly more common than vertebrate–vertebrate interactions. Although our lizard models indicated birds were major predators to small lizards, predatory invertebrates were the second most important predatory group, larger than mammals and other reptiles. Our lizard models provide a different kind of measure from that determined from visual observations. We suspect that birds were more likely to attack the sedentary models because many birds are visual foragers and actively search for prey items (Barker and Vestjens, 1989, 1990). Furthermore, many predatory invertebrates, such as huntsman spiders are predominantly sit-and-wait foragers (Framenau et al., 2014), and therefore are less likely to encounter or attack a lizard model that is stationary. Finally, our lizard models were designed to match the size and shape of adult *Gehyra dubia* (snout-vent length = 40 – 60 mm; mass = 4 – 6 g), therefore we suspect that only the largest of invertebrates would likely attack the models. Thus, both our estimates of predation were, therefore, likely conservative estimates of predation pressure.

Although we have shown that sub-adult and adult herpetofauna groups are prey items of large invertebrates, we suspect smaller ages classes may be even more likely to be targets of predation by large predatory invertebrates, simply due to size differences. Both adult and juvenile life stages are known to be consumed by predatory spiders (Menin et al., 2005, Pramuk and Alamillo, 2002).

While the diets of many vertebrates can be classified by means other than visual observations, such as dissection of stomach contents (e.g., Shine, 1977;

Manicom and Schwarzkopf, 2011), stomach flushing (e.g., Legler and Sullivan 1979), or faecal dissection (e.g., McKnight et al., 2015; Nordberg et al., 2017), many invertebrates cannot be examined in the same way. Invertebrates, such as spiders, do not retain body parts of prey items during digestion and often consume primarily liquefied body material (Foelix, 2011). Spiders often retain body parts of prey items in their webs, but not all spiders use webs. For example, large huntsman spiders (Sparassidae), which we suggest are major predators of small herpetofauna, are active foragers and do not use webs for prey capture. Little is known about the ecology and natural history of many webless huntsman spiders, and therefore details regarding diet remain largely unknown (but see Henschel, 1994), with the exception of anecdotal and visual observations (Shine and Tamayo, 2015). Huntsman spiders occupy many of the same ecological niches as small lizards; in fact, a few species of huntsman spider (*Typostola barbata* and *Holconia immanis*) co-occurred on the main trunks of trees, presumably waiting to ambush prey (i.e., invertebrates or geckos). With the onset of new technology, such as stable isotope analysis or DNA extraction techniques, it may be possible to identify prey items from faecal samples of many predatory invertebrates (Symondson, 2002; Akamatsu et al., 2004; Sheppard and Harwood, 2005; Wise et al., 2006; King et al., 2008). We hypothesize that future examination of predatory invertebrate diets, via DNA testing or other methods, may indicate a greater proportion of vertebrates in the diet of many invertebrate predators than currently expected.

Conclusion

Disentangling food webs can be difficult, but understanding what eats what is critical for environmental management of communities (Johnson et al., 2007; Yugovic, 2015). While many aquatic systems have substantial bodies of work on predator–prey interactions, including knowledge of the diet of many invertebrate predators, there is a major knowledge gap in terrestrial systems. Many predation events are captured opportunistically in the form of photos or videos that appear on the internet (which can still provide valuable information on the food habits of predator groups), but few scientific studies have been designed to investigate the impacts of invertebrates on small vertebrate groups. Our data from visual observations, as well as attack frequencies on model lizards indicate that invertebrate predators do attack small vertebrates. In fact, in some systems where small vertebrate groups (e.g., herpetofauna) and large predatory invertebrates (e.g., spiders, centipedes) co-exist, predation rate on small herpetofauna may be similar. Not only are invertebrate predators abundant in the environment, but they often occupy the same microhabitats as many small vertebrate groups.

The relationship between small herpetofauna and large predatory invertebrates warrants more exploration. Due to the cryptic nature and rarity of observing predation events *in situ*, it is difficult to quantify the true predation pressure on small vertebrates by large predatory invertebrates. Furthermore, we illustrate a continued need for studying natural history and ecology of many cryptic species, including many predatory invertebrate groups such as spiders and centipedes.

TABLES

Table 6.1. Vertebrate–vertebrate and invertebrate–vertebrate predation events from 500 man-hours of visual searches.

Predator Type	Location	Date	Predator	Prey	Figure
Vertebrate	TCCP	May-16	Slaty-grey snake (*Stegonotus cucullatus*)	Green tree frog (*Litoria caerulea*)	
	TCCP	Sep-16	Asian house gecko (*Hemidactylus frenatus*)	Asian house gecko (*H. frenatus*)	
	TCCP	Nov-16	Slaty-grey snake (*S. cucullatus*)	Green tree frog (*L. caerulea*)	
	WGT	Aug-15	Blue-winged kookaburra (*Dacelo leachii*)	Unknown lizard sp.	
Invertebrate	TCCP	May-16	Huntsman spider (Sparassidae)	Green tree frog (*L. caerulea*)	
	TCCP	Jul-16	Huntsman spider (Sparassidae)	Native house gecko (*G. dubia*)	Figure 6.2B
	TCCP	Aug-16	Praying mantis (Mantodea)	Green tree frog (*L. caerulea*)	Figure 6.2C
	WGT	Feb-15	Whistling spider (Theraphosidae)	Fledgling bird (Unknown sp.)	
	WGT	Aug-15	Centipede (Scolopendromorpha)	Native house gecko (*G. dubia*)	Figure 6.2A

TCCP = Town Common Conservation Park, Townsville QLD; WGT = Wambiana Grazing Trial, Campase QLD.

Table 6.2. Attack frequencies (percentages) on model lizards at the Wambiana Grazing Trial, QLD, Australia.

	August 2015 Dry Season	January 2016 Wet Season
Total models deployed	400	400
Missing/removed[†]	10 (2.5%)	31 (7.8%)
Not Attacked	316 (79%)	326 (81.5%)
Attacked	74 (18.5%)	43 (10.8%)
Birds	68 (91.9%)	31 (72.1%)
Invertebrates	5 (6.8%)	10 (23.3%)
Other	1 (1.3%)	2 (4.6%)

[†] Models that went missing and therefore could not be recovered for inspection were not scored as "attacked" or "not attacked". Some missing models were likely removed from their location by birds, but we often found models trampled on the ground or models that we suspect had been removed from trees by cattle, and were therefore not counted in the predation estimates.

FIGURES

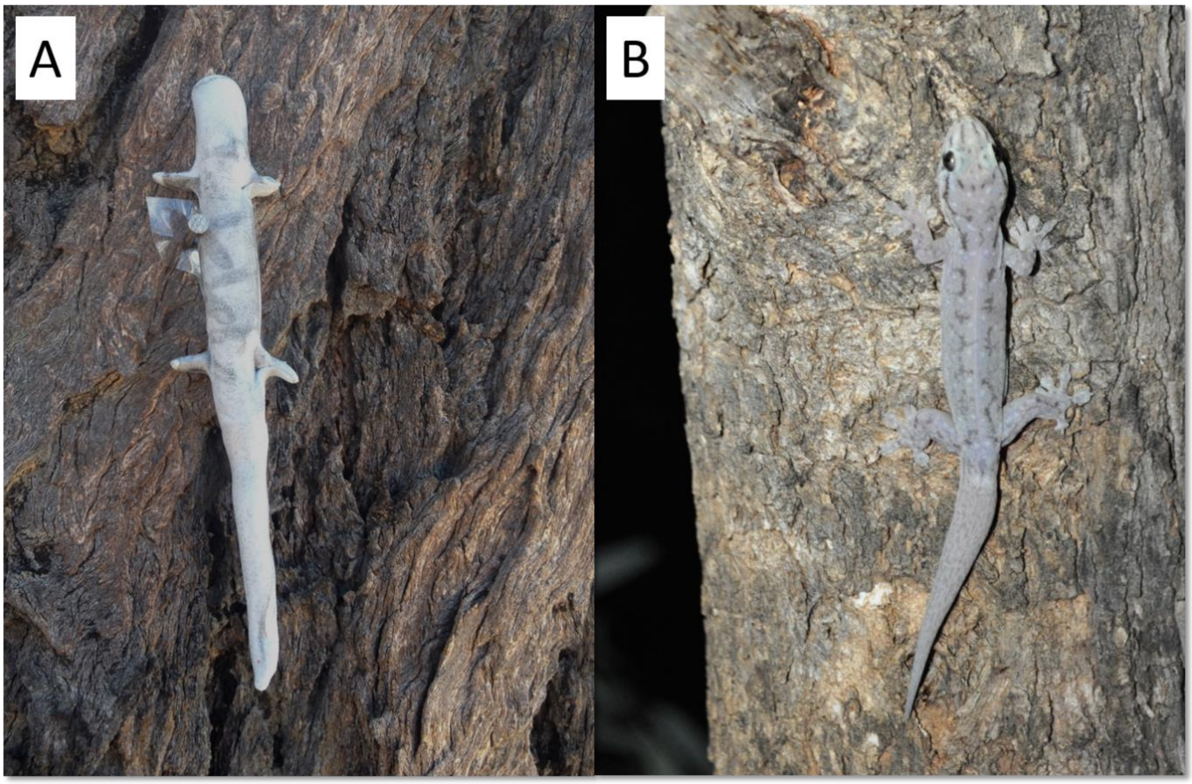


Figure 6.1. Blu-Tack® model (A) tacked to the main trunk of a Silver-leaf ironbark (*Eucalyptus melanophloia*) to estimate predation on lizards. Blu-Tack® models were made to resemble the Australian native house gecko (*Gehyra dubia*; B). Photographs (A and B) taken at Wambiana Grazing Trial, QLD, Australia by E. Nordberg.

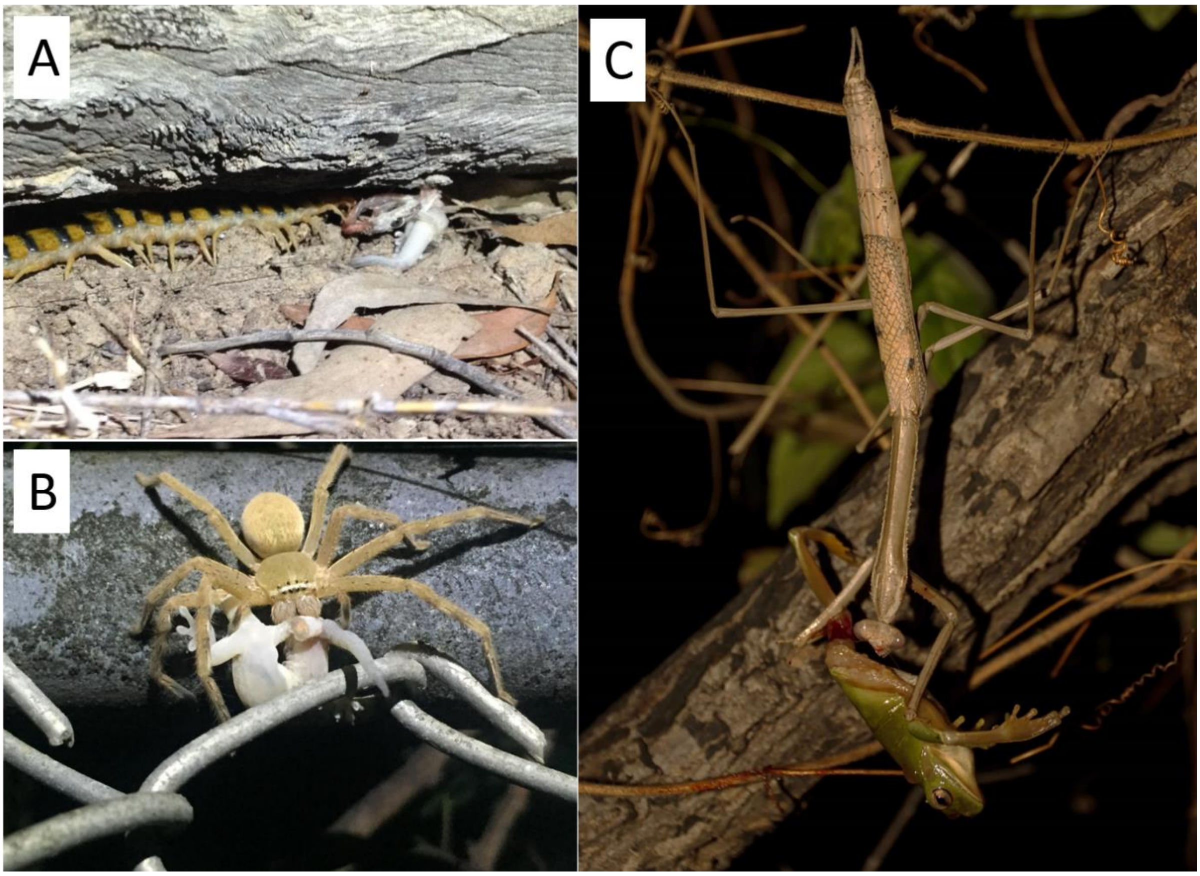


Figure 6.2. Predatory invertebrates consuming vertebrate prey. (A) Centipede (Scolopendridae) consuming an adult Australian native house gecko (*Gehyra dubia*); (B) Huntsman spider (Sparassidae) consuming a sub-adult *G. dubia*; (C) Praying mantis (Mantidae) consuming a sub-adult green tree frog (*Litoria caerulea*). (A) photographed by E. Nordberg near Charters Towers, QLD Australia; (B) photographed by L. Edwards and (C) photographed by R. Pillai in Townsville, QLD, Australia.

Chapter 7 – Mechanisms Allowing Generalist Species to Benefit from Habitat Homogenization

Under review as: Nordberg, E.J., and L. Schwarzkopf. Under review. Mechanisms allowing generalist species to benefit from habitat homogenization. Functional Ecology.

ABSTRACT

Complex environments support high biodiversity because they have abundant resources and diverse microhabitat availability, which may reduce the intensity of competition among species. Both natural and anthropogenic disturbances reduce the structural complexity of habitats, leading to homogenization. The high abundance of common, generalist species in disturbed habitats may be driven by reduced competition from specialists in similar habitats. We compared habitat utilization of three co-occurring arboreal geckos (northern velvet geckos, *Oedura castelnaui*, Australian native house geckos, *Gehyra dubia*, and eastern spiny-tailed geckos, *Strophurus williamsi*) in four replicated grazing regimes in an experimental grazing trial in northeast Queensland, Australia. In our system, native house geckos were most abundant in heavily grazed habitats where the two other species rarely co-occur (either with each other or with native house geckos). Geckos displayed resource partitioning of habitat features, such as tree species and tree structural characteristics. We found evidence of interspecific competition between gecko species, in which native house geckos shifted their habitat selection in the presence of velvet geckos. In the absence of other geckos, native house geckos preferred rough, peeling bark and dead trees; yet in the presence of velvet geckos, native house geckos used more structurally complex trees, probably due to high niche overlap (O = 0.74) between these species. Further, native house geckos were more resistant to the negative effects of livestock grazing than either velvet geckos or spiny-tailed geckos. In the absence of other species, native house geckos used a wider range of microhabitats. Our data suggest that grazing by livestock leads to the homogenization and simplification of habitat features. Further, the homogenization of the habitat then acts as the mechanism that homogenizes the arboreal lizard community, such that a reduction in competition from other gecko species has allowed expansion of a generalist (native house geckos) and habitat disturbance has caused reductions in specialist species (velvet geckos and spiny-tailed geckos).

KEYWORDS

Australia, cattle grazing, disturbance, habitat selection, homogenization, lizards, niche

INTRODUCTION

Anthropogenic disturbances modify habitats, often reducing habitat complexity (Connell 1978; Petraitis et al. 1989) and leading to environmental homogenization, in which the biodiversity of both plant and animal communities are reduced, presumably because only disturbance–tolerant species persist (Jones 1981; Milchunas et al. 1998; Olden 2006). Disturbed environments are often the sites of colonization by invasive species (see reviews by Sakai et al. 2001; Daehler 2003; Goodenough 2010), and a few disturbance–tolerant native species, reducing overall diversity (McKinney and Lockwood 1999). For example, the homogenizing impacts of livestock grazing on vegetation communities and structural complexity have been well documented (e.g., Milchunas and Lauenroth 1993; Fleischner 1994). Typically, grazing simplifies plant biodiversity by selecting for grazing–tolerant species (McNaughton 1984; Milchunas and Lauenroth 1993), and opens habitat, reducing the cover of grass and leaf litter, and increasing the amount of bare ground (Landsberg et al. 2003, Kutt and Woinarski 2007). Such effects over time lead to the homogenization of the vegetation community and a predictable suite of invasive and native species (McKinney and Lockwood 1999; Olden and Poff 2003).

The impacts of anthropogenic disturbance, including livestock grazing, on wildlife biodiversity are less well studied than those on plants (Belsky and Blumenthal 1997; Belsky 2003; McIntyre et al. 2003; Landsberg et al. 2003), but such studies often find that decreases in habitat heterogeneity lead to decreases in wildlife biodiversity

(Woinarski and Ash 2002; Martin and McIntyre 2007; Neilly et al. 2017). As in plants, however, while some fauna species may respond negatively to grazing and become extirpated locally, some species are successful in such habitats, becoming more common (Woinarski and Ash 2002; McIntyre et al. 2003; Newbold and MacMahon 2008; Neilly et al. 2017). For example, in some grazed landscapes, some reptile species become more common, which is often attributed to increases in solar radiation reaching the ground and improving the environment for ectotherms (Heath 1964; Hacking et al. 2014). In other cases, reptile biodiversity decreases, or stays the same in grazed landscapes (Woinarski and Ash 2002; Germano et al. 2012; Neilly et al. 2017). Because of the complexity of animal behavior and the many possible factors driving specific wildlife responses to disturbances, including livestock grazing, few studies quantify the contributions of specific mechanisms to changes in faunal communities (but see Pringle et al. 2007; Newbold and MacMahon 2008; Germano et al. 2012). Thus, the mechanisms driving faunal responses to disturbance are often poorly known, inferred from generalizations about an animal's biology and not specifically tested. Understanding mechanisms driving such faunal changes may help predict fauna community outcomes from disturbance.

Species, often with similar ecologies, often response to disturbances in different ways, which can be difficult to explain (Denslow 1987). In response to disturbance, some species become more common while others disappear, in a process called homogenization (McKinney and Lockwood 1999; Olden 2006). Simplification through homogenization has effects of habitat structure as well as animal communities and diversity. It is important to identify the mechanisms responsible for changes to both habitat structure and wildlife populations. One mechanism thought to drive differences in abundance among similar species is competition (Schoener 1974; Grace and Wetzel 1981; Chase et al. 2002). In theory, generalist species should have broader niches than specialists (Clavel et al. 2011), and if homogenization makes the habitat overall less suitable for a group, the generalists, which can, by definition, exploit a wider range of resources than specialists, should tolerate the disturbance better, persisting after the specialists have been extirpated (Munday 2004; Devictor et al. 2008). On the other hand, if a disturbance makes some habitat feature more available, or better in some way, and a specialist can exploit that feature, then we expect the specialist to outcompete the generalist (Auttum et al. 2006; Clavero et al. 2011). It is, therefore, difficult to predict the outcomes of species interactions such as competition in response to disturbance without detailed knowledge of the requirements of the individual species, and how habitat changes influence the availability of specific habitat features.

In this study, we described the habitat requirements and use of an assemblage of three species of nocturnal reptiles, with specific reference to the mechanisms leading to assemblage homogenization by livestock grazing. We described changes in community structure, species composition, and habitat selectively in this assemblage of arboreal geckos in a long-term, replicated, cattle grazing trial in northeast Australia. We set out to answer the following questions: 1 – Do some species benefit from livestock grazing, i.e., are they more abundant where grazing is more intense? If so, are the species that benefit microhabitat generalists or specialists? 2 – Does the availability of specific habitat features vary with disturbance (grazing pressure)? 3 – How do competitive interactions in the face of this disturbance shape community composition?

METHODS

Study site

Our study was conducted at the Wambiana Grazing Trial (WGT), an experimental grazing site located within the Wambiana Cattle Station, 70 km southwest of Charters Towers, Queensland, Australia. The WGT was designed by Queensland’s Department of Agriculture and Fisheries in 1997 to examine the impact of varying stocking rates and grazing strategies on land condition and beef production (O’Reagain et al. 2011). The WGT has replicated grazing regimes varying from moderate stocking (at the long-term carrying capacity of the site) to heavy stocking (at twice the long-term carrying capacity of the land), including different grazing strategies (i.e., when cattle numbers are adjusted annually, and how much area is protected from grazing by fencing). Each 100-ha paddock (two for each grazing treatment) includes equal proportions of two major eucalypt woodland forest types, Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*). We sampled 24, one-ha sites in both eucalypt forest types nested within four major grazing treatments (long term average stocking rates of: moderate stocking [MSR] = 8–10 ha/head; rotational wet-season spelling [ROT] = 7–8 ha/head, a lower impact grazing method in which 1/3rd of the paddock has no grazing for 4-6 months of the year; variable stocking [VAR] = 3–12 ha/head the same stocking rate, but animals roam freely; and heavy stocking [HSR] = 4–5 ha/head; Table 7.1).

Study species

Australian native house geckos (*Gehyra dubia*; Figure 7.1a) are common medium-sized geckos (snout-to-vent (SVL) length = 65mm) found throughout eastern Australia (Wilson 2015). They forage on invertebrates, including spiders and beetles (Nordberg et al. 2017) and are commonly found around human dwellings and buildings foraging around lights in tropical areas (Zozaya et al. 2015). Northern velvet geckos (*Oedura castelnaui*; Figure 7.1b) are large (SVL = 90mm) insectivorous geckos that often shelter under loose bark or in dead trees (Wilson 2015). Northern velvet geckos occupy dry woodlands and rocky outcrops throughout northeastern Australia. Eastern spiny-tailed geckos (*Strophurus williamsi*; Figure 7.1c) are medium-sized (SVL = 60mm) arboreal geckos found throughout eastern eucalypt woodlands and sclerophyll scrub (Wilson 2015). They often occur on small trees, bushes, and slender twigs.

Gecko surveys

We sampled arboreal lizards at the WGT from 2015–2017. Lizards were captured by hand using two survey methods: nocturnal spotlight surveys, and arboreal cover boards (ACBs; Nordberg and Schwarzkopf 2015), or both. We used timed, area-constricted spotlight searches to capture lizards: two researchers searched a one-ha site for 20 min (40 total search-minutes). We also used ACBs to facilitate capture of arboreal lizards. ACBs act as artificial bark that lizards use as diurnal refuge. The use of ACBs also helps maintain natural refugia, such as loose and peeling bark, which can be damaged while searching for sheltering lizards. We deployed eight ACBs at each site, which were checked daily, and moved to new trees after two days. By the end of each survey period, ACBs had been attached to 24 different trees throughout each site. All lizards were captured and brought back to the field station for individual marking with visible implant elastomer tags (Northwest Marine Technology, Shaw Island, WA, USA) and to record morphometric data. Captured lizards were linked to specific trees (see habitat assessment below) and released at the tree of capture the following night. By linking the presence of geckos to specific trees during surveys, we were able to identify how frequently multiple geckos (within and among species) occupied the same tree at the same time.

Habitat assessment

We measured available habitat features at each site from three parallel 100 m transects. We classified the percent ground cover (e.g., bare ground, grass cover, coarse woody debris) along each transect and characterized tree species within 2 m of each transect. We measured the composition of trees that fell within each transect to get an unbiased estimate of available tree species at each site. In addition, we assessed the structural characteristics and complexity of a subset of trees available to lizards (Table 7.2). This subset of trees were selected randomly within the site and from trees on which geckos were found during both ACB and spotlight surveys. Each tree was tagged with a unique numbered tree tag so we could relate the occupancy of each gecko to particular trees.

Niche breadth and overlap

We used two measures to estimate resource use and niche overlap among species. Niche breadth (*B*; Levins 1968) was calculated as a measure of resource use from the proportion (*p*) of individuals using the resource (*i*). We used a variation of this calculation, the adjusted niche breadth (B_{adj}; Equation 1; Hurlbert 1978), which standardizes the niche breadth to values between 0 (very specialized) and 1 (generalist). Niche overlap (*O*; Equation 2; Pianka 1973) was used as a measure of similarity in resource use among species. This compares the proportion of resource *i* used by species *j* (P_{ij}) compared to the proportion of resource *i* used by species *k* (P_{ik}). This value also ranges from 0 (no resources in common) to 1 (total overlap in resource use) between species.

Data analysis

We classified habitat selection by calculating Manly selection ratios using a type I design from the *adehabitatHS* package in the statistical program R (Calenge 2006; R Core Team 2016). We measured habitat use and availability on a population level. Manly selection ratios were used to compare the proportion of resource use to resource availability (Manly et al. 2007). We calculated Manly selection ratios for each gecko species for all of our habitat features, including tree species and structural complexity measures.

We compared the habitat selection of each gecko species when they co-occurred with other arboreal gecko species, and when they were the only arboreal species present at a site, where possible. Habitat availability and use were recalculated for each subset of data to account for changes in habitat features among the subset data. We used a multivariate analysis of variance (Type II MANOVA Tests: Pillai test) and canonical discriminant analysis (CDA; *candisc*, Friendly and Fox 2016) to test if there were significant differences in habitat selection among gecko species. We used the Manly selection ratios for each habitat characteristic (structure and tree species) as our response variable, and the gecko species occurrences (e.g. *Gehyra* only, *Gehyra* co-occurring with *Oedura*, *Gehyra* co-occurring with *Oedura* and *Strophurus*, etc.) as our grouping variable vectors. We used principal component analysis (PCA; *vegan*, Oksanen et al. 2017) to visualize the separation and shift in habitat selection among the three gecko species when alone and when co-occurring.

We ran generalized linear mixed-effects models (GLMM) with model selection to identify the habitat composition variables important to geckos, and therefore to determine which habitat variables should be included in subsequent analyses. We ran GLMMs with a negative binomial distribution for each gecko species with abundance (counts) as the response variable, environmental habitat composition variables as fixed effects, and site as a random factor. We used the ‘dredge’ function in the package *MuMIn* (Barton 2016) to identify a top model (ΔAICc < 2) with a subset of important habitat variables to be included in further analyses. We then used the same methodology described above (MANOVA and CDA analyses) to quantify differences in available habitat features among the four grazing regimes by using the habitat variables included in the top models as our response variables, and grazing regime as our grouping variable. All analyses were conducted using the program R (R Core Team, 2016).

RESULTS

Gecko abundance

We captured a total of 1566 geckos (Australian native house geckos, *Gehyra dubia*; n = 1493; northern velvet geckos, *Oedura castelnaui*; n = 52; and eastern spiny-tailed geckos, *Strophurus williamsi*; n = 21) over six survey periods from 2015–2017. All geckos were captured in 145 hours of spotlighting or flipping ACBs (n = 4992 boards). Native house geckos were the most abundant gecko species and were present at all 24 sites. Velvet and spiny-tailed geckos were less abundant, and were present at 11 and 6 sites, respectively.

We found a significant positive effect of grazing on abundance of native house geckos ($F_{3,19} = 5.349$, $P = 0.007$) such that native house geckos were more abundant in the heavily stocked paddocks, and there was no significant effect of woodland type on their abundance (Silver-leaf ironbark sites versus Reid River box sites; $F_{1,19} = 3.135$, $P = 0.092$; Figure 7.2a). The abundances of velvet geckos were low in general, and we were unable to detect a significant effect on abundance of velvet geckos of either grazing ($F_{3,19} = 0.185$, $P = 0.905$) or woodland type ($F_{1,19} = 1.545$, $P = 0.229$; Figure 7.2b). The abundance of spiny-tailed geckos showed a significant trend opposite to native house geckos, with the lowest abundances in the heavily grazed areas, and highest abundance in the lowest stocked paddocks ($F_{3,19} = 3.414$, $P = 0.038$), and no significant effect of woodland type on their abundance ($F_{1,19} = 3.470$, $P = 0.078$; Figure 7.2c).

Habitat assessment

We classified the structure and identity of a subset of available trees across the study area (n = 1045), including nine dominant tree species: Beefwood (*Grevillea striata*), Blackbutt (*Eucalyptus cambageana*), Bloodwood (*Corymbia clarksoniana*), Brigalow (*Acacia harpophylla*), Box (*Eucalyptus brownii*), Coolabah (*Eucalyptus* *coolabah*), dead trees (which included multiple species), False sandalwood (*Eremophila mitchellii*), and Ironbark (*Eucalyptus melanophloia*). We assessed the structural complexity of 43.5 ± 4.6 (mean ± SE) trees per one-ha site. Canonical discriminant analysis indicated significant separation in the available habitat structure among the grazing treatments on habitat composition ($F_{36,33} = 2.289$, $P = 0.040$; Figure 7.3). We found that sites with heavy stocking rates (HSR) were less structurally complex (e.g., characterized by less leaf-litter cover, and grass cover, shorter grass height, less coarse woody debris, and more bare ground) than other grazing regimes. We found that heavily stocked (HSR) paddocks clustered furthest from any of the other grazing regimes. Ground cover features, such as grass cover and leaf litter cover clustered near the moderate stocking rate (MSR) and rational (ROT) grazing regimes, with lower stocking rates.

Habitat selection

Overall habitat selection by arboreal gecko species, in terms of tree species ($F_{18,62} = 7.857$, $P < 0.001$; Figure 7.4a) and structural characteristics of trees ($F_{18,62} = 3.461$, $P < 0.001$; Figure 7.4b), was significantly different. Native house geckos (*G. dubia*) were the most generalist species in terms of tree selection; they were found on all nine species of tree throughout the study area. In terms of selectivity overall, native house geckos preferred (showed a positive selection) for Silver-leaf ironbark trees, whereas they avoided Reid River box and False sandalwood trees, and used all the other species at random (Table 7.3). Native house geckos preferred high bark indices (high 'flakiness') and complexity values, in terms of both the number of branching nodes as well as the number of trunks in the tree system. In the absence of other geckos, native house geckos preferred dead trees and high bark indices, yet in the presence of velvet geckos (*O. castelnaui*), native house geckos shifted their habitat selection away from dead trees, and towards high measures of tree structural complexity (Figure 7.5).

Northern velvet geckos (*O. castelnaui*) preferred dead trees and trees that contained hollows and dead branches. They were found on only five species of tree throughout the study area. Velvet geckos did not show a positive selection for any tree species in particular, just dead trees, but showed significant avoidance of Reid River box, Beefwood, Brigalow, Bloodwood, and Coolabah trees. Similar to native house geckos, velvet geckos also preferred high bark indices, preferring trees with flaking and peeling bark.

Eastern spiny-tailed geckos (*S. williamsi*) were the most specialized geckos, and occurred on only four tree species. Spiny-tailed geckos preferred False sandalwood trees, avoided Reid River box, Beefwood, Blackbutt, Bloodwood, Coolabah, and dead trees. They showed strong positive selection for small shrub-type trees (False sandalwood, Brigalow trees, and shrubs). They showed strong associations with trees that did not contain hollows, dead branches, and low bark indices, all of which were characteristic of small shrubby trees.

We rarely found multiple gecko species occupying the same tree, further suggesting competition among species. Native house geckos and velvet geckos both showed positive selection for dead trees, yet in sites where they both occurred, we only observed a velvet gecko and a native house gecko occupying the same tree (live Reid River Box tree) at the same time once throughout our study. Similarly, we did not observe native house geckos and spiny-tailed geckos occupying the same tree at the same time, likely due to their dissimilar habitat preferences. While native house geckos are generally aggressive and tend to avoid each other in confined spaces (Cisterne et al., ms submitted), we did find multiple native house geckos occupying the same tree at the same time, accounting for 15% of our observations of native house geckos. Co-occupying a tree by two or more native house geckos was more common in the dry season (72% of co-occupied observations) than the wet season (28%) and were predominantly male-female associations (52%), followed by female-female (26%) and male-male (22%) associations.

Niche breadth and overlap

Native house geckos (*G. dubia*) had the widest niche breadth overall, both when they were the only arboreal gecko occupying a site, and when co-occupying sites with other arboreal gecko species (Table 7.4). While the niche breadth of native house geckos remained fairly consistent (B_{adj} = 0.27–0.32 [range]), habitat selection varied depending on the presence or absence of other arboreal geckos (see above). On the other hand, the niche breadth of velvet geckos (*O. castelnaui*) and spiny-tailed geckos

(*S. williamsi*) remained consistent regardless of the presence of other geckos (velvet geckos, B_{adj} = 0.17–0.17; spiny-tailed geckos, B_{adj} = 0.16–0.18). Native house geckos and velvet geckos exhibited high niche overlap both when they co-occurred (*O* = 0.74) and when all three arboreal gecko species co-occurred (*O* = 0.76). Native house geckos and spiny-tailed geckos exhibited minimal niche overlap when they co-occurred (*O* = 0.07), but overlapped more when all three geckos co-occurred (*O* = 0.30). Spiny-tailed geckos and velvet geckos exhibited the least niche overlap when all three species co-occurred (*O* = 0.18), as their habitat preferences were dissimilar. Native house geckos increased in niche breadth with increasing stocking rate, while spiny-tailed geckos and velvet geckos showed a decrease in niche breadth (Table 7.5).

DISCUSSION

Homogenization of the habitat was clearly occurring, with greater grazing impact in this agricultural system. Habitat characteristics relevant to the geckos had less cover, were less common, or were not present in the heavily grazed sites. In addition, two of the three gecko species were generally absent in the heavily grazed areas, whereas the most common species was more abundant and often occurred alone in heavily grazed areas. A reduction in habitat structure and complexity will lead to decreased diversity in animal communities and disturbance sensitive fauna associated with those habitat characteristics (Manning et al. 2013; Howland et al. 2014). Further, few studies have documented the change in competitive interactions that ensue as a result of habitat homogenization, and specifically how they impact faunal community structure, except to predict low diversity.

Habitat partitioning

All three species of gecko (*G. dubia*, *O. castelnaui*, and *S. williamsi*) used trees and vertical structures as their primary microhabitat, although native house geckos (*G. dubia)* and northern velvet geckos (*O. castelnaui)* also used terrestrial habitats at times (Nordberg, pers obs). The arboreal habitat at our study site included multiple tree species of varying structural complexity, ranging from simple, dead (standing) trees, to complex branching living trees, shrubs, and small trees. The geckos we studied varied from microhabitat generalists to specialists. Native house geckos used microhabitat features most generally, with no strong preference for particular tree species, but positive selection of trees with loose, peeling bark, and hollows or cavities. Velvet geckos were more specialized, preferring dead trees and hollows. Eastern spiny-tailed geckos (*Strophurus williamsi*) were most selective in their microhabitat use, preferring False sandalwood, and short, shrub-like trees. Given that both native house and velvet geckos preferred dead trees, we expected some level of competition for resources, whereas habitat preferences for spiny-tailed geckos were the least similar to the others, and so we expected little or no competition among species.

Competition, niche breadth, and niche overlap

While each gecko species used slightly different microhabitats, we begin tease apart whether these differences were due to habitat preferences or competitive exclusion. Native house geckos occurred at every site (n = 24), and were the only arboreal geckos occupying nine of our sites. We examined their habitat selection and niche breadth when they were the sole arboreal gecko at a site and compared it to their habitat selection when they co-occupied a site with velvet or spiny-tailed geckos, or both species. We expected the niche breadth of native house geckos to increase when they were the sole arboreal geckos at a site, having unimpeded access to all microhabitats and resources. In the absence of other competitors, animals should increase their realized niche to more closely match their fundamental niche (Diamond 1970; Lister 1976; Luiselli 2003). However, this was not the case; the niche breadth for native house geckos did not increase greatly when it was the sole occupant of a site. Although the niche breadth did not increase, however, niche breadth only examines the *breadth* of resources used, not the nature of those resources. Thus, while native house geckos used approximately the same proportion of available habitat features and microhabitats as when competitors were present, they shifted their microhabitat use in the presence of other species. Native house geckos showed no positive selection for tree species (i.e., using tree species in proportion to their availability) when occupying a site without other arboreal gecko species, although they preferred dead trees, and trees with a high bark indices. Yet, in the presence of velvet geckos, native house geckos changed their habitat selection to prefer Silver-leaf ironbark trees, trees with high bark indices, and high tree complexity measures (branching and trunks).

Velvet gecko habitat preferences overlap with those of native house geckos (dead trees and high bark indices values). Velvet geckos likely outcompete where they occur with native house geckos because velvet geckos are almost twice the size of native house geckos, and therefore competitive exclusion probably prevents native house geckos from occupying dead trees in the presence of velvet geckos. The abundance of velvet geckos were much lower than native house geckos, and therefore it is difficult to quantify the effect of completive exclusion in this natural experiment. It would be beneficial to replicate this experiment in an artificial manor to directly test competition among species. Further, it remains unclear to what extent intraspecific competition among native house geckos may contribute to changes in habitat selection both when other gecko species co-occupy a site, and when native house geckos are the sole arboreal gecko species present. The habitat selection of native house geckos in the presence of only spiny-tailed geckos did not change much compared to their habitat selection when alone, as these two species had minimal niche overlap and preferred different tree species and structure.

Response to livestock grazing

Native house geckos were more generalist in terms of microhabitat selection (tree species), habitat types, and even disturbance levels, i.e., they had the highest abundance in all the grazing treatments. While all three geckos occurred in both the Silver-leaf ironbark and Reid River box woodlands, spiny-tailed geckos only occurred at sites where short shrub–like trees (e.g., False sandalwood trees) were more abundant. In terms of disturbance, spiny-tailed geckos were found only in areas with low stocking rate and low grazing pressure from livestock. False sandalwood trees were more closely associated with paddocks with low to intermediate stocking levels (MSR and ROT), where spiny-tailed geckos were most abundant. This suggests that spiny-tailed geckos were constrained by habitat availability, influenced by grazing (Figure 7.3). We suspect that spiny-tailed geckos may be more susceptible to the impacts of grazing compared to velvet or native house geckos, in part because they occur close to the ground, where foraging cattle can directly disturb and alter the structure of shrubs and small trees (Seifan and Kadmon 2006; Neilly et al. 2017). Velvet and native house geckos occurred in all grazing treatments, but velvet geckos were less abundant in areas with heavy stocking rates. As a microhabitat specialist, velvet geckos were apparently less able to use heavily grazed sites due to reduced habitat suitability. The abundance of native house geckos was greatest in the most heavily stocked paddocks, indicating they were resistant to, and even benefitted from, disturbance by livestock grazing (Neilly et al. 2017; Nordberg et al. 2017). We have demonstrated that this benefit is, at least partly, driven by the absence of their competitor, velvet geckos, rather than the availability of preferred habitat.

Homogenization: winners and losers

Habitat modification by grazing led to landscape-level homogenization on our sites, producing changes in fauna species composition. We found livestock grazing altered vegetation complexity and structure, as in other studies (Landsberg et al. 2003; Dias et al. 2007) which can have major effects on lizard diversity (this study; Jones 1981; James 2003; Castellano and Valone 2006). While some species may benefit from open habitats produced by grazing (Brown et al. 2011; Nordberg et al. 2017; Neilly et al. 2017), many species show negative responses to grazing by livestock (Bock et al. 1990; Woinarski and Ash 2002; Hellgren et al. 2010). A reduction in lizard diversity in disturbed habitats may benefit those that are more tolerant to, or prefer disturbed habitat, and therefore reduce competition for resources. We predicted an increase in niche breadth by remaining lizards (native house geckos in this study, *G. dubia*) in areas with less competition (heavy stocking rates). Our data support this hypothesis, the niche breadth of native house geckos increased slightly but consistently with increasing stocking rates and impacts from grazing (where the abundance of competitors decreased), indicating that native house geckos used a wider variety of resources in areas with heavy grazing and less competitors. While multiple factors are likely responsible for community level changes to species composition, our data suggests reduced competition (completive release; Connell 1961) from specialist species allowed an abundant, generalist species to increase in abundance and occupy a wide variety of niches. Grazing by livestock acted as the mechanism that homogenized the environment by reducing vegetative complexity, but also homogenized the lizard community by promoting the success of a generalist through competitive release in areas where specialists suffered.

In summary, we found that native house geckos were more abundant in disturbed environments, and increased their resource use in the absence of competitors. Velvet and spiny-tailed geckos were both microhabitat specialists, and were less abundant in disturbed sites due to a lack of available habitat structure associated with heavy grazing. Our results suggest that habitat disturbance by livestock grazing homogenized the structural habitat, reduced the ability of the two specialist species (*O. castelnaui* and *S. williamsi*) to live in these areas, and lack of competition promoted the abundance of the generalist species (*G. dubia*). In addition, direct habitat change driven by cattle grazing (suppression of False sandalwood trees) apparently reduced the abundance of spiny-tailed geckos, a shrub specialist. Livestock grazing was the mechanism leading to the homogenization and simplification of habitat structure, which ultimately led to changes in the species composition, driven by multiple processes. With decreased abundance and competitive pressure from velvet geckos, native house geckos became more abundant and used habitat features otherwise preferred by, and dominated by velvet geckos. In contrast, in the presence of spiny-tailed geckos, we saw minimal changes in resource use by native house geckos as their preferred habitats were dissimilar. The greater abundance of native house geckos in heavily grazed environments, taken together with a decline in abundance of other geckos suggests reduced competition may facilitate native house geckos in expanding their niche, both in terms of habitat features, but also landscape scale occurrences (disturbed environments).

It is important to highlight that homogenization happens, but it is even more important to identify the mechanism(s) that lead to homogenization. Here, we have used cattle grazing as the mechanism that leads to homogenization of the habitat, where vegetative structure and complexity have been simplified by livestock grazing. Further, the homogenization of the habitat then acts as the mechanism that homogenizes the arboreal lizard community, in which reduced competition among gecko species has resulted in the expansion of a generalist (native house geckos) and reduction in specialist species (velvet geckos and spiny-tailed geckos). Without understanding the cause of homogenization (of the environment or species assemblages) to occur, we cannot prevent, mitigate, or predict it from happening in the future. We can use this information to increase or maintain biodiversity by understanding species responses to disturbances, such as livestock grazing, and ultimately habitat complexity.

EQUATIONS

Eq. 1:

$$Levins\ Niche\ Bredth\text{:}\quad B = \frac{1}{\sum P_i^2} \quad ; \quad B_{adj} = \frac{B-1}{n-1}$$

Eq. 2:

$$Pianka\text{'}s\ Niche\ Overlap\text{:}\quad O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum {P_{ij}}^2 {P_{ik}}^2}}$$

TABLES

Table 7.1. Descriptions and rationale for the stocking regimes at the Wambiana Grazing Trial, Queensland, Australia. Stocking rate represents the number of hectares available per adult equivalent (AE; based on a 450kg steer). Adapted from O'Reagain and Bushell 2011.

Stocking Regime	Stocking Rate (ha/AE)	Description
Moderate Stocking (MSR)	8–10	Constant stocking rate equal to the long-term carrying capacity of the paddocks. Considered a low stocking rate.
Rotational Wet Season Spelling (ROT)	7–8	Relatively constant stocking rate 50% above the long-term carrying capacity. Two-thirds of the paddock are used for grazing while one-third is rested during the wet season.
Variable Stocking (VAR)	3–12	Variable stocking rate in which cattle are adjusted up or down at the end of the wet season depending on the remaining available pasture feed, reduces land condition more than the rotational method, although mean stocking rates are similar.
Heavy Stocking (HSR)	4–5	Constant stocking rate at 2x the long-term carrying capacity of the paddock.

Table 7.2. Description of arboreal habitat features measured from the subset of available trees (n = 1045). All dead trees were identified as “dead trees” under the tree species category, as standing dead trees were often unidentifiable to species level.

Category	Description
Tree species	Tree species were identified.
Canopy connectivity	Whether tree canopy was connected to adjacent trees (yes/no).
Bark roughness	Tree bark was classified as "smooth" or "rough".
Branching complexity	Number of major branching events split from of the main trunk.
Trunk complexity	Number of major trunks growing out of the ground in a single tree cluster or system.
Bark index (1-3)	An index of bark roughness and flakiness ranging from 1–3; 1 represents little or no flaking bark, with few refuge options for sheltering lizards; 3 represents very flaky and loose bark with ample refuge microhabitats available for sheltering lizards.
Hollows present	Whether trees contained hollows or cavities visible from the ground (yes/no).

Table 7.3. Habitat selection ratios (Manly selection ratios) for structural characteristics and tree species for the gecko community. Overall selection represents the habitat selection for each species with all sites combined, regardless of other species presence. Gecko community columns represent the selection ratio value for varying gecko occupancies (“G” = *Gehyra dubia*, “O” = *Oedura castelnaui*, and “S” = *Strophurus williamsi*). Combinations of gecko codes (e.g., “O.G”) represents the selection of the first species listed (*Oedura castelnaui*) in the presence of any remaining species codes listed (*Gehyra dubia*). Manly selection ratios greater than 1.0 represent a positive selection, whereas values below 1.0 represent a negative selection or avoidance. Selection ratios significantly different from random selection (1.0) are represented in bold.

		Overall Selection			Gecko Community Occupancy							
		G.dubia	*O.castelnaui*	*S.williamsi*	*G.*	*G.O.*	*G.S.*	*G.O.S.*	*O.G.*	*O.G.S.*	*S.G.*	*S.G.O.*
Structural Characteristics	Canopy.Connected	0.989	0.722	0.812	1.001	0.999	1.026	1.088	0.706	**0.452**	0.749	0.968
	Canopy.Seperated	1.006	1.163	1.110	0.999	1.001	0.983	0.930	1.178	**1.435**	1.168	1.025
	Bark.rough	1.015	0.990	1.000	0.931	**1.027**	**1.074**	**1.113**	0.997	1.114	1.066	1.023
	Bark.smooth	0.846	1.098	0.998	1.029	**0.747**	**0.572**	**0.417**	1.025	0.411	0.617	0.882
	Bark.Index.1	0.721	0.239	1.319	**0.772**	**0.648**	**0.857**	**0.827**	**0.258**	**0.366**	0.116	1.045
	Bark.Index.2	**1.182**	**1.576**	0.931	1.094	**1.173**	**1.243**	1.182	1.450	2.011	1.019	0.958
	Bark.Index.3	**1.364**	**1.885**	0.405	**1.360**	**1.435**	1.101	1.261	1.800	1.293	0.560	0.923
	Hollows.Present	0.962	**3.339**	0.000	1.044	0.823	0.734	**0.392**	**3.276**	**3.382**	**0.000**	**0.000**
	Hollows.Absent	1.005	0.720	1.120	0.995	1.022	1.033	1.082	**0.722**	**0.680**	**1.126**	**1.134**
	Complexity.low	0.859	1.086	1.037	0.942	**0.841**	**0.796**	**0.834**	1.123	0.745	0.878	**0.357**

	Complexity.high	**1.294**	0.821	0.923	1.133	**1.300**	**1.393**	**1.278**	0.769	1.427	1.063	**1.384**
	Trunks.1	0.928	0.987	0.658	**0.936**	**0.955**	0.954	1.034	1.047	1.058	0.673	0.625
	Trunks.2+	**1.473**	1.086	**3.259**	**1.721**	**1.202**	1.261	0.864	0.787	0.769	2.838	2.500
Tree Species	Beefwood	0.805	**0.000**	**0.000**	0.000	0.717	0.767	0.000	0.000	0.000	0.000	0.000
	Blackbutt	1.395	0.620	**0.000**	0.000	1.213	0.384	1.300	0.329	0.294	0.000	0.000
	Box	**0.906**	**0.300**	0.392	1.039	**0.752**	0.961	**0.667**	0.327	0.579	**0.402**	0.723
	Brigalow	0.715	**0.000**	6.302	0.000	0.448	0.844	0.393	**0.000**	**0.000**	4.393	0.000
	Bloodwood	0.553	**0.000**	**0.000**	**0.225**	0.922	0.000	0.590	**0.000**	**0.000**	0.000	0.000
	Dead	1.116	**3.403**	**0.000**	**1.501**	1.149	**1.611**	0.806	**3.289**	1.763	0.000	0.000
	Sandalwood	**0.212**	1.957	**20.89**	0.450	**0.165**	**0.192**	**0.079**	1.316	1.528	**11.71**	**11.93**
	Ironbark	**1.123**	0.863	0.351	0.868	**1.252**	0.986	**1.879**	0.865	1.491	0.854	0.582
	Coolabah	1.073	**0.000**	**0.000**	1.802	0.717	0.000	0.000	**0.000**	**0.000**	0.000	0.000

Table 7.4. Adjusted niche breadth (0–1; Hurlbert 1978) and overlap (0–1; Pianka 1973) values for three arboreal gecko species on grazed land in northern Australia. Grouped species represent sites where these geckos co-occur.

Species Present	Niche Breadth (B_{adj})	Niche Overlap (O)
Gehyra dubia	0.28	
Gehyra dubia	0.27	0.74
Oedura castelnaui	0.17	
Gehyra dubia	0.32	0.07
Strophurus williamsi	0.16	
Gehyra dubia	0.29	*Gehyra* vs. *Oedura* = 0.76
Oedura castelnaui	0.17	*Gehyra* vs. *Strophurus* = 0.07
Strophurus williamsi	0.18	*Oedura* vs. *Strophurus* = 0.18

Table 7.5. Adjusted niche breadth (Hurlbert 1978) for each gecko species in four grazing regimes with different stocking rates; heavy stocking at twice the carrying capacity of the land (HSR), variable stocking to more than twice carrying capacity (VAR), fairly low stocking with spelled areas (ROT), and moderate stocking levels at the carrying capacity of the land (MSR). Note the trend to wider niches in moderately stocked paddocks, except in native house geckos (*G. dubia*).

	Niche Breadth (B_{adj})			
Species	HSR	VAR	ROT	MSR
Gehyra dubia	0.37	0.35	0.30	0.32
Oedura castelnaui	0.19	0.15	0.17	0.30
Strophurus williamsi	0.00	0.00	0.19	0.31

FIGURES

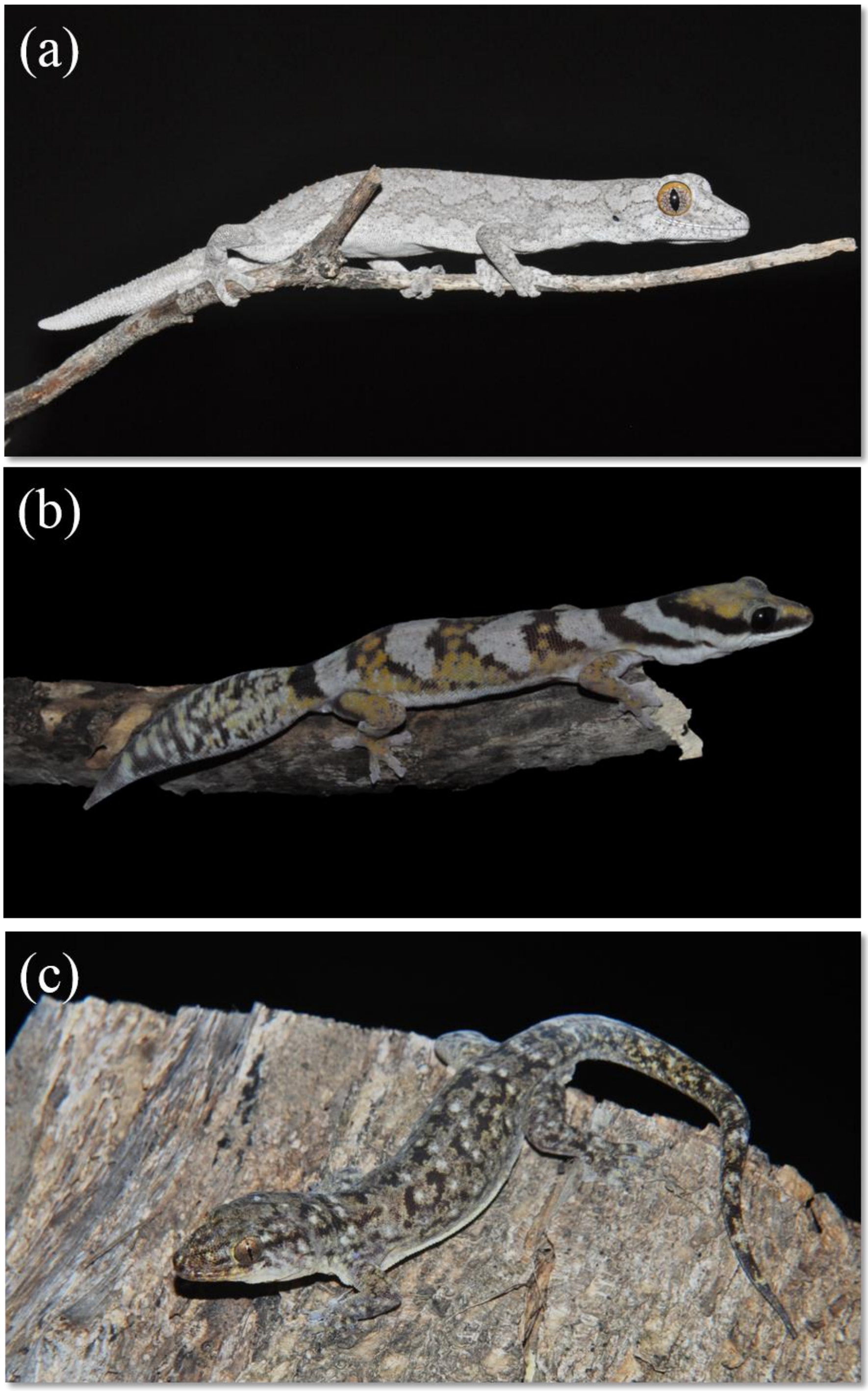


Figure 7.1. Eastern spiny–tailed gecko (*Strophurus williamsi*; (a)), Northern velvet gecko (*Oedura castelnaui*; (b)) and Australian native house gecko (*Gehyra dubia*; (c)). All photographs by E. Nordberg 2017.

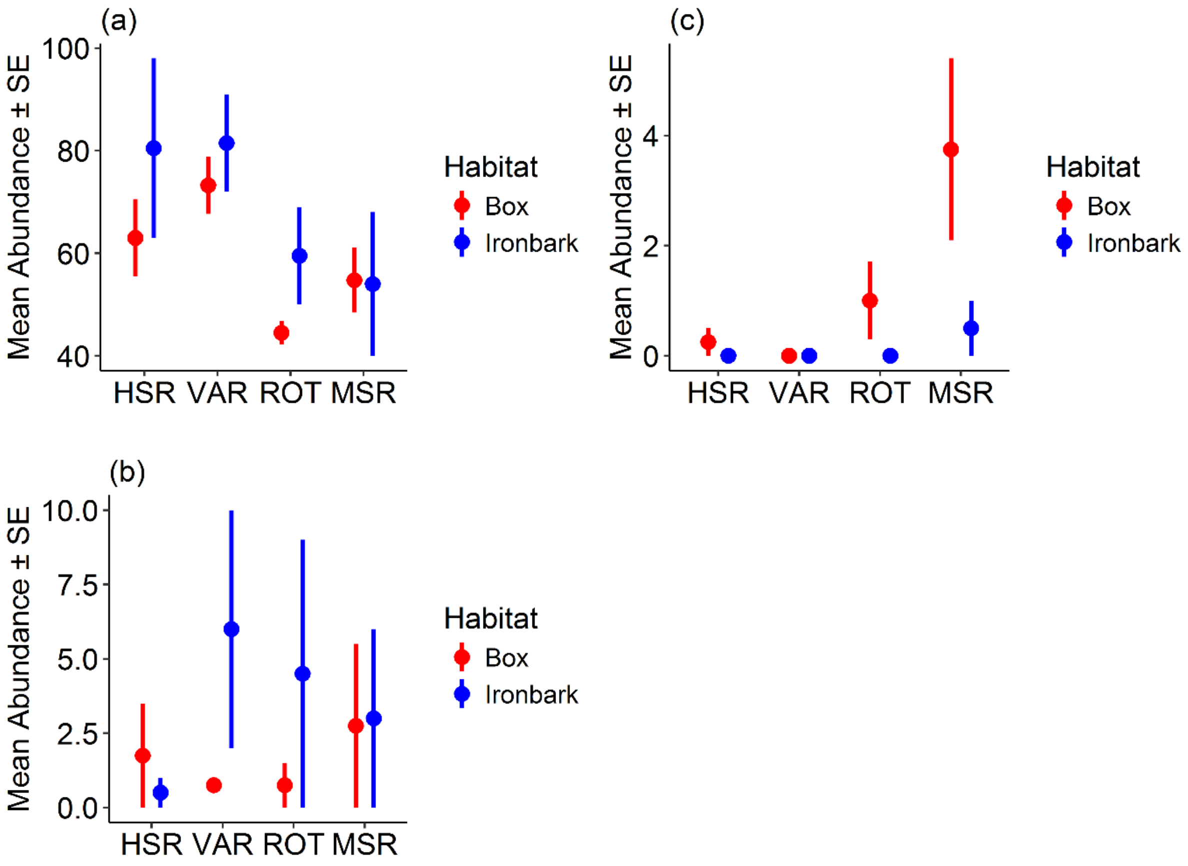


Figure 7.2. Abundance (mean ± SE) of three arboreal geckos Australian native house geckos (*Gehyra dubia)* [a], northern velvet geckos (*Oedura castelnaui)* [b], and eastern spiny-tailed geckos (*Strophurus williamsi*) [c]) in four grazing regimes and two habitat types. Stocking regimes range from heavy – light from left to right; heavy stocking – HSR, variable stocking – VAR, rotational wet season spelling – ROT, and moderate stocking – MSR. Habitat represents woodland types, Reid River box (*Eucalyptus brownii*; Box) and Silver-leaf ironbark (*Eucalyptus melanophloia*; Ironbark).

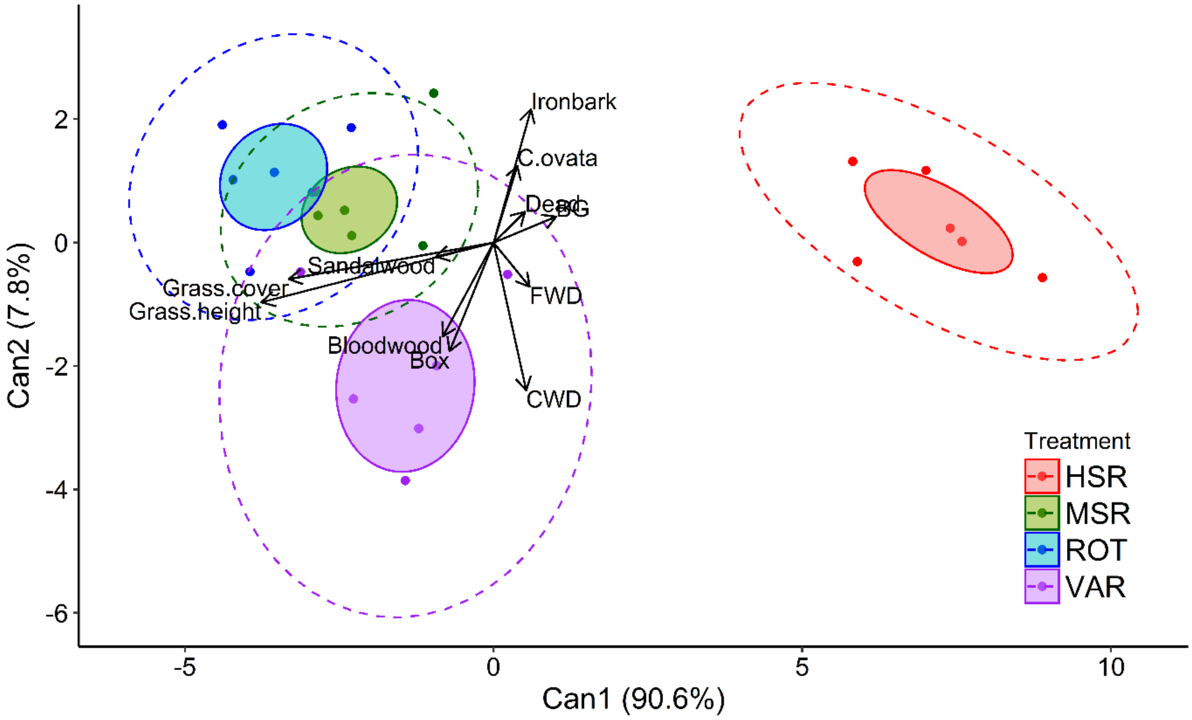


Figure 7.3. Variation in habitat availability relevant to geckos among four grazing regimes (canonical scores and confidence ellipses (50% = solid; 95% = dashed)) (Heavy stocking [HSR] = red; variable stocking [VAR] = green; rotational wet-season spelling [ROT] = blue; and moderate stocking [MSR] = purple). Vectors indicate tree species or habitat cover measures (*Eucalyptus melanophloia* [Ironbark]; dead trees [Dead]; *Eremophila mitchellii* [Sandalwood]; *Corymbia clarksoniana* [Bloodwood]; *Eucalyptus brownii* [Box]; *Carissa ovata* [C.ovata]; grass cover [grass.cover]; course woody debris [CWD]; fine woody debris [FWD]; bare ground [BG]). Grazing treatments show significant separation based on available habitat (Type II MANOVA Tests: Pillai test; $F_{33,36}$ = 1.818, P = 0.040).

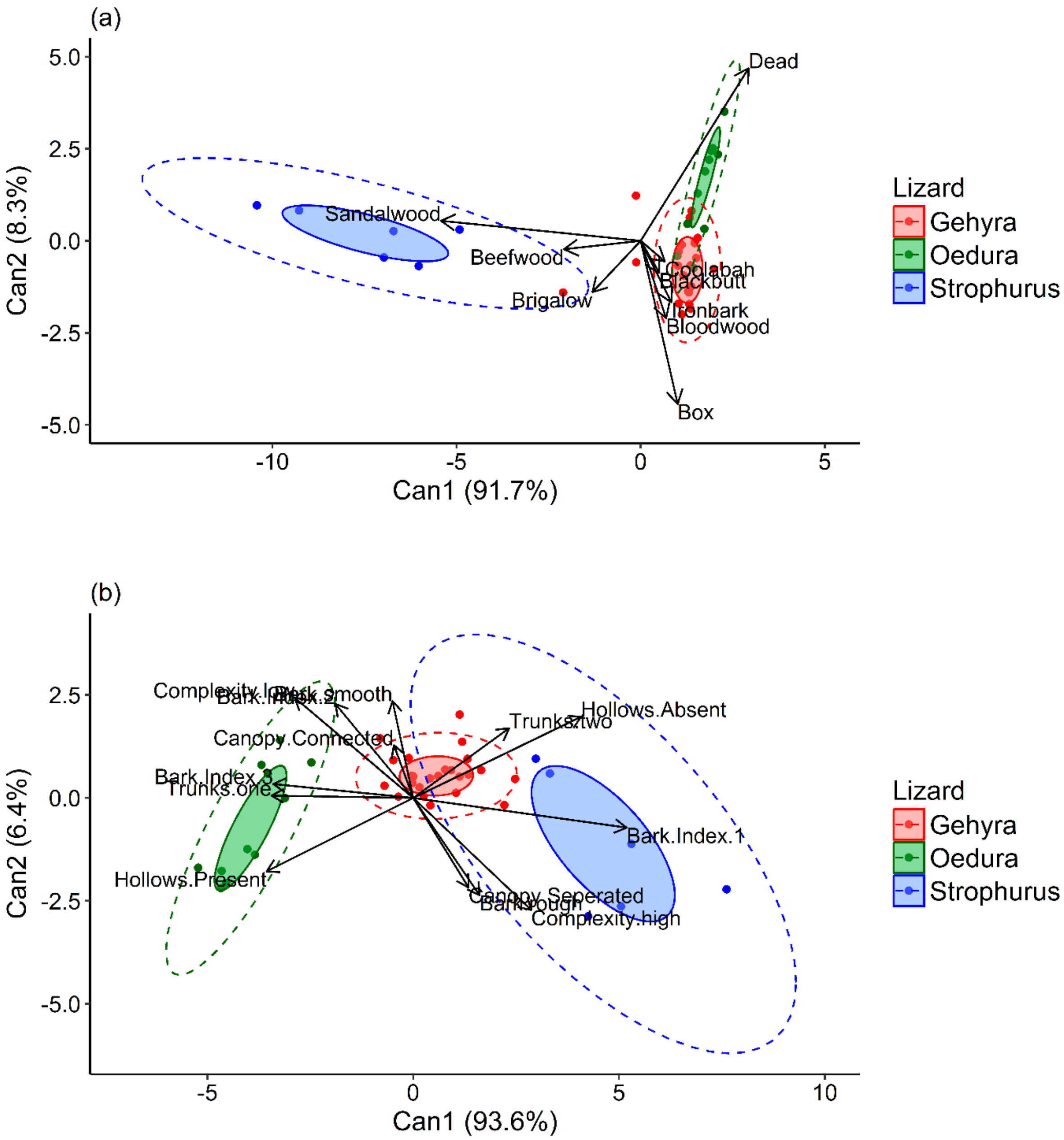


Figure 7.4. Habitat use (canonical scores and confidence ellipses (50% = solid; 95% = dashed)) for three gecko species (eastern spiny-tailed gecko, *Strophurus williamsi* = blue; Australian native house gecko, *Gehyra dubia* = red; and northern velvet gecko, *Oedura castelnaui* = green). Vectors indicate tree species (a) and tree structural complexity measures (b). All three species are statistically separated by differences in selection (Manly selection ratios) of tree species and structural complexity features (MANOVA; (a) $F_{18,62} = 7.857$, $P < 0.001$; (b) $F_{18,62} = 3.461$, $P < 0.001$).

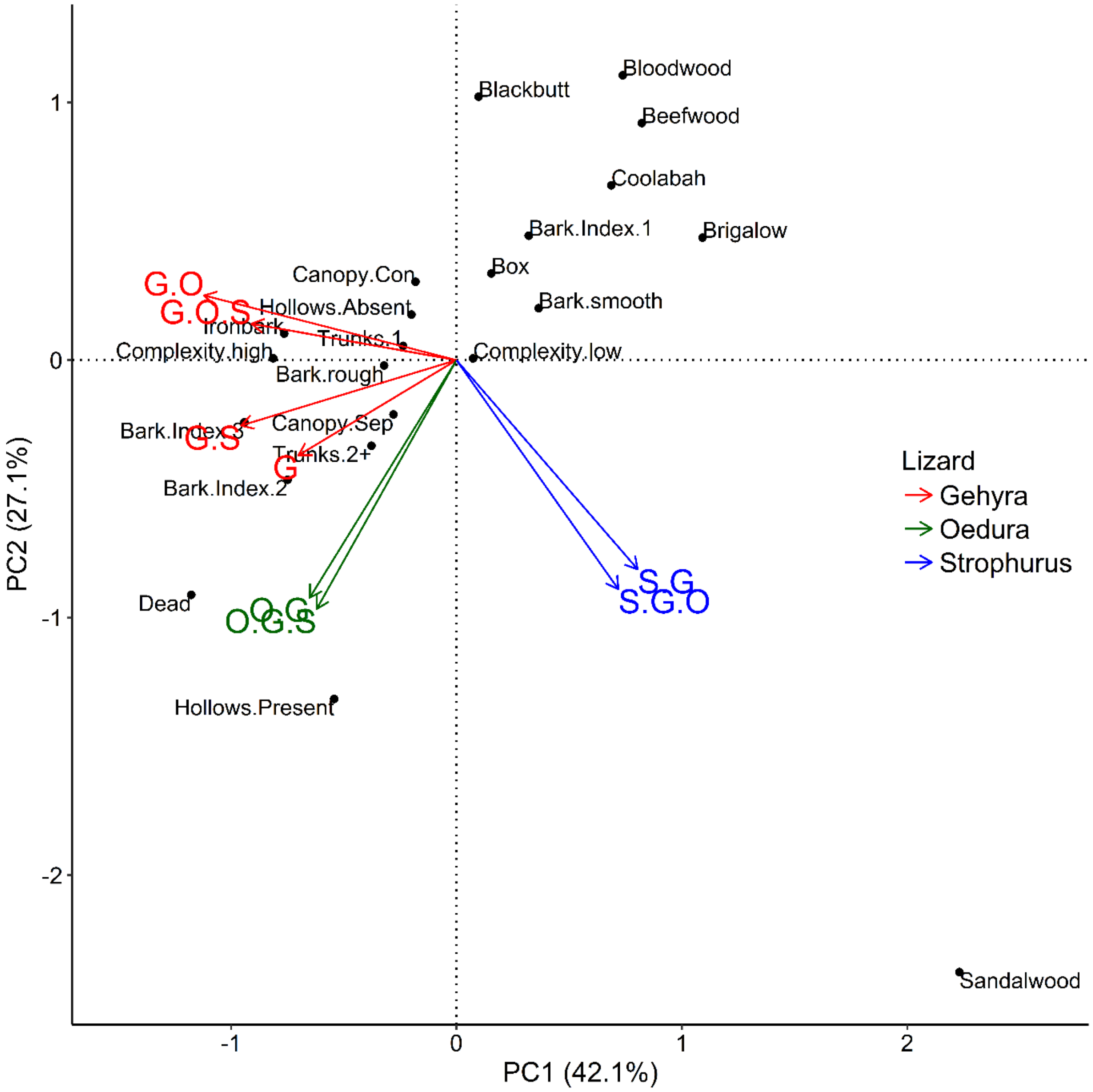


Figure 7.5. Principal component analysis of Manly selection ratios for different habitat attributes for geckos alone and in co-occupancy. Vectors indicate habitat selection by each species (first letter) when they are occupying sites with other species (second and third letters – indicate those species are also present). For example, the blue vector “S.G” indicates the selection of *Strophurus williamsi* (S) when *Gehyra dubia* (G) are also present. Points represent arboreal habitat features. *Gehyra* clearly change their habitat selection in the presence of *Oedura,* whereas there is little change in habitat selection for species in other combinations.

Chapter 8 – Concluding Remarks and Synthesis

Habitat disturbances are wide-spread across the world as a result of both natural and human-mediated processes (Short and Wyllie-Echeverria 1996; McKinney 2006, 2008). In either case, changes to habitat structure and complexity have cascading effects on the diversity and richness of flora and fauna (Landsberg et al. 2003; Belsky 1992; Neilly et al. 2017). While disturbances to habitat are often associated with declines in species or diversity (Belsky 2003; Kutt and Woinarski 2007), some ecosystems require some level of disturbance to function and maintain biodiversity (Connell 1978; Brisson et al. 2003). Disturbances like wildfire or severe storms can create habitat gaps or patches in which some species thrive ("increasers") and others decline ("decreasers"). For example, Longleaf pine (*Pinus palustris*) ecosystems in the southeastern United States, are rich in biodiversity, support many endemic species, and are resistant to wildfires (Noss 1988; Means 2006). Longleaf pine ecosystems benefit from wildfire through the suppression of woody vegetation encroachment on the forest floor, minimizing competition for nutrients and sunlight (Frost 1993; Glitzenstein et al. 1995). Other systems also benefit from low levels of disturbance, including closed canopy forests. Small canopy gaps created from fallen trees create thermal hot-spots on the forest floor, which benefit many ectotherms, by creating increased basking and nesting sites (Greenberg 2001; Roznik et al. 2015).

Grazing by livestock is one of the most extensive land-uses, and therefore habitat disturbances, across the world (Asner et al. 2004). While this thesis is not the first study to identify the impacts of livestock grazing on wildlife, I highlight the impacts on an arboreal fauna, which is often overlooked. Further, I have focused my studies on identifying the mechanisms that benefit an "increaser" species, the Australian native house gecko (*Gehyra dubia*). This thesis is a collection of works that have tested various mechanisms as potential reasons explaining why native house geckos respond positively to grazing intensity. My work is unique in that I have examined the impacts of grazing on reptile communities at multiple scales: 1 – I have described how grazing affects habitat features and reptile community composition of terrestrial and arboreal systems differently (Chapter 3); and 2 – how grazing affects the natural history of arboreal geckos, including diet and prey availability (Chapter 4), predation risk (Chapter 5), and competition (Chapter 7). I have been able to answer questions about the impacts of livestock grazing on arboreal reptiles by incorporating natural history data and community level effects, such as predator–prey relationships and competition to understand a community level response to disturbance. Further, I have explored not only the impacts of grazing on reptiles, but also identified the mechanisms that lead to changes in community composition and species responses.

Ecology and natural history

Natural history and field ecology studies provide baseline data for our understanding of the natural world. For many years, ecologists and explorers have filled journals and field notebooks with observations of new species, behaviors, and interactions that had not been observed previously. Every year, we continue to learn more about cryptic and elusive animals and their behaviors, yet the field of natural history is becoming viewed as increasingly less valuable, and perhaps more importantly, less fundable. Even baseline ecological surveys to establish the occurrence of species, often fail to catch the attention of many organizations. Funding agencies often fail to see the broad importance of species specific traits, such as home range and movement patterns, foraging behavior, or habitat selection. While these natural history focused studies may not appeal to a “broad audience” on their own, many studies incorporate these types of data into large scale species distribution models, mapping the impacts of fragmentation or climate change, or even ecological assessments prior to infrastructure projects (e.g. roads, mining, urban development). So how can we protect threatened or endangered species if we don’t know where it lives, how far it moves, what it eats, or where to find it?

Predator–prey dynamics

Food webs and predator–prey dynamics are an important part of understanding how ecosystems function (Ives et al 2005); although teasing apart these complex interactions can be challenging. Populations of both predators and prey often fluctuate through time in relation of external factors such as weather patterns, resource availability, or disturbances (Huffaker 1958; Rosenzweig and MacArthur

1963). While we may think of species or groups as predominantly either “predators” or “prey”, in reality, all animals are predators to some, and prey to others. I studied the predator–prey dynamics of arboreal lizards as both predators (Chapters 4) and prey (Chapters 5 and 6), which has rarely been done previously. In general, studies on predator–prey dynamics focus on either the perspective of predators, by answering questions about functional and numerical responses (Miller et al. 2006; Gilg et al. 2003), or from the perspective of the prey, by looking at consumptive and non-consumptive effects, including predator avoidance behavior, changes in habitat selection, or foraging behavior (Lima & Dill 1990; Cowlishaw 1997; Schmitz et al. 1997; Heithaus & Dill 2002). Rarely are these two perspectives looked at simultaneously within the same system.

As predators, Australian native house geckos (*Gehyra dubia*) and inland snake-eyed skinks (*Cryptoblepharus australis*) were both insectivorous and selective in their diets (Chapter 4). Both species showed high selectivity for beetles, spiders, and scorpions and exhibited high niche overlap in their diet (O = 0.97). Although dietary niche overlap was high, these two lizard species were temporally segregated based on activity time (*G. dubia* – nocturnal, *C. australis* – diurnal). While invertebrates, particularly spiders, make up a large proportion of the diet of these small arboreal lizards, I found an interesting dynamic within these two groups. Small spiders are often prey to lizards (Chapter 4), yet some groups of spiders, such as Huntsman spiders (Sparassidae) quickly grow larger than many small lizard species and become predators. Large spiders are formidable predators to not only small lizards, but also frogs and other small vertebrates (Chapter 6).

There is a general assumption that predation risk is predator–density dependent, i.e. the more predators that are present, the higher the risk of predation. This assumption seems logical in that as prey, the likelihood of being found and captured by a predator should be greater if there are 100 predators around than if there are only 10. Yet, surprisingly, this has been largely untested (but see Hereu et al 2005; Schmitt and Holbrook 2007; Hollander et al. 2015). I found that predation risk was not related to predator abundance, in fact, predation risk to lizards was lowest when predator abundance was highest (Chapter 5). Although predation risk was not predator–density dependent, I found predation risk was inversely related to the abundance of alternative prey populations. This pattern is represented by the alternative prey hypothesis (Lack 1954; Hornfeldt 1978). Predation risk was greatest to lizards when the abundance of alternative prey (invertebrates) was lowest, and vise – versa.

Response to livestock grazing

Changes to habitat complexity and structure have a large impact on community composition. This has been well studied in plant communities (Landsberg et al. 2003; McIntyre et al. 2003; Dorrough et al. 2004), and to a lesser degree, wildlife (Woinarski and Ash 2002; Read and Cunningham 2010; Neilly et al. 2017). As discussed in Chapters 3 and 7, species level responses are varied, resulting in changes to species composition. Extensive grazing by livestock results in habitats with more open space and less structural complexity due to the consumption of vegetation. Few studies have indicated the impacts of livestock grazing show a varied response in wildlife populations, as some species decline in abundance, some remain unaffected, and others increase (Woinarski and Ash 2002; Kutt and Woinarski 2007; Neilly et al. 2017). While many studies focus on species in decline, often threatened or endangered species, my research has focused on the species that are resistant to the negative effects of grazing. Arboreal lizards are often representatives of typical "increaser" species as they respond positively in disturbed environments (Romero-Schmidt and Ortega-Rubio 1999; Smart et al. 2005; Pringle 2008), yet until now, little has been done to identify the mechanisms behind this response.

A few arboreal lizard species, including the Australian native house gecko (*Gehyra dubia*) and inland snake-eyed skink (*Cryptoblepharus australis*) responded as typical "increaser" species in my studies, with high abundances in the heavily grazed areas (Chapters 3, 4, and 7). These generalist species take advantage of a wide variety of resources, and are generally better suited to cope with environmental changes to habitat features than many specialist species (Mac Nally and Brown 2001). In contrast, many terrestrial lizards, including leaf-litter skinks, followed typical "deacreaser" patterns, and showed reduced abundance in heavily grazed environments (Chapter 3).

Leaf-litter skinks are dependent on the accumulation of leaf-litter and ground debris for shelter, thermoregulation, foraging, and predator avoidance, which is often absent in paddocks with high stocking rates.

Livestock grazing acts as a catalyst that facilitates changes to species composition by homogenizing habitat structure (Chapter 7). Environments that are less structurally complex often support less biodiversity (Menge and Sutherland 1976; Gratwicke and Speight 2005; Garden et al. 2007). While few studies have focused on the impacts of grazing and subsequent changes in wildlife populations, few have identified the mechanisms responsible for these changes. I have identified changes to species composition, including both “increasers” and “decreasers”, I have also tested mechanism such as food availability (Chapter 4), predation pressure (Chapter 5), habitat availability and competition (Chapter 7) that explain changes in species composition.

Management strategies and implications

Arboreal animals are often difficult to study; by occupying arboreal habitat, they are often simply out of reach. To mitigate this problem, I designed and implemented a trapping/monitoring technique using simple closed-cell foam cover boards to increase my capture success and sample sizes (Chapter 2). Arboreal cover boards (ACBs) were beneficial for 3 main reasons: 1 – ACBs acted as an area-defined and quantifiable survey method to compare captures of animals across multiple sites over time; 2 – capture success of animals under ACBs was greater than from visual encounter surveys because animals sheltering under ACBs were all within a catchable height (<2 m); and 3 – ACBs minimize permanent or long-term damage to arboreal microhabitats, such as loose and peeling bark. Traditional survey methods for arboreal lizards often rely on removing dead or peeling bark off trees to reveal sheltering species, but this technique results in permanent or long-term damage to loose bark – an important microhabitat for many species.

In addition, I found that ACBs resulted in a more evenly distributed age and sex class distribution compared to standard visual encounter surveys. I was able to capture individuals ranging from hatchlings to adults using ACBs, while visual encounter surveys generally biased towards adult lizards. Although arboreal lizards were my main target, I found this methodology was also an effective survey method for arboreal invertebrates (Chapters 2, 4 and 6). Additionally, ACBs and other artificial shelters such as terrestrial cover boards, rocks, or hides have proven to be successful in various habitat restoration and enhancement projects (Webb and Shine 2000; Souter et al. 2004; Croak et al. 2010; Bowie et al. 2014).

Implementing conservation strategies to manage wildlife populations in rangelands can be extremely difficult. As discussed in Chapters 3 and 7, there is generally no overall trend in which a wildlife community responds; some species decline while other increase. While habitat alternation is generally a driving factor in shaping wildlife communities in rangelands (Chapters 3 and 7), the indirect effects that lead to changes in community structure and species composition also have a major impact on community level responses (Chapter 7). In some areas, managers may want to target species of concern, in which species–specific management plans can be implemented to improve habitat quality, reduce predation risk, or improve foraging success. Other managers may want to implement conservation strategies that cover a broad spectrum of benefits to multiple species. One overarching conservation tool that can be applied to benefit both arboreal and terrestrial fauna is the retention of trees (Chapter 3). Trees are keystone structures in that they directly and indirectly benefit wildlife across multiple scales (Manning et al. 2006). For arboreal fauna, trees provide primary habitat and refugia, such as hollows, but also provide food for many species that consume leaves, flowers, fruits, and seeds. Terrestrial fauna benefit from trees by increasing the heterogeneity in the landscape. Trees provide a mosaic of shade patches and microhabitats that increase plant diversity and structure, and benefit ectotherms by increasing the potential to thermoregulate in the environment. Further, the accumulation of leaf-litter and woody debris are often the primary habitat of many ground–dwelling species, which are all byproducts of trees.

Conclusion and future research

Understanding the impacts of disturbance on ecosystems is an important and constant conservation need around the world. An increasing number of natural environments are being replaced by anthropogenic landscapes of varying levels of disturbance, ranging from livestock grazing in native pasture, to complete habitat destruction and urbanization. We need to understand how these practices impact native flora and fauna, and ultimately shape ecosystems and communities. Further, in order to understand the impacts of disturbance, we need to understand the ecology and dynamics among species. In this regard, many studies focus on endangered or threatened species, or species in decline, and try to mitigate the negative impacts contributing to their population declines. Yet, it is also important to understand how and why some species are "increasers", and what mechanisms allow them to thrive where others have declined.

By testing a series of mechanisms, I found that reduced competition, as a result of homogenization, is a major contributing factor in the success and persistence of native house geckos in heavily grazed landscapes (Chapter 7). There are many factors that contribute to community composition and function, and in most cases, a combination of mechanisms contribute to community level changes. To better manage and understand community–level responses, we need a holistic knowledge of how ecosystems function.

Although I have tested multiple mechanisms (i.e., food availability, habitat availability, predation, competition) and their effects on native house geckos, there are still other potential mechanisms that may play an important role. I am interested in looking at the thermal ecology of geckos and how changes to habitat structure affect the thermal environment. Changes to habitat structure likely have an effect on the thermal heterogeneity of the habitat, including basking and egg-laying sites, which may limit or benefit reptiles. Further, life history traits such as fecundity, offspring survival, and identifying breeding cycles may differ in regards to grazing strategies and may contribute to the long–term success or decline of some species. There are countless other areas of research in which I would like to further explore to better understand the population dynamics in this system. While I have primarily focused on native house geckos for my Ph.D., I would like to identify the responses of other lizards, both arboreal and terrestrial, to see if "increasers" and "decreasers" respond in predictable ways in regards to the mechanisms explored in this thesis.

Literature Cited

Abensperg-Traun, M. A. X., and D. Steven. 1997. Ant- and termite-eating in Australian mammals and lizards: a comparison. Australian Journal of Ecology 22:9–17.

Abensperg-Traun, M. A. X., G. T. Smith, and B. Main. 2000. Terrestrial arthropods in a fragmented landscape: a review of ecological research in the Western Australian central wheatbelt. Pacific Conservation Biology 6:102–119.

Abom, R., and L. Schwarzkopf. 2016. Short-term responses of reptile assemblages to fire in native and weedy tropical savannah. Global Ecology and Conservation 6:58–66.

Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. Ecology 74:726–733.

Abrams, P. A., and H. Matsuda. 1996. Positive indirect effects between prey species that share predators. Ecology 77:610–616.

Abrams, P. A., and H. Matsuda. 2003. Population dynamical consequences of reduced predator switching at low total prey densities. Population Ecology 45:175–185.

Akamatsu, F., H. Toda, and T. Okino. 2004. Food source of riparian spiders analyzed by using stable isotope ratios. Ecological Restoration 19:655–662.

Allen, J. A. 1988. Frequency-dependent selection by predators. Philosophical Transactions of the Royal Society B 319:485–503.

Angelstam, P., E. Lindström, and P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62:199–208.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29:261–299.

Attum, O., P. Eason, G. Cobbs, and S. M. Baha El Din. 2006. Response of a desert lizard community to habitat degradation: Do ideas about habitat specialists/generalists hold? Biological Conservation 133:52–62.

Ayala, F. J., and C. A. Campbell. 1974. Frequency-dependent selection. Annual Review of Ecology, Evolution, and Systematics 5:114–138.

Barker, M. G., and M. A. Pinard. 2001. Forest canopy research: Sampling problems and some solutions. Plant Ecology 153:23–38.

Barker, R. D., and W. J. M. Vestjens. 1989. *The food of Australian birds. I. Non-passerines*. CSIRO Publishing, Lyneham, Australia.

Barker, R. D., and W. J. M. Vestjens. 1990. *The food of Australian birds. II. Passerines*. CSIRO Publishing, Lyneham, Australia.

Barton, K. 2016. MuMIn: Multi-model inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bastos, R. P., O. C. Oliveira, J. P. Pombal Jr. 1994. *Hyla minuta* (NCN). Predation. Herpetological Review 25:118.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Batson, W. G., C. F. J. O. Donnell, N. J. Nelson, and J. M. Monks. 2015. Placement period of artificial retreats affects the number and demographic composition but not the body condition of skinks. New Zealand Journal of Ecology 39:273–279.

Batzli, G. O., H. J. G. Jung, and G. Guntenspergen. 1981. Nutritional ecology of microtine rodents: linear foraging-rate curves for brown lemmings. Oikos 37:112–116.

Bauer, A. M. 1990. Gekkonid lizards as prey of invertebrates and predators of vertebrates. Herpetological Review 21:83–87.

Bell, T. P. 2009. A novel technique for monitoring highly cryptic lizard species in forests. Herpetological Conservation and Biology 4:415–425.

Belsky, A. J. 2003. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187–200.

Belsky, J. A., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. Conservation Biology 11:315–327.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 1999:419–431.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18:182–188.

Beruldsen, G. 2003. *Australian birds: their nests and eggs*. G. and E. Berulsen, Kenmore Hills, Australia.

Beutel, T. S., G. S. Baxter, and R. J. S. Beeton. 2002. Geckos and grazers: A perspective on reptiles in the assessment of rangeland biodiversity. Environment Australia, Centre for Arid Zone Research, CSIRO Sustainable Ecosystems.

Bittner, T. D. 2003. Polymorphic Clay Models of *Thamnophis Sirtalis* Suggest Patterns of Avian Predation. Ohio Journal of Science 103:62–66.

Blackburn, L. M., C. D. Hoefler, and P. Nanjappa. 2002. *Acris crepitans blanchardi* (Blanchard's Cricket Frog). Predation. Herpetological Review 33:299.

Bock, C. E., H. M. Smith, and J. H. Bock. 1990. The effect of livestock grazing upon abundance of the lizard, *Sceloporus scalaris*, in Southeastern Arizona. Journal of Herpetology 24:445–446.

Borges, L. M., C. M. da Rosa, G. F. Dri, and R. Bertani. 2016. Predation of the snake *Erythrolamprus almadensis* (Wagler, 1824) by the tarantula *Grammostola quirogai* Montes De Oca, D'Elia & Pérez-Miles, 2016. Herpetology Notes 9:321–322.

Bowie, M. H., W. J. Allen, J. Mccaw, and R. Van Heugten. 2014. Factors influencing occupancy of modified artificial refuges for monitoring the range-restricted Banks Peninsula tree weta *Hemideina ricta* (Anostostomatidae). New Zealand Journal of Ecology 38:132–138.

Brisson, J. A, J. L. Strasburg, and A. R. Templeton. 2003. Impact of fire management on the ecology, of collared lizard (*Crotaphytus collaris*) populations living on the Ozark Plateau. Animal Conservation 6:247–254.

Brodeur, R. D., C. L. Suchman, D. C. Reese, T. W. Miller, and E. A. Daly. 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California current. Journal of Marine Biology 154:649–659.

Brodie, E.D. III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution 47:227–235.

Brodie Jr., E. D., and D. R. Formanowicz Jr. 1983. Prey size preference of predators: differential vulnerability of larval anurans. Herpetologica 39:67–75.

Bromham, L., M. Cardillo, A. F. Bennett, and M. A. Elgar. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Austral Ecology 24:199–207.

Brooks, D. M. 2012. Birds caught in spider webs: a synthesis of patterns. Journal of Ornithology 124:345–353.

Brown G. W. 1986. The diet of *Pseudemoia spenceri* (Lucas and Frost, 1884) (Lacertilia: Scincidae), a species endemic to south-eastern Australia. Victorian Naturalist 103:48–55.

Brown G. W. 1988. The diet of *Leiolopisma entrecasteauxii* (Lacertilia: Scincidae) from south-western Victoria, with notes on its relationship with the reproductive cycle. Wildlife Research 15:605–14.

Brown, G. W. 1991. Ecological feeding analysis of South-eastern Australian scincids (Reptilia: Lacertilia). Australian Journal of Zoology 39:377–380.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution 5:344–352.

Brown, G. W., J. W. Dorrough, and D. S. L. Ramsey. 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. Landscape and Urban Planning 103:277–288.

Bryant, G. L., S. J. Dundas, and P. A. Fleming. 2012. Tree hollows are of conservation importance for a near-threatened python species. Journal of Zoology 286:81–92.

Bury, B. R. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetological Conservation and Biology 1:56–61.

Busack, S. D., and R. B. Bury. 1974. Some effects of off-road vehicles and sheep grazing on lizard populations in the Mojave Desert. Biological Conservation 6:179–183.

Bustard, H. R. 1967. Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. Copeia 1967:753–758.

Bustard, H. R. 1968. The ecology of the Australian gecko, *Gehyra variegata*, in northern New South Wales. Journal of Zoology 1968:113–138.

Bustard, R. H. 1969. The Population Ecology of the Gekkonid Lizard (*Gehyra variegata* (Dumeril & Bibron)) in Exploited Forests in Northern New South Wales. Journal of Animal Ecology 38:35–51.

Bylo, L. N., N. Koper, and K. A. Molloy. 2014. Grazing intensity influences ground squirrel and American badger habitat use in mixed-grass prairies. Rangeland Ecology and Management 67:247–254.

Cabrera-Guzmán, E., M. R. Crossland, and R. Shine. 2015. Invasive cane toads as prey for native arthropod predators in tropical Australia. Herpetological Monographs 29:28–39.

Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4:765–781.

Castellano, M. J., and T. J. Valone. 2006. Effects of livestock removal and perennial grass recovery on the lizards of a desertified arid grassland. Journal of Arid Environments 66:87–95.

Castellano, M. J., and T. J. Valone. 2007. Livestock, soil compaction and water infiltration rate: Evaluating a potential desertification recovery mechanism. Journal of Arid Environments 71:97–108.

Castilla, A. M., A. Gosa, P. Galan, and V. Perez-Mellado. 1999. Green tails in lizards of the genus *Podarcis*: do they influence the intensity of predation? Herpetologica 55:530–537.

Cisterne, A., D. A. Pike, and L. Schwarzkopf. *Submitted*. Native lizards are more aggressive than a successful invasive species. Behavioral Ecology.

Chambers, J. C., J. D. Maestas, D. A. Pyke, C. S. Boyd, M. Pellant, and A. Wuenschel. 2016. Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sage-grouse. Rangeland Ecology and Management 70:149–164.

Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. Ecology Letters 2002:302–315.

Clavel, J., R. Julliard, and V. Devictor. 2010. Worldwide decline of specialist species: Toward a global functional homogenization? Frontiers in Ecology and the Environment 9:222–228.

Clavero, M., L. Brotons, and S. Herrando. 2011. Bird community specialization, bird conservation and disturbance: The role of wildfires. Journal of Animal Ecology 80:128–136.

Cogger H. 2014. *Reptiles and Amphibians of Australia, Seventh Edition*. CSIRO Publishing, Melbourne, Australia.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–743.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities, *in* “Ecology and Evolution of Communities” pp. 460–491, (M. L. Cody and J. M. Diamond, Eds.), Harvard University Press, Cambridge, United States.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs high diversity of trees and corals is maintained. Science 199:1302–1310.

Cooper, R. J. 1988. Dietary relationships among insectivorous birds of an eastern deciduous forest. Ph.D. Thesis, West Virginia University, Morgantown, WV, USA.

Cornell, H. 1976. Search strategies and the adaptive significance of switching in some general predators. American Naturalist 110:317–320.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour 1997:667–686.

Croak, B. M., D. A. Pike, J. K. Webb, and R. Shine. 2010. Using artificial rocks to restore non-renewable shelter sites in human-degraded systems: colonization by fauna. Restoration Ecology 18:428–438.

Croak, B. M., J. K. Webb, and R. Shine. 2013. The benefits of habitat restoration for rock-dwelling velvet geckos *Oedura lesueurii*. Journal of Applied Ecology 50:432–439.

Crome B. 1981. The diet of some ground-layer lizards in three woodlands of the New England tableland of Australia. Herpetofauna 13:4–11.

Curry, P. J., and R. B. Hacker. 1990. Can pastoral grazing management satisfy endorsed conservation objectives in arid Western Australia? Journal of Environmental Management 30:295–320.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics 2003:183–211.

Davis, C., P. Fleming, M. Craig, A. Grigg, and G. Hardy. 2008. A funnel trap for capture of small arboreal reptiles. Amphibia-Reptilia 29:413–423.

Dayton, P. K. 2003. The importance of the natural sciences to conservation. The American Naturalist 162:1–13.

DeGregorio, B. A., P. J. Weatherhead, and J. H. Sperry. 2014. Power lines, roads, and avian nest survival: effects on predator identity and predation intensity. Ecology and Evolution 4:1589–1600.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology, Evolution, and Systematics 18:431–451.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17:252–261.

Diamond, J. M. 1970. Ecological consequences of island colonization by southwest pacific birds, I. Types of niche shifts. Proceedings of the National Academy of Sciences 67:529–536.

Dias, E., and C. F. D. Rocha. 2007. Niche differences between two sympatric whiptail lizards (*Cnemidophorus abaetensis* and *C. ocellifer*, Teiidae) in the restinga habitat of northeastern Brazil. Brazilian Journal of Biology 67:41–46.

Diaz, J. A, and L. M. Carrascal. 1991. Regional distribution of a Mediterranean lizard - influence of habitat cues and prey abundance. Journal of Biogeography 18:291–297.

Dickman, C. R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313–322.

Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe’s farmland bird populations. Proceedings of the Royal Society B: Biological Sciences 268, 25–29.

Dorcas, M. E., and J. D. Willson. 2009. Innovative methods for studies of snake ecology and conservation. *In* “Snakes: Ecology and Conservation” pp. 5–37, (J. Mullin and R. A. Seigel Eds.), Cornell University Press, Ithaca, United States.

Dorrough, J., J. Ash, and S. McIntyre. 2004. Plant responses to livestock grazing frequency in an Australian temperate grassland. Ecography 27:798–810.

Dorrough, J., S. McIntyre, G. Brown, J. Stol, G. Barrett, and A. Brown. 2012. Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. Austral Ecology 37:569–582.

Dubas, G., and C. Bull. 1991. Diet choice and food availability in the omnivorous lizard, *Trachydosaurus rugosus*. Wildlife Research 18:147–155.

Ekroos, J., J. Heliölä, and M. Kuussaari. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology 47:459–467.

Eldridge, D. J., J. Val, and A. I. James. 2011 Abiotic effects predominate under prolonged livestock-induced disturbance: Livestock-induced disturbance in woodlands. Austral Ecology 36:367–377.

Essington, T. E., and S. Hansson. 2004. Predator-dependent functional responses and interaction strengths in a natural food web. Canadian Journal of Fisheries and Aquatic Sciences 61:2215–2226.

Fischer, J., D. B. Lindenmayer, and A. Cowling. 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. Journal of Applied Ecology 41:32–44.

Fischer, J., J. Stott, A. Zerger, G. Warren, K. Sherren, and R. I. Forrester. 2009. Reversing a tree regeneration crisis in an endangered ecoregion. Proceedings of the National Academy of Sciences 106:10386–10391.

Fitzgerald, M., B. Lazell, and R. Shine. 2010. Ecology and conservation of the Pale-headed Snake (*Hoplocephalus bitorquatus*, Elapidae). Australian Zoologist 35:283–290.

Fitzgerald, M., R. Shine, and F. Lemckert. 2002. Spatial ecology of arboreal snakes *Hoplocephalus stephensii*, Elapidae) in an eastern Australian forest. Austral Ecology 2002:537–545.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Floyd, H. B., T. A. Jenssen, S. Copeia, and N. May. 1983. Food habits of the Jamaican lizard *Anolis opalinus*: resource partitioning and seasonal effects examined. Copeia 1983:319–331.

Foelix, R., 2011. *Biology of Spiders*. Oxford University Press, New York.

Framenau, V. W., B. C. Baehr, and P. Zborowski. 2014. *A Guide to the Spiders of Australia*. CSIRO Publishing, Melbourne, Australia.

Francke, J. V. A. 2005. Ecological implications of habitat fragmentation and restoration for the gecko *Hoplodactylus maculatus*. M.Sc. Thesis, Victoria University of Wellington, New Zealand.

Friendly, M. and J. Fox. 2016. candisc: visualizing generalized canonical discriminant and canonical correlation analysis. R package version 0.7-2. https://CRAN.R-project.org/package=candisc

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. *In* "18th Tall Timbers Fire Ecology Conference" pp. 17–43, (S. M. Hermann Ed.), Tall Timbers Research, Inc., Tallahassee, United States.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625.

Garden, J. G., C. A. Mcalpine, H. P. Possingham, and D. N. Jones. 2007. Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane, Australia. Austral Ecology 32:669–685.

Germaine, S. S., and B. F. Wakeling. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97:229–237.

Germano, D. J., G. B. Rathbun, and L. R. Saslaw. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. Journal of Wildlife Management 76:670–682.

Gertsch, W.J. 1979. *American Spiders*. D. Van Nostrand Reinhold Co., New York.

Gibbons, P., and D. Lindenmayer. 2002. *Tree hollows and wildlife conservation in Australia*. CSIRO Publishing, Collingwood, Australia.

Gilg, O. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. Science 302:866–868.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441–476.

Goldingay, R. L., and D. A. Newell. 2000. Experimental rock outcrops reveal continuing habitat disturbance for an endangered Australian snake. Conservation Biology 14:1908–1912.

Goode, M. J., W. C. Horrace, M. J. Sredl, and J. M. Howland. 2005. Habitat destruction by collectors associated with decreased lizard abundance. Biological Conservation 125:1–24.

Goode, M. J., D. E. Swann, and C. R. Schwalbe. 2004. Effects of destructive collecting practices on reptiles: a field experiment. Journal of Wildlife Management 68:429–434.

Goodenough, A. E. 2010. Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. Community Ecology 11:13–21.

Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. American Naturalist 118:463-474.

Grant, B. W., A. D. Tucker, J. E. Lovich, A. M. Mills, P. M. Dixon, and J. W. Gibbons. 1992. The use of coverboards in estimating patterns of reptile and amphibian biodiversity. *In* “Wildlife 2001: Populations” pp. 379–403, (D. R. McCullough and R. H. Barrett, Eds.), Kluewer Academic Publishers Group, Dordrecht, Netherlands.

Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650–667.

Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management 148:135–144.

Greene, H. W. 1994. Systematics and natural-history, foundations for understanding and conserving biodiversity. American Zoologist 34:48–56.

Greenspan, S. E., D. S. Bower, R. J. Webb, E. A. Roznik, L. A. Stevenson, L. Berger, G. Marantelli, D. A. Pike, L. Schwarzkopf, and R. A. Alford. 2017. Realistic heat pulses protect frogs from disease under simulated rainforest frog thermal regimes. Functional Ecology 2017:1–13.

Griffiths, A. D., and K. A. Christian. 1995. Diet and habitat use of frillneck lizards in a seasonal tropical environment. Oecologica 106:39–48.

Griffiths, A. D., and K. A. Christian. 1996. The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. Austral Ecology 21:386–398.

Gruber, B., and K. Henle. 2004. Linking habitat structure and orientation in an arboreal species *Gehyra variegata* (Gekkonidae). Oikos 2:406–414.

Gruber, B., and K. Henle. 2008. Analysing the effect of movement on local survival: a new method with an application to a spatially structured population of the arboreal gecko *Gehyra variegate*. Oecologia 154:679–690.

Gruber, B. 2004. Measuring activity of geckos with an automatic movement monitoring system. Herpetological Review 35:245–247.

Hacking, J., R. Abom, and L. Schwarzkopf. 2014. Why do lizards avoid weeds? Biological Invasions 16:935–947.

Hamilton, A. M., R. Klein, Elaine, M. E. Eckstut, and E. E. Hartfield. 2007. A simple, inexpensive method to capture arboreal lizards. Herpetological Conservation and Biology 2:164–167.

Hansen, R. A. 2000. Effects of habitat complexity and composition on a diverse litter microarthropod. Ecology 81:1120–1132.

Hayward, B., E. J. Heske, and C. W. Painter. 1997. Effects of livestock grazing on small mammals at a desert cienaga. Journal of Wildlife Management 61:123–129.

Heath, J. E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146:784–785.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

Hellgren, E. C, A. L. Burrow, R. T. Kazmaier, and D. C. Ruthven. 2010. The effects of winter burning and grazing on resources and survival of Texas Horned Lizards in a thornscrub ecosystem. Journal of Wildlife Management 74:300–309.

Hendrickx, F., J. P. Maelfait, W. Van Wingerden, O. Schweiger, M. Speelmans, S. Aviron, I. Augenstein, R. Billeter, D. Bailey, R. Bukacek, F. Burel, T. Diekötter, J. Dirksen, F. Herzog, J. Liira, M. Roubalova, V. Vandomme, and R. Bugter. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44:340–351.

Henle, K. 1990. Population ecology and life history of the arboreal gecko *Gehyra variegata* in arid Australia. Herpetological Monographs 4:30–60.

Henschel, J.R., 1994. Diet and foraging behaviour of huntsman spiders in the Namib dunes (Araneae: Heteropodidae). Journal of Zoology 234:239–251.

Hereu, B., M. Zabala, C. Linares, and E. Sala. 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Marine Biology 146:293–299.

Herman, S. G. 2002. Wildlife biology and natural history: time for a reunion. Journal of Wildlife Management 66:933–946.

Hódar, J. A., J. M. Pleguezuelos, and J. C. Poveda. 2000. Habitat selection of the common chameleon (*Chamaeleo chamaeleon*) (L.) in an area under development in southern Spain: Implications for conservation. Biological Conservation 94:63–68.

Hodge, S., C. J. Vink, J. C. Banks, and M. H. Bowie. 2007. The use of tree-mounted artificial shelters to investigate arboreal spider communities in New Zealand nature reserves. Journal of Arachnology 35:129–136.

Hollander, F. A., H. Van Dyck, G. S. Martin, and N. Titeux. 2015. Nest predation deviates from nest predator abundance in an ecologically trapped bird. PLoS ONE 10:1–20.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91:293–320.

Holt, R. A. and Lawton, J. H. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology, Evolution, and Systematics 25:495–520.

Hoopes, M. F., R. D. Holt, and M. Holyoak. 2005. The effects of spatial processes on two species interactions. *In* “Metacommunities: Spatial Dynamics and Ecological Communities” pp. 35–67, (M. Holyoak, M. A. Leibold and R. D. Holt, Eds.), University of Chicago Press, Chicago, USA.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. Oecologia 32:141–152.

Howland, B., D. Stojanovic, I. J. Gordon, A. D. Manning, and D. B. Lindenmayer. 2014. Eaten out of house and home: impacts of grazing on ground-dwelling reptiles in Australian grasslands and grassy woodlands. PloS ONE 9:1–25.

Huey, R. B., E. R. Pianka, and T. Schoener. 1983. *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, United States.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist 19:357–366.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia, 27:343–383.

Hughes, R. D., and M. I. Croy. 1993. An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. Journal of Animal Ecology 62:341–352.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67–435 77.

Iles, D. T., R. F. Rockwell, P. Matulonis, G. J. Robertson, K. F. Abraham, J. C. Davies, and D. N. Koons. 2013. Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. Journal of Animal Ecology 82:683–693.

Ineich, I. 2010. How habitat disturbance benefits geckos: Conservation implications. Comptes rendus biologies 333:76–82.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. Ecology Letters 8:102–116.

Jacobs, J. 1974. Quantitative measurement of food selection: A modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

James, C. D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. Oecologia 85:553–561.

James, C. D. 2003. Response of vertebrates to fenceline contrasts in grazing intensity in semi-arid woodlands of eastern Australia. Austral Ecology 28:137–151.

James, C. D., J. Landsberg, and S. R. Morton. 1999 Provision of watering points in the Australian arid zone: a review of effects on biota. Journal of Arid Environments 41:87–121.

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C. N, J. L. Isaac, and D. O. Fisher. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. Proceedings of the Royal Society B: Biological Sciences 274:341–346.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist 60:155–164.

Jones, K. B. 1981. Effects of grazing on lizard abundance and diversity in western Arizona. Southwestern Naturalist 26:107–115.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications. . . a review. Journal of Rangeland Management 37:430-438.

King, M. 1983. The *Gehyra australis* species complex (Sauria: Gekkonidae). Amphibia-Reptilia 4:147–169.

King, R. A., D. S. Read, M. Traugott, and W. O. C. Symondson. 2008. INVITED REVIEW: Molecular analysis of predation: a review of best practice for DNA-based approaches. Molecular Ecology 17:947–963.

Knox, C. D. 2010. Habitat requirements of the jewelled gecko (*Naultinus gemmeus*): effects of grazing, predation and habitat fragmentation. MS Thesis. University of Otago, New Zealand.

Knox, C. D., A. Cree, and P. J. Seddon. 2012. Direct and indirect effects of grazing by introduced mammals on a native, arboreal gecko (*Naultinus gemmeus*). Journal of Herpetology 46:145–152.

Kopp, K., M. Wachlevski, and P. C. Eterovick. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84:136–140.

Korpimiiki, E., K. Huhtala, and S. Sulkava. 1990. Does the year-to-year variation in the diet of eagle and ural owls support the alternative prey hypothesis? Oikos 58:47–54.

Kutt, A. S., and I. J. Gordon. 2012. Variation in terrestrial mammal abundance on pastoral and conservation land tenures in north-eastern Australian tropical savannas. Animal Conservation 15:416–425.

Kutt, A. S., and T. G. Martin. 2010. Bird foraging height predicts bird species response to woody vegetation change. Biodiversity and Conservation 19:2247–2262.

Kutt, A. S., E. P. Vanderduys, and P. O’Reagain. 2012. Spatial and temporal effects of grazing management and rainfall on the vertebrate fauna of a tropical savanna. The Rangeland Journal 34:173–182.

Kutt, A. S., and J. C. Z. Woinarski. 2007. The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. Journal of Tropical Ecology 23:95–106.

Kutt, A. S., E. P. Vanderduys, J. J. Perry, G. C. Perkins, J. E. Kemp, B. L. Bateman, J. Kanowski, and R. Jensen. 2013 Signals of change in tropical savanna woodland vertebrate fauna 5 years after cessation of livestock grazing. Wildlife Research 39:386–396.

Kuznetsova A., P. B. Brockhoff, and R. H. B. Christensen. 2016 lmerTest: tests in linear mixed effects models. R package version 2.0–30.

Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London, United Kingdom.

Landsberg, J., C. D. James, S. R. Morton, W. J. Muller, and J. Stol. 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. Journal of Applied Ecology 40:1008–1024.

Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography 36:1276–1290.

Legler, J. M., and L. J. Sullivan. 1979. The application of stomach-flushing to lizards and anurans. Herpetologica 35:107–110.

Lettink, M., C. F. J. O. Donnell, and J. M. Hoare. 2011. Accuracy and precision of skink counts from artificial retreats. New Zealand Journal of Ecology 35:236–246.

Lettink, M., and B. H. Patrick. 2006. Use of artificial cover objects for detecting red katipo, *Latrodectus katipo* Powell (Araneae: Theridiidae). New Zealand Entomologist 29:99–102.

Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, United States.

Liebezeit, J. R., and S. Zack. 2008. Point counts underestimate the importance of arctic foxes as avian nest predators: evidence from remote video cameras in arctic Alaskan oil fields. Arctic 61:153–161.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 1990:619–640.

Lisboa, C. M. C. A., R. F. D. Sales, and E. M. X. Freire. 2012. Feeding ecology of the pygmy gecko *Coleodactylus natalensis* (Squamata: Sphaerodactylidae) in the Brazilian Atlantic forest. Zoologia (Curitiba) 29:293–299.

Lister, B. C. 1976. The nature of niche expansion in West Indian Anolis lizards I: ecological consequences of reduced competition. Evolution 30:659-676.

Lotka, A.J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, United States.

Lovich, R. E., W. K. Hayes, H. Mushinsky and G. H. Rodda. 2012. Transect surveys, including line distance. *In* "Reptile Biodiversity: Standard Methods for Inventory and Monitoring" pp. 227–234, (R. W. McDiarmid, M.S. Foster, C. Guyer, J. W. Gibbons and N. Chernoff, Eds.), University of California Press, Berkeley, United States.

Ludwig, J. A., I. R. W. Eager, A. C. Liedloff, J. C. Mccosker, D. Hannah, N. Y. Thurgate, J. C. Z. Woinarski, and C. P. Catterall. 2000. Clearing and grazing impacts on vegetation patch structures and fauna counts in eucalypt woodland, Central Queensland. Pacific Conservation Biology 6:254–272.

Luiselli, L. 2003. Do snakes exhibit shifts in feeding ecology associated with the presence or absence of potential competitors? A case study from tropical Africa. Canadian Journal of Zoology 81:228–236.

Lusk, J. S., and N. Koper. 2013 Grazing and songbird nest survival in southwestern Saskatchewan. Rangeland Ecology and Management 66:401–409.

Mac Nally, R., and G. W. Brown. 2001. Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: Predictions, compositional change and faunal nestedness. Oecologia 128:116–125.

Maffei, F., F. K. Ubaid, and J. Jim. 2014. Predation of herps by spiders (Araneae) in the Brazilian Cerrado. Herpetology Notes 3:167–170.

Manicom, C. 2010. Beyond abundance: the direct and indirect effects of predation. Ph.D. Thesis. James Cook University, Queensland, Australia.

Manicom, C., and L. Schwarzkopf. 2011. Diet and prey selection of sympatric tropical skinks. Austral Ecology 36:485–496.

Manly, B. F. L., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2007. *Resource selection by animals: statistical design and analysis for field studies*. Springer, Dordrecht, Netherlands.

Manning, A. D., R. B. Cunningham, and D. B. Lindenmayer. 2012. Bringing forward the benefits of coarse woody debris in ecosystem recovery under different levels of grazing and vegetation density. Biological Conservation 157:204–214.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures - Implications for conservation. Biological Conservation 132:311–321.

Martin, T. G., and S. McIntyre. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology 21:504–514.

Martin, T. G., and H. P. Possingham. 2005. Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology 42:400–408.

McCallum, M. L., and J. L. McCallum. 2006. Publication trends of natural history and field studies in herpetology. Herpetological Conservation and Biology 1:62–67.

McCollum, S. A., and J. D. Leimberger. 1997. Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. Oecologia 109:615–621.

McCormick, S., and G. A. Polis. 1982. Arthropods that prey on vertebrates. Biological Reviews 57:29–58.

McCoy E. D., Bell S. S. 1991 Habitat structure: The evolution and diversification of a complex topic. *In* “Habitat Structure. Population and Community Biology”, (S. S. Bell, E. D. McCoy, H. R. Mushinsky, Eds.) Springer, Dordrecht, Netherlands.

McCreary, D. D., and M. R. George. 2005. Managed grazing and seedling shelters enhance oak regeneration on rangelands. California Agriculture 59:217–222.

McIntyre, S., K. M. Heard, and T. G. Martin. 2003. The relative importance of cattle grazing in subtropical grasslands: does it reduce or enhance plant biodiversity? Journal of Applied Ecology 40:445–457.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

McKnight, D. T., A. C. Jones, and D. B. Ligon. 2015. The omnivorous diet of the western chicken turtle (*Deirochelys reticularia miaria*). Copeia 103:322–328.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 128:765–770.

Means, D. Bruce. 2006. Chapter 6. Vertebrate faunal diversity in longleaf pine savannas. *In* “Longleaf Pine Ecosystems: Ecology, Management, and Restoration” pp. 155–213, (S. Jose, E. Jokela, and D. Miller, Eds.), Springer, New York, United States.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

Menin, M., D. de Jesus Rodrigues, and C. Salette de Azevedo. 2005. Predation on amphibians by spiders (Arachnida, Araneae) in the Neotropical region. Phyllomedusa 4:39–47.

Mester, B., M. Szalai, T. O. Méro, M. Puky, and S. Lengyel. 2015. Spatiotemporally variable management by grazing and burning increases marsh diversity and benefits amphibians: a field experiment. Biological Conservation 192:237–246.

Michael, D. R., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 2012. Comparative use of active searches and artificial refuges to survey reptiles in temperate eucalypt woodlands. Wildlife Research 2012:149–162.

Milchunas, D. G., W. K. Lauenroth, and I. C. Burke. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos 83:65–74.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:328–366.

Milchunas, D.G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87–106.

Miller, D. A., J. B. Grand, T. F. Fondell, and M. Anthony. 2006. Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. Journal of Animal Ecology 75:101–110.

Mitchell, J. C. 1990. *Pseudacris feriarum* (Upland Chorus Frog). Predation. Herpetological Review 21: 89–90.

Mitrovich, M. J., and R. A. Cotroneo. 2006. Use of plasticine replica snakes to elicit antipredator behavior in the California ground squirrel (*Spermophilus beecheyi*). Southwestern Naturalist 51:263–267.

Monti, L., M. Hunter, and J. Witham. 2000. An evaluation of the artificial cover object (ACO) method for monitoring populations of the redback salamander *Plethodon cinereus*. Journal of Herpetology 34:624–629.

Mori, A., Ohba, S., 2004. Field observations of predation on snakes by the giant water bug. Bulletin of the Herpetological Society of Japan 2004:78–81.

Morrissey, C. A., J. E. Elliott, and S. J. Ormerod. 2010. Diet shifts during egg laying: implications for measuring contaminants in bird eggs. Environmental Pollution 158:447–454.

Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology 10:1642–1647.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335–354.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1–131.

Murphy, S. A., and S. M. Legge. 2007. The gradual loss and episodic creation of Palm Cockatoo (*Probosciger aterrimus*) nest-trees in a fire- and cyclone-prone habitat. Emu 107:1–6.

National Land and Water Resources Audit. 2001. Australian natural resources atlas, v2.0, land, land use Australia, national land and water resources audit. http://audit.ea.gov.au/ANRA/land/land_frame.cfm?region_type=AUSandregion_code=AUSandinfo=land_use

Neilly, H., E. Nordberg, J. VanDerWal, and L. Schwarzkopf. 2017. Arboreality increases reptile community resistance to disturbance from livestock grazing. Journal of Applied Ecology (available online) DOI: 10.1111/1365-2664.12982.

Neilly, H., P. O'Reagain, J. VanDerWal, and L. Schwarzkopf. 2017. Profitable and sustainable cattle grazing strategies support reptiles in a tropical savanna rangeland. Rangeland Ecology & Management.

Neilly, H., J. VanDerWal, and L. Schwarzkopf. 2016. Balancing biodiversity and food production: a better understanding of wildlife response to grazing will inform off-reserve conservation on rangelands. Rangeland Ecology and Management 69:430–436.

Newbold, T. A. S., and J. A. MacMahon. 2008. Consequences of cattle introduction in a shrubsteppe ecosystem: indirect effects on desert horned lizards (*Phrynosoma platyrhinos*). Western North American Naturalist 68:291–302.

Nordberg, E. J., and L. Schwarzkopf. 2015. Arboreal cover boards: using artificial bark to sample cryptic arboreal lizards. Herpetologica 71:268–273.

Nordberg, E.J., L. Edwards, and L. Schwarzkopf. *In review.* Terrestrial invertebrates: an underestimated predator guild for small vertebrate groups. Food Webs.

Nordberg, E.J., P. Murray, R. Alford, and L. Schwarzkopf. 2017. Abundance, diet, and prey selection of arboreal lizards in a grazed tropical woodland. Austral Ecology (Available online) DOI: 10.1111/aec.12570.

Norrdahl, K., and E. Korpimak. 2000. Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predator. Oikos 91:528–540.

Noss, R. F. 1988. The longleaf pine landscape of the southeast: almost gone and almost forgotten. University of Michigan School of Natural Resources, Endangered Species Update 5:1–8.

Nyffeler, M., and M. Knornschild. 2013. Bat predation by spiders. PLoS ONE, 8: e58120.

Nyffeler, M., M. R. Maxwell, J. V Remsen, and J. Rivera. 2017. Bird predation by praying mantises: a global perspective. The Wilson Journal of Ornithology 129:331–344.

O'Reagain, P. O., and J. Bushell. 2011. The Wambiana grazing trial: Key learnings for sustainable and profitable management in a variable environment. Agri-Science Queensland November:1–60.

O'Reagain, P. O., J. Bushell, and B. Holmes. 2011. Managing for rainfall variability: long-term profitability of different grazing strategies in a northern Australian tropical savanna. Animal Production Science 51:210–224.

O'Reagain, P., J. Bushell, C. Holloway, and A. Reid. 2009. Managing for rainfall variability: effect of grazing strategy on cattle production in a dry tropical savanna. Animal Production Science 49:85–99.

Ogada, D. L., M. E. Gadd, R. S. Ostfeld, T. P. Young, and F. Keesing. 2008. Impacts of large herbivores on bird diversity and abundance in an African savanna. Oecologia 156:387–397.

Ohba, S. 2011. Field observation of predation on a turtle by a giant water bug. Entomological Science 14:364–365.

Oksanen J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner 2017. vegan: community ecology package. R package version 2.4–3.

Olden, J. D. 2006. Biotic homogenization: A new research agenda for conservation biogeography. Journal of Biogeography 33:2027–2039.

Olden, J. D., and N. L. Poff. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. American Naturalist 162:442–460.

Orrock, J. L., and R. J. Fletcher. 2014. An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. Proceedings of the Royal Society B: Biological Sciences 281:20140391.

Owen, R. D., and S. A. Johnson. 1997. *Pseudacris ocularis* (Little Glass Frog). Predation. Herpetological Review 28:200.

Pafilis, P., I. Anastasiou, K. Sagonas, and E. D. Valakos. 2013. Grazing by goats on islands affects the populations of an endemic Mediterranean lizard: Grazing affects lizard populations on islands. Journal of Zoology 290:255–264.

Parsons, S. A., A. Kutt, E. P. Vanderduys, J. J. Perry, and L. Schwarzkopf. 2017. Exploring relationships between native vertebrate biodiversity and grazing land condition. Rangeland Journal 39:25–37.

Pech, R. P., A. R. E. Sinclair, and A. E. Newsome. 1995. Predation models for primary and secondary prey species. Wildlife Research 22:55–64.

Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. The Quarterly Review of Biology 64:393–418.

Petren, K., and T. J. Case. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. Proceedings of the National Academy of Sciences 95:11739–11744.

Pettigrew, M., and C. M. Bull, C.M. 2014. Prey capture behaviour by pygmy bluetongue lizards with simulated grazing. New Zealand Journal of Ecology 38:45–52.

Piana, R. P., and S. J. Marsden. 2014. Impacts of cattle grazing on forest structure and raptor distribution within a neotropical protected area. Biodiversity and Conservation 23:559–572.

Pianka, E., and H. Pianka. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. Copeia 1:90–103.

Pianka, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012–1030.

Pianka, E. R. 1971. Notes on the biology of *Varanus tristis*. The Western Australian Naturalist 11:180–183.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology, Evolution, and Systematics 4:53–74.

Pianka, E. R. 1982. Observations on the ecology of *Varanus* in the Great Victoria Desert. The Western Australian Naturalist 1982:37–44.

Pianka, E. R. 1994. Comparative ecology of *Varanus* in the Great Victoria Desert. Australian Journal of Ecology 19:395–408.

Pianka, E. R., and W. S. Parker. 1975. Ecology of horned lizards - a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141–162.

Pianka, E. R., and H. D. Pianka. 1976. Australian desert comparative ecology of twelve species of nocturnal lizards (gekkonidae) in the Western Australian desert. Copeia 1976:125–142.

Pitt, M. D., R. F. Newman, P. L. Youwe, B. M. Wikeem, and D. A. Quinton. 1998. Using a grazing pressure index to predict cattle damage of regenerating tree seedlings. Journal of Range Management 51:417–422.

Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet. 2012. Who is eating what: diet assessment using next generation sequencing. Molecular Ecology 2012:1931–1950.

Poulin, B., G. Lefebvre, R. Ibáñez, C. Jaramillo, C. Hernández, and A. S. Rand. 2001. Avian predation upon lizards and frogs in a neotropical forest understorey. Journal of Tropical Ecology 17:21–40.

Pramuk, J. B., and H. Alamillo. 2002. *Hyla nana* (Dwarf Tree Frog). Predation. Herpetological Review 33: 46–47.

Pringle, R. M. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. Ecology 89:26–33.

Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences 104:193–197.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rabinowitz, A., and M. D. Tuttle. 1982. A test of the validity of two currently used methods of determining bat prey preferences. Acta Theriologica 27:13–24.

Raven, R. J. 1990. Spider predators of reptiles and amphibia. Memoirs of the Queensland Museum 29:448.

Read, J. L. 1995. Subhabitat variability: a key to the high reptile diversity in chenopod shrublands. Australian Journal of Ecology 20:494–501.

Read, J. L. 2002. Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. Austral Ecology 27:55–66.

Read, J. L., and R. Cunningham. 2010. Relative impacts of cattle grazing and feral animals on an Australian arid zone reptile and small mammal assemblage. Austral Ecology 35:314–324.

Recher, H. F., J. D. Majer, and S. Ganesh. 1996. Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. Australian Journal of Ecology 21:64–80.

Reif, V., R. Tornberg, S. Jungell, and E. Korpimaki. 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. Ecography 24:267–274.

Ribeiro, R., X. Santos, N. Sillero, M. a. Carretero, and G. a. Llorente. 2009. Biodiversity and Land uses at a regional scale: Is agriculture the biggest threat for reptile assemblages? Acta Oecologica 35:327–334.

Ribi, W. A. 1981. The phenomenon of eye glow. Endeavour 5:2–8.

Romera–Schmidt, H. L., and A. Ortega–Rubio. 1999. Changes in lizard abundance on protected versus grazed desert scrub in Baja California Sur, Mexico. Brazilian Archives of Biology and Technology 42:175–180.

Rosenzweig, M., and R. H. Macarthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist 97:209–223.

Rosi, M. I., S. Puig, M. I. Cona, F. Videla, E. Mendez, and V. G. Roig. 2009. Diet of a fossorial rodent (Octodontidae), above-ground food availability, and changes related to cattle grazing in the Central Monte (Argentina). Journal of Arid Environments 73:273–279.

Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation 88:289–299.

Roznik, E. A., S. J. Sapsford, D. A. Pike, L. Schwarzkopf, and R. A. Alford. 2015. Natural disturbance reduces disease risk in endangered rainforest frog populations. Scientific Reports 5:1–11.

Sakai, A. K., F. W. Allendorf, J. S. Holt, M. Lodge, J. Molofsky, K. A. With, R. J. Cabin, J. E. Cohen, C. Norman, D. E. McCauley, P. O. Neil, M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology, Evolution, and Systematics 32:305–332.

Sales, R. F. D., and E. M. X. Freire. 2015. Diet and foraging behavior of *Ameivula ocellifera* (squamata: teiidae) in the Brazilian Semiarid Caatinga. Journal of Herpetology 49:579–585.

Saporito, R. A., R. Zuercher, M. Roberts, G. Kenneth, and M. A. Donnelly. 2007. Experimental evidence for aposematism in the Dendrobatid poison frog *Oophaga pumilio*. Copeia 2007:1006–1011.

Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20:495–503.

Schmitt, R. J., and S. J. Holbrook. 2007. The scale and cause of spatial heterogeneity in strength of temporal density dependence. Ecology 88:1241–1249.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Seifan, M., and R. Kadmon. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a Mediterranean scrub community. Basic and Applied Ecology 7:496–506.

Shannon, C. E., and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana, United States.

Shepard, D. B. 2007. Habitat but not body shape affects predator attack frequency on lizard models in the Brazillian Cerrado. Herpetologica 63:193–202.

Sheppard, S. K., J. D. Harwood. 2005. Advances in molecular ecology: tracking trophic links through predator–prey food-webs. Functional Ecology 19:751–762.

Shine, R. 1977. Habitats, diets, and sympatry in snakes: a study from Australia. Canadian Journal of Zoology 55:1118–1128.

Shine, R. 1986. Food habits, habitats and reproductive biology of four sympatric species of varanid lizards in tropical Australia. Herpetologica 42:346–360.

Shine, R., and R. Lambeck. 1989. Ecology of frillneck lizards, *Chlamydosaurus kingii* (Agamidae), in tropical Australia. Wildlife Research 16:491–500.

Shine, R., and B. Tomayo, 2015. Some little known aspects of spider behavior. Australian Zoologist 38:212–213.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17–27.

Sidorovich, V. 2011. *Analysis of vertebrate predator-prey community: Studies within the European Forest zone in terrains with transitional mixed forest in Belarus*. Tesey, Minsk, Belarus.

Sih, A., P. Crowley, M. Mcpeek, J. Petranka, and K. Strohmeier. 1985. A review of field experiments. Annual Review of Ecology, Evolution, and Systematics 16:269–311.

Sint, D., I. Thurner, R. Kaufmann, and M. Traugott. 2015. Sparing spiders: faeces as a non-invasive source of DNA. Frontiers in Zoology 12:1–5.

Smart, R., M. J. Whiting, and W. Twine. 2005. Lizards and landscapes: Integrating field surveys and interviews to assess the impact of human disturbance on lizard assemblages and selected reptiles in a savanna in South Africa. Biological Conservation 122:23–31.

Smith, R. L. 1980. Daddy water bugs. Natural History 89:57–63.

Smith, G. T., G. W. Arnold, S. Sarre, M. Abensperg-Traun, and D. E. Steven. 1996. The effect of habitat fragmentation and livestock grazing on animal communities in remnants of Gimlet Eucalyptus salubris woodland in the Western Australia Wheatbelt. 2. Lizards. Journal of Applied Ecology 33:1302–1310.

Souter, N. J., C. M. Bull, and N. Hutchinson, Mark. 2004. Adding burrows to enhance a population of the endangered pygmy blue tongue lizard, *Tiliqua adelaidensis*. Biological Conservation 116:403–408.

Stamps, J., and S. Tanaka. 1981. The relationship between selectivity and food abundance in a juvenile lizard. Ecology 62:1079–1092.

Steffen, J. E. 2009. Perch-height specific predation on tropical lizard clay models: implications for habitat selection in mainland neotropical lizards. Revista de Biologia Tropical 57:859–864.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, United States.

Stowasser, G. 2004. Squid and their prey: insights from fatty acid and stable isotope analysis. PhD Thesis, University of Aberdeen, United Kingdom.

Stuart-Fox, D. M., A. Moussalli, N. J. Marshall, and I. P. F. Owens. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Animal Behaviour 66:541–550.

Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. Molecular Ecology 11:627–641.

Szaro, R. C., S. C. Belfit, J. K Aitkin, and J. N. Rinne. 1985. Impact of grazing on a riparian garter snake. *In* “Riparian ecosystems and their management: Reconciling conflicting uses” pp. 359–363 (R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and F. H. Hamre, technical coordinators). General Technical Report RM-120. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Taylor, S. G. 2008. Leaf litter invertebrate assemblages in box-ironbark forest: Composition, size and seasonal variation in biomass. Victorian Naturalist 125:19–27.

Terborgh, J., R. D. Holt, and J. A. Estes. 2010. Trophic cascades: what they are, how they work and why they matter. *In* “Trophic cascades: predators, prey, and the changing dynamics of nature” pp. 55–69, (J. Terborgh, and J. A. Estes, Eds.), Island Press, Washington D.C., United States.

Thompson, G. G., M. De Boer, and E. R. Pianka. 1999. Activity areas and daily movements of an arboreal monitor lizard, *Varanus tristis* (Squamara: Varanidae) during the breeding season.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, United States.

Toledo, L.F., 2003. Predation on seven South American anuran species by water bugs (Belostomatidae). Phyllomedusa 2:105–108.

Toledo, L. F. 2005. Predation of juvenile and adult anurans by lnvertebrates: current knowledge and perspectives. Herpetological Review 36:395–400.

Towns, D. R., and G. P. Elliott. 1996. Effects of habitat structure on distribution and abundance of lizards at Pukeru Bay, Wellington, New Zealand. New Zealand Journal of Ecology 20:191–206.

Trainor, C. R., and J. C. Z. Woinarski. 1994. Responses of lizards to three experimental fires in the savanna forests of Kakadu national park. Wildlife Research 1994:131–148.

Trauth, S. E. 2006. A personal glimpse into natural history and a revisit of a classic paper by Fred R. Cagle. Herpetological Conservation and Biology 1:68–70.

Trent, T. T., and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. The Journal of Wildlife Management 38:459–472.

Turchin P. 2003*. Complex Population Dynamics*. Princeton University Press, Princeton, United States.

Underwood, A. H., and J. E. Seymour. 2007. Venom ontogeny, diet and morphology in *Carukia barnesi*, a species of Australian box jellyfish that causes Irukandji syndrome. Toxicon 49:1073–1082.

Valeix, M., A. J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Behavioural adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30.

Valentine, L. E. 2006. Habitat avoidance of an introduced weed by native lizards. Austral Ecology 31:732–735.

Valentine, L. E., and L. Schwarzkopf. 2009. Effects of weed-management burning on reptile assemblages in Australian tropical savannas. Conservation Biology 23:103–13.

Van Buskirk, J., J. Aschwanden, I. Buckelmüller, S. Reolon, S. Rüttiman. 2004. Bold tail coloration protects tadpoles from dragonfly strikes. Copeia 2004:599–602.

Vanderduys, E. P., and A. S. Kutt. 2012. Is the Asian house gecko, *Hemidactylus frenatus*, really a threat to Australia's biodiversity? Australian Journal of Zoology 60:361–367.

Vesterinen, E. J., T. Lilley, V. N. Laine, and N. Wahlberg. 2013. Next generation sequencing of fecal DNA reveals the dietary diversity of the widespread insectivorous predator Daubenton's bat (*Myotis daubentonii*) in southwestern Finland. PLoS ONE 8:e82168.

Villar, N., X. Lambin, D. Evans, R. Pakeman, and S. Redpath. 2013. Experimental evidence that livestock grazing intensity affects the activity of a generalist predator. Acta Oecologica 49:12–16.

Vitt L., and E. R. Pianka. 2007. Feeding ecology in the natural world. *In* "Lizard Ecology" pp. 141–172, (S. M. Reilly, L. D. McBrayer, and D. B. Miles, Eds.), Cambridge University Press, Cambridge, United Kingdom.

Vitt, L. J., and E. R. Pianka. 2014. *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, United States.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560.

Wang, Y., U. Naumann, S. Wright, and D. I. Warton. 2012. mvabund: an R package for model-based analysis of multivariate data. Methods in Ecology and Evolution, 3:471–474.

Wangvoralak, S., L. C. Hastie, and G. J. Pierce. 2011. Temporal and ontogenetic variation in the diet of squid (*Loligo forbesii Streenstrup*) in Scottish waters. Hydrobiologia 670:223–240.

Webb, J. K., and R. Shine. 2000. Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? Biological Conservation 92:93–99.

Webb, J. K., and M. J. Whiting. 2005. Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. Oikos 110:515–522.

Webb, R. H. 1979. Sheep grazing effects on Mojave Desert vegetation and soils. Environmental Management 3:517–529.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

Whiles, M. R., and J.W. Grubaugh. 1996. Importance of coarse woody debris to southern forest herpetofauna. *In* “Biodiversity and Coarse Woody Debris in Southern Forests” pp. 94–100, (J. W. McMinn, and D. A. Crossley Jr., Eds.), General Technical Report SE-94. USDA Forest Service.

White, J. W. 2007. Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality. Ecology Letters 10:1054–1065.

White, J. W., and J. F. Samhouri. 2011. Oceanographic coupling across three trophic levels shapes source – sink dynamics in marine metacommunities. Oikos 120:1151–1164.

Wilgers, D. J., and E. A. Horne. 2007. Spatial variation in predation attempts on artificial snakes in a fire-disturbed tallgrass prairie. Southwestern Naturalist 52:263–270.

Wilson, D. J., R. L. Mulvey, and R. D. Clark. 2007. Sampling skinks and geckos in artificial cover objects in a dry mixed grassland – shrubland with mammalian predator control. New Zealand Journal of Ecology 31:169–185.

Wilson, S. K. 2015. *A Field Guide to Reptiles of Queensland*, New Holland, Chatswood, Australia.

Wise, D. H., D. M. Moldenhauer, and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. Ecological Applications 16:865–876.

Woinarski, J. C. Z., and A. J. Ash. 2002. Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. Austral Ecology 27:311–323.

Yates, C. J., D. A. Norton, and R. J. Hobbs. 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecology 25:36–47.

Yonge, C. M. 1928. Feeding mechanisms in the invertebrates. Biological Reviews 3:21–76.

Yugovic, J. 2015. Do ecosystems need top predators? A review of native predator-prey imbalances in south-east Australia. Victorian Naturalist 132:4–11.

Zozaya, S. M., R. A. Alford, and L. Schwarzkopf. 2015. Invasive house geckos are more willing to use artificial lights than are native geckos. Austral Ecology 40:982–987.

Appendices

APPENDIX 3.S1. Habitat characteristics

Table 1. Two-way ANOVA results exploring the effect of grazing treatment: Heavy (H), Moderate (M), Variable (V) and Rotational wet season spelling (R), and vegetation type: Box (B) and Ironbark (I), on terrestrial and arboreal habitat characteristics. Post-hoc Tukey's test are used to explore significant results (p<0.05).

	Mean ± SE	**Explanatory Variables**	**F Statistic**	**P Value**	**Post Hoc**
Terrestrial Habitat Features					
Bare ground (% cover)	20.52 ± 2.49	Veg*Graze	5.906	**0.001**	HI>HB HI>MB HI>MI HI>VB HI>RB HI>VI HI>RI
Leaf litter <0.5mm (% cover)	45.32 ± 2.17	Veg*Graze	7.419	**<0.001**	HB>HI HB>MB HB>RB VB>HI VI>HI
Leaf litter>5mm (% cover)	0.82 ± 0.28	Veg*Graze	4.041	**0.009**	MI>HB MI>MB MI>RB MI>RI MI>VB
Grass (% cover)	18.85 ± 1.79	Veg	1.437	0.234	-
		Graze	10.993	**<0.001**	M>H R>H V>H
Grass height (cm)	40.27 ± 2.28	Veg	1.245	0.268	-
		Graze	49.672	**<0.001**	M>H R>H V>H
Carrissa ovata (% cover)	11.80 ± 0.91	Veg	206.840	**<0.001**	B>I
		Graze	10.010	**<0.001**	H>V M>R M>V
Coarse woody debris (% cover)	0.76 ± 0.09	Veg*Graze	9.521	**<0.001**	VI>HB VI>HI VI>MB VI>MI VI>RB VI>RI VI>VB
Fine woody debris (% cover)	0.69 ± 0.09	Veg	0.005	0.942	-
		Graze	0.531	0.662	-

Termite mounds (% cover)	0.69 ± 0.07	Veg*Graze	8.970	**<0.001**	RI>HI VB>HI RI>MB VB>MB RI>VI
		Veg	2.958	0.102	-
Canopy cover (%)	34.70 ± 3.23	Graze	2.244	0.116	-
Arboreal Habitat Features					
Mean distance to nearest tree (m)	4.11 ± 0.05	Veg	0.537	0.472	-
		Graze	0.984	0.421	-
Hollows (%)	11.34 ± 1.46	Veg	0.151	0.702	-
		Graze	0.057	0.981	-
Canopy connectivity (%)	34.70 ± 3.23	Veg	0.338	0.568	-
		Graze	5.757	**0.005**	H>R
Trees dead	1.16 ± 0.16	Veg	6.962	**0.016**	B>I
		Graze	0.998	0.415	-
Trees <5cm Diametre at breast height (DBH)	3.04 ± 0.86	Veg	3.509	0.076	-
		Graze	2.139	0.129	-
Trees 5-10cm DBH	1.45 ± 0.20	Veg	0.713	0.409	-
		Graze	0.431	0.733	-
Trees 10-20 DBH	1.80 ± 0.23	Veg	6.156	**0.022**	B>I
		Graze	1.000	0.414	-
Trees 20-30 DBH	1.01 ± 0.16	Veg	0.003	0.955	-
		Graze	0.422	0.739	-
Trees >30 DBH	0.50 ± 0.10	Veg	1.125	0.302	-
		Graze	3.908	**0.024**	V>H V>R
Mean Bark Index (1-3)	2.0 ± 0.03	Veg	2.028	0.171	-
		Graze	0.497	0.689	-

APPENDIX 3.S2. Model coefficients

Table 1. The estimated regression parameters, standard errors, t-values and P-values for the fixed effects in the negative binomial GLMM: Terrestrial reptile abundance ~ grazing treatment + vegetation type + (1|year) + (1|season)

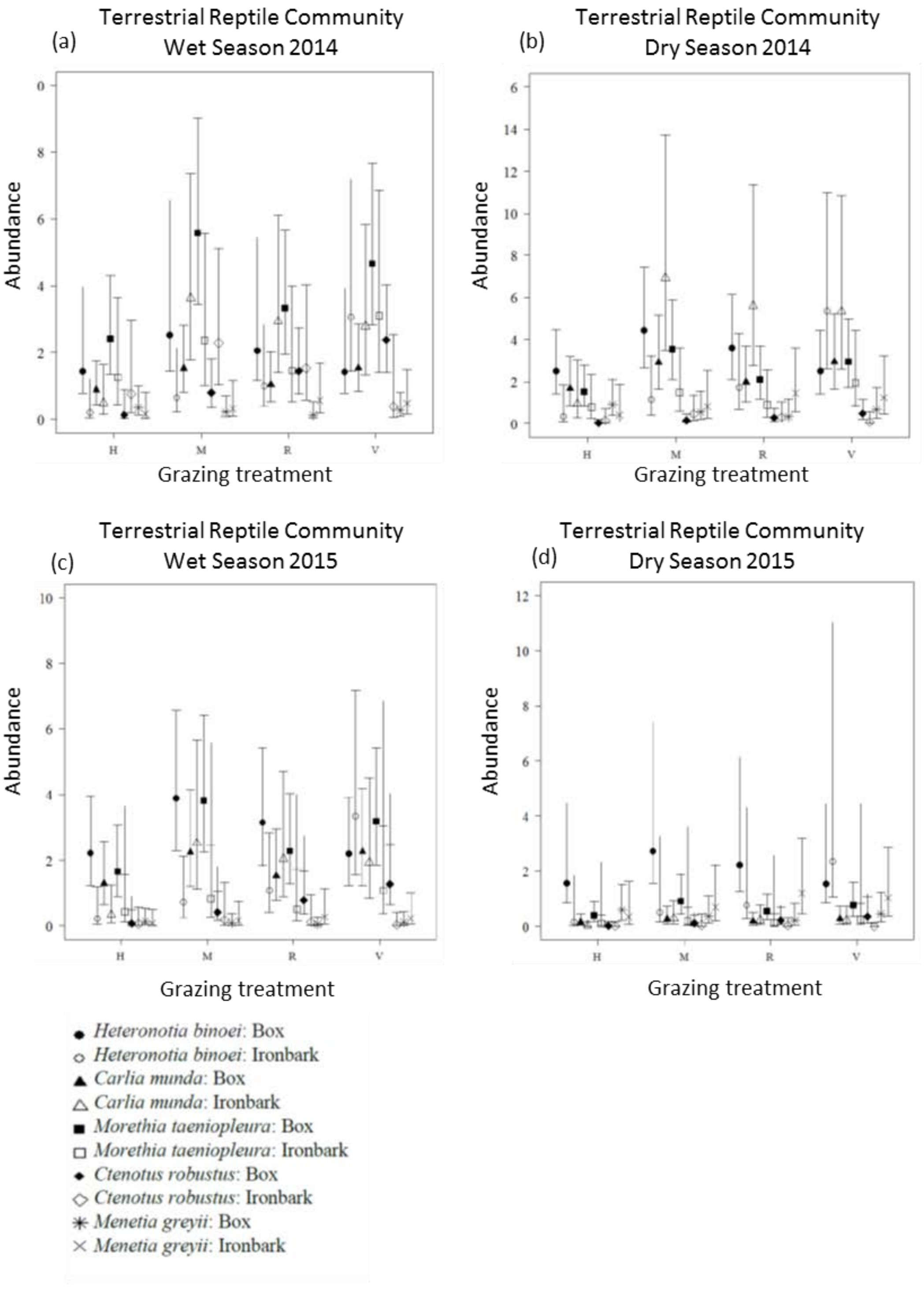
	Estimate	Std. error	*t*-value	*P*-value
Intercept	1.49	0.259	5.755	<0.01
Graze.Moderate	0.75	0.179	4.201	<0.01
Graze.Rotational	0.502	0.183	2.751	0.01
Graze.Variable	0.704	0.18	3.918	<0.01
Veg.Ironbark	-0.305	0.132	-2.313	0.021

Table 2. The estimated regression parameters, standard errors, t-values and P-values for the fixed effects in the negative binomial GLMM: Arboreal reptile abundance ~ grazing treatment + vegetation type + (1|year) + (1|season).

	Estimate	Std. error	*t*-value	*P*-value
Intercept	1.304	0.229	5.7	<0.01
Graze.Moderate	-0.512	0.207	-2.48	0.01
Graze.Rotational	-0.461	0.204	-2.258	0.024
Graze.Variable	0.021	0.19	0.108	0.914
Veg.Ironbark	0.455	0.147	3.094	<0.01

APPENDIX 3.S3. Manyglm community analysis

Figure 1. The fitted values with 95% confidence intervals of the negative binomial multivariate GLM for: the terrestrial reptile community at (a) the end of the wet season 2014; (b) the end of the dry season 2014; (c) the end of the wet season 2015; and the end of the dry season 2015, for each of the grazing treatments Heavy (H), Moderate (M), Variable (V) and Rotational wet season spelling (R).



APPENDIX 3.S4. Terrestrial and arboreal reptile functional groups.

Taxonomy follows Wilson (2015)

Wilson, S. (2015) *A field guide to the reptiles of Queensland*. Reed New Holland Publishers, London, UK.

Litter Skinks

Carlia munda

Morethia taeniopleura

Ctenotus robustus

Ctenotus strauchii

Menetia greyii

Carlia rubigo

Pygmaeascincus timlowi

Proablepharus tenuis

Terrestrial Geckos

Lucasium steindachneri

Diplodactylus platyurus

Heteronotia binoei

Arboreal Geckos

Gehyra dubia

Strophurus williamsi

Oedura castelnaui

APPENDIX 4.S1. Grazing treatments and invertebrate availability

Table 1. Cattle stocking regimes for the Wambiana Grazing Trial. Rate (ha/AE) = the stocking rate in terms of hectares per adult equivalent (AE); AE = 450 kg steer; LTCC = long-term carrying capacity. HSR = heavy stocking rate; MSR = moderate stocking rate; ROT = rotational stocking rate; VAR = variable stocking rate. Adapted from O’Reagain et al 2011.

Stocking Regime	**Rate (ha/AE)**	**Description**	**Rationale**
HSR	4 - 5	Constant stocking rate at twice the LTCC of the land	Highest profitability/beef production
MSR	8 - 10	Constant stocking rate equal to the LTCC of the land	Maintains land condition, minimal losses during drought years
ROT	7 - 8	Relatively constant stocking rate 50% above the LTCC where 2/3^{rds} of the paddock is used for grazing and 1/3rd is allowed to recover during the wet season	Buffers impact of rainfall variability
VAR	3 - 12	Variable stocking rate in which the stock is adjusted up/down at the end of the wet season in relation to the remaining pasture feed available	Match stock to feed availability, take advantage of periods with high pasture yield

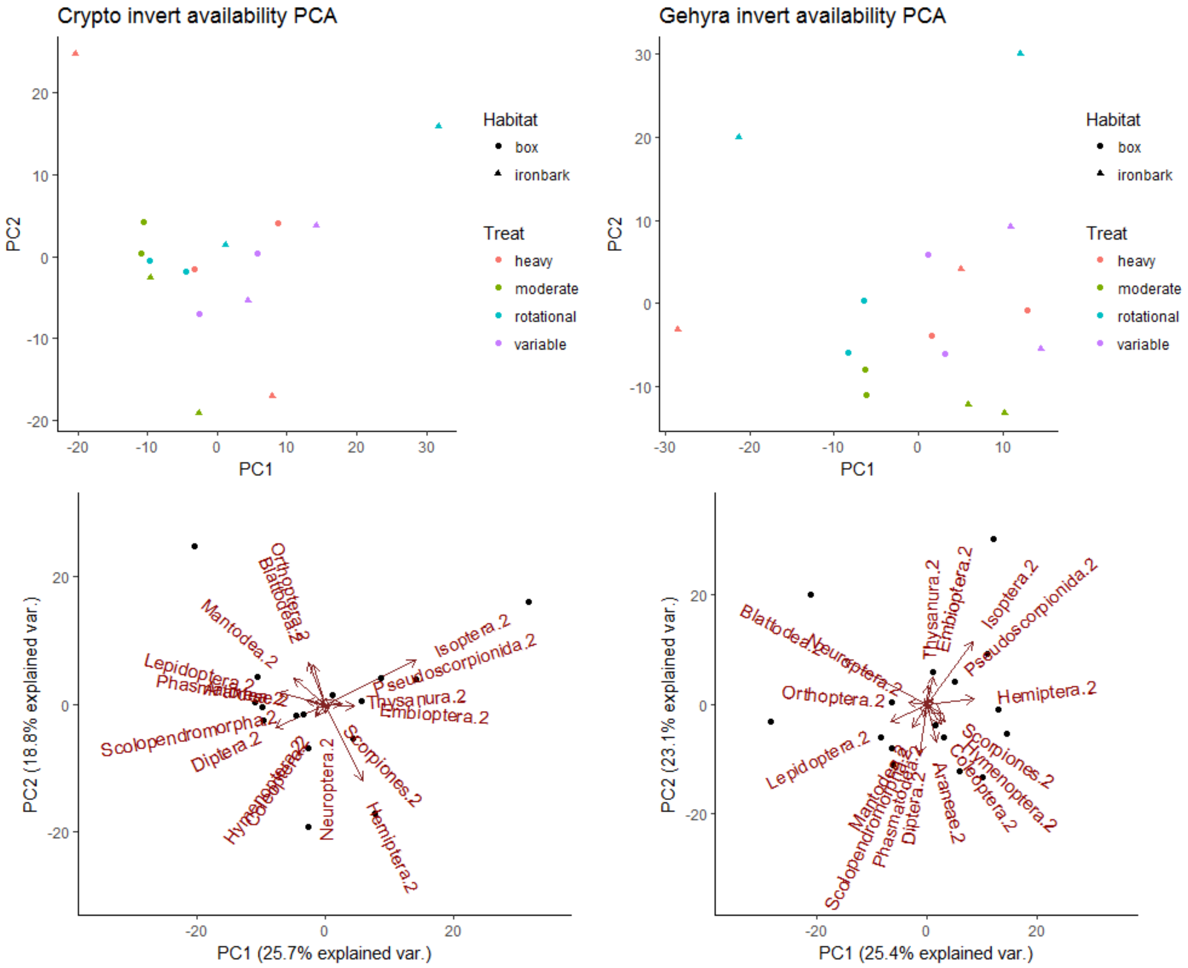


Figure 1. PCA plots (top) and biplots (bottom) indicating minimal separation of invertebrate prey groups for *Cryptoblepharus australis* (left) and *Gehyra dubia* (right).

APPENDIX 5.S1. Biological and environmental model selection.

Biological Models

Lizard Model Attacks

Global model call: glmer(formula = Attacks ~ BirdPreds + InvertPrey + InvertPreds + (1|Habitat:Treatment), data = model.pred.data, family = poisson())

model	intercept	*BirdPreds*	*InvertPreds*	*InvertPrey*	df	logLik	AICc	delta	weight
5	2.56			-0.04	3	-39.79	87.60	0.00	0.39
1	1.99				2	-41.76	88.40	0.87	0.25
7	2.55		0.03	-0.04	4	-39.13	89.90	2.33	0.12
2	2.08	-0.01			3	-41.50	91.00	3.42	0.07
6	2.60	-0.01		-0.03	4	-39.69	91.00	3.44	0.07
3	1.95		0.01		3	-41.69	91.40	3.80	0.06
8	2.60	-0.01	0.03	-0.04	5	-38.98	94.00	6.38	0.02
4	2.04	-0.01	0.01		4	-41.37	94.40	6.80	0.01

Predatory Bird Abundance

Global model call: glmer(formula = BirdPreds ~ 1 + Gecko + InvertPreds + InvertPrey + (1|Habitat:Treatment), data = model.pred.data, family = poisson)

model	intercept	*Geckos*	*InvertPreds*	*InvertPrey*	df	logLik	AICc	delta	weight
1	2.14				2	-62.67	130.30	0.00	0.36
2	2.55	-0.03			3	-61.46	130.90	0.65	0.26
5	1.87			0.02	3	-62.36	132.70	2.45	0.11
4	2.88	-0.05	-0.05		4	-60.66	133.00	2.69	0.09
3	2.21		-0.02		3	-62.53	133.10	2.79	0.09
6	2.98	-0.05		-0.02	4	-61.31	134.30	3.98	0.05
7	1.85		-0.03	0.02	4	-61.93	135.50	5.23	0.03
8	3.22	-0.06	-0.04	-0.01	5	-60.58	137.20	6.89	0.01

Gecko Abundance

Global model call: glmer(formula = Gecko ~ InvertPrey + BirdPreds + InvertPreds + (1|Habitat:Treatment), data = model.pred.data, family = poisson)

model	intercept	BirdPreds	InvertPreds	InvertPrey	df	logLik	AICc	delta	weight
5	3.31			-0.05	3	-44.33	96.70	0.00	0.66
7	3.35		-0.03	-0.05	4	-43.99	99.60	2.95	0.15
6	3.35	-0.01		-0.05	4	-44.15	99.90	3.26	0.13
8	3.39	-0.01	-0.02	-0.05	5	-43.83	103.70	6.99	0.02
1	2.44				2	-49.66	104.20	7.58	0.02
3	2.62		-0.05		3	-48.41	104.80	8.15	0.01
2	2.56	-0.01			3	-49.17	106.30	9.68	0.01
4	2.73	-0.01	-0.05		4	-47.95	107.50	10.87	0.00

Invertebrate Prey Abundance

Global model call: glmer(formula = InvertPrey ~ Gecko + BirdPreds + InvertPreds + (1|Habitat:Treatment), data = model.pred.data, family = poisson)

model	intercept	BirdPreds	*Geckos*	InvertPreds	df	logLik	AICc	delta	weight
3	3.26		-0.04		3	-44.70	97.40	0.00	0.69
7	3.18		-0.04	0.01	4	-44.53	100.70	3.31	0.13
4	3.29	0.00	-0.04		4	-44.68	101.00	3.60	0.12
1	2.80				2	-49.74	104.40	7.00	0.02
8	3.21	0.00	-0.04	0.01	5	-44.51	105.00	7.63	0.02
5	2.69			0.03	3	-48.57	105.10	7.75	0.01
2	2.75	0.01			3	-49.58	107.20	9.77	0.01
6	2.65	0.00		0.03	4	-48.47	108.60	11.19	0.00

Predatory Invertebrate Abundance

Global model call: glmer(formula = InvertPreds ~ 1 + Gecko + BirdPreds + InvertPrey + (1|Habitat:Treatment), data = model.pred.data, family = poisson)

model	intercept	BirdPreds	*Geckos*	InvertPrey	df	logLik	AICc	delta	weight
1	1.20				2	-37.21	79.30	0.00	0.35
3	1.78		-0.05		3	-36.06	80.10	0.78	0.24
5	0.52			0.04	3	-36.24	80.50	1.15	0.20
2	1.28	-0.01			3	-37.13	82.30	2.91	0.08
4	1.88	-0.01	-0.05		4	-35.97	83.60	4.24	0.04
7	1.33		-0.04	0.02	4	-35.99	83.60	4.29	0.04
6	0.59	-0.01		0.04	4	-36.20	84.00	4.69	0.03
8	1.48	-0.01	-0.04	0.01	5	-35.93	87.90	8.51	0.01

Environmental Models

Lizard Model Attacks

Global model call: glmer(formula = Attacked ~ + 1 + Season + Habitat + Micro.Habitat + (1|Habitat:Treatment), data = glmm.pred.data2, family = binomial)

model	intercept	*Habitat*	*MicroHab*	*Season*	df	logLik	AICc	delta	weight
5	-1.45			+	3	-322.31	650.60	0.00	0.39
6	-1.57	+		+	4	-321.67	651.40	0.74	0.27
7	-1.39		+	+	4	-322.12	652.30	1.65	0.17
8	-1.51	+	+	+	5	-321.48	653.00	2.39	0.12
1	-1.70				2	-326.25	656.50	5.87	0.02
2	-1.82	+			3	-325.65	657.30	6.70	0.01
3	-1.63		+		3	-326.02	658.10	7.43	0.01
4	-1.75	+	+		4	-325.42	658.90	8.26	0.01

Predatory Bird Abundance

Global model call: glmer(formula = BirdPreds ~ +Season + Habitat + (Season:Habitat) + (1|Habitat:Treatment), data = raw.pred.data, family = poisson())

model	intercept	*Habitat*	*Season*	*Hbt:Ssn*	df	logLik	AICc	delta	weight
8	-1.07	+	+	+	5	-125.55	261.90	0.00	0.99
4	-0.23	+	+		4	-131.94	272.40	10.50	0.01
3	0.10		+		3	-134.41	275.10	13.22	0.00
2	0.20	+			3	-141.27	288.90	26.95	0.00
1	0.53				2	-143.74	291.60	29.72	0.00

Gecko Abundance

Global model call: glmer(formula = Gecko ~ Season + Habitat + (Season:Habitat) + (1|Habitat:Treatment), data = model.pred.data, family = poisson())

model	intercept	Habitat	Season	Hbt:Ssn	df	logLik	AICc	delta	weight
3	2.60		+		3	-46.80	101.60	0.00	0.64
1	2.44				2	-49.66	104.20	2.65	0.17
4	2.68	+	+		4	-46.57	104.80	3.19	0.13
2	2.52	+			3	-49.44	106.90	5.28	0.05
8	2.66	+	+	+	5	-46.53	109.10	7.47	0.02

Invertebrate Prey Abundance

Global model call: glmer(formula = invert.total ~ +1 + Habitat * Season + (1|Site), data = invert.abund.raw, family = poisson())

model	intercept	*Habitat*	*Season*	*Hbt:Ssn*	df	logLik	AICc	delta	weight
3	1.04		+		3	-164.51	335.30	0.00	0.57
4	1.03	+	+		4	-164.50	337.50	2.19	0.19
1	1.19				2	-167.10	338.40	3.02	0.13
8	1.06	+	+	+	5	-164.41	339.60	4.30	0.07
2	1.18	+			3	-167.09	340.50	5.16	0.04

Invertebrate Predator Abundance

Global model call: glmer(formula = InvertPreds ~ +1 + Habitat + Season + (Season:Habitat) + (1|Habitat:Treatment), data = raw.pred.data, family = "poisson")

model	intercept	*Habitat*	*Season*	*Hbt:Ssn*	df	logLik	AICc	delta	weight
2	-0.76	+			3	-92.59	191.50	0.00	0.31
1	-0.41				2	-93.69	191.50	0.04	0.31
8	-0.98	+	+	+	5	-91.24	193.30	1.79	0.13
3	-0.34		+		3	-93.50	193.30	1.81	0.13
4	-0.68	+	+		4	-92.39	193.30	1.82	0.13

APPENDIX 5.S2. Additional information and discussion of alternative predators.

Invertebrates: Predators, competitors, prey, or all of the above?

The presence of small lizards and large spiders make for an interesting predator–prey dynamic. Many lizards, including *G. dubia*, are insectivorous and consume a wide variety of prey items, including spiders (Nordberg et al. *in review*). Although infrequently studied and observed, many large spiders consume small vertebrates, such as lizards and frogs (see McCormick and Polis 1982; Nordberg et al. *in review*). We suspect that due to the high abundance of *G. dubia* and huntsman spiders at our study site, these two groups are not only competitors for invertebrate prey, but also eat each other. Adult *G. dubia* probably feed on juvenile huntsman spiders, while adult huntsman spiders can consume juvenile (and even some adult) geckos (Nordberg pers. obs). The diets of many web-spinning spiders can be determined by examining food remains and body parts left in the web; whereas for active-foraging spiders, such as huntsmen, diet analysis can be much more difficult. The diets of active-foraging spiders may require burrow excavation (Henschel 1994) or modern techniques such as DNA sequencing of stomach or fecal samples (King et al. 2008) to identify prey items. Nevertheless, we have observed large huntsman spiders consuming *G. dubia* (Nordberg pers. obs.). Others have used plasticine models to record invertebrate “attacks” (Posa et al. 2007; Saporito et al. 2007) providing insight into predation attempts by predatory invertebrates.

Snake predators

Snakes are likely important predators of *G. dubia* and other small herpetofauna. The most common snake species in our study were pale-headed snakes (*Hoplocephalus bitorquatus*), arboreal specialists that probably feed on a variety of small vertebrates (Wilson 2015; Cogger 2014). Unfortunately, we could not detect predation attempts on model lizards by snakes because *H. bitorquatus* are ambush predators; not likely to attack a motionless model (Huey and Pianka 1981). Active foraging snakes, such as coachwhips (*Masticophis flagellum*), do attack even sedentary plasticine models of lizards (Husak et al. 2006). Brown tree snakes (*Boiga irregularis*) are nocturnal active foraging snakes present at the study site, but were not observed during our survey periods. Likely, our models underestimated attacks by snakes, but the estimates of survival include predation by snakes.

References

Cogger, H. (2014). Reptiles and amphibians of Australia. CSIRO Publishing, ACT, Australia.

Henschel, J.R. (1994). Diet and foraging behaviour of huntsman spiders in the Namib dunes (Araneae: Heteropodidae). *J. Zool.*, 234, 239–251.

Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. *Ecology*, 62, 991–999.

Husak, J.F., Macedonia, J.M., Fox, S.F. & Sauceda, R.C. (2006). Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): An experimental test using clay-covered model lizards. *Ethology*, 112, 572–580.

King, R.A., Read, D.S., Traugott, M. & Symondson, W.O.C. (2008). INVITED REVIEW: Molecular analysis of predation: a review of best practice for DNA-based approaches. *Mol. Ecol.*, 17, 947–963.

McCormick, S. & Polis, G.A. (1982). Arthropods that prey on vertebrates. *Biol. Rev.*, 57, 29–58.

Nordberg, E. J., L. Edwards, and L. Schwarzkopf. *In review*. Invertebrates as formidable predators: An underestimated guild. *Food Webs*.

Posa, M.R.C., Sodhi, N.S. & Koh, L.P. (2007). Predation on artificial nests and caterpillar models across a disturbance gradient in Subic Bay, Philippines. *J. Trop. Ecol.*, 23, 27–33.

Saporito, R.A., Zuercher, R., Roberts, M., Kenneth, G. & Donnelly, M.A. (2007). Experimental evidence for aposematism in the Dendrobatid poison frog *Oophaga pumilio*. *Copeia*, 2007, 1006–1011.

Wilson, S.K. (2015). A Field Guide to Reptiles of Queensland, New Holland, Chatswood, NSW, Australia.

Table 5.1. Total counts of predator groups. RRB = Reid River box; SLI = Silver-leaf ironbark.

		Dry Season			Wet Season		
			Habitat			Habitat	
Predator Group	Species	Count	RRB	SLI	Count	RRB	SLI
Birds	Blue-faced Honey-eater	3	3	0	8	6	2
	Brown Goshawk	0	0	0	1	0	1
	Corvids	11	0	11	23	5	18
	Grey Butcherbird	4	1	3	0	0	0
	Pied Butcherbird	6	0	6	23	17	6
	Grey-crowned Babbler	9	1	8	0	0	0
	Kookaburra	3	1	2	7	4	3
	Magpie	6	0	6	31	7	24
	Pheasant Coucal	2	1	1	0	0	0
	Southern Boobook Owl	0	0	0	1	1	0
	Tawney Frogmouth	0	0	0	2	2	0
	Whistling Kite	4	0	4	4	1	3
Invertebrates	Centipedes	9	7	2	19	19	0
	Huntsman	67	30	37	81	45	36
	Redback Spider	11	4	7	1	1	0
Snakes	Pale-headed Snake	0	0	0	2	2	0

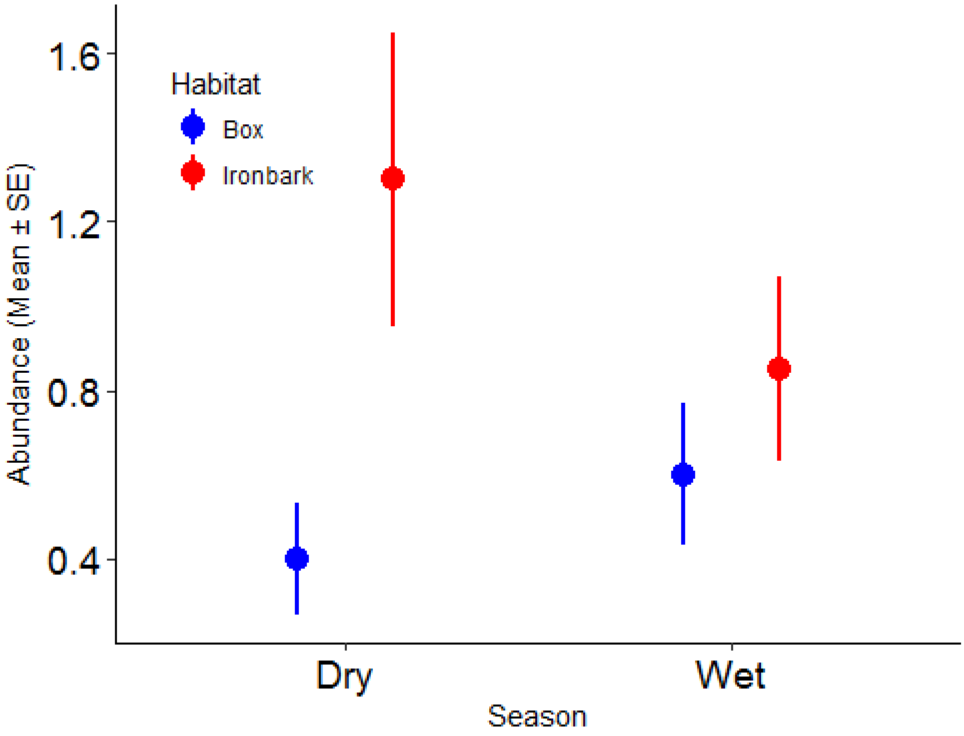


Figure 1. Seasonal and habitat differences in the abundance of predatory invertebrates. Habitat types represent Reid River box (*Eucalyptus brownii*; “Box”; blue) and Silver-leaf ironbark (*Eucalyptus melanophloia*; “Ironbark”; red).

APPENDIX 7.S1. Gecko captures

Table 1. Total lizard captures from 24 sites, two major habitat woodland types, and four major grazing regimes.

Site	Habitat	Grazing Regime	Species	Count
5	Box	Heavy	*Gehyra dubia*	59
15	Box	Heavy	*Gehyra dubia*	44
15a	Box	Heavy	*Gehyra dubia*	70
5a	Box	Heavy	*Gehyra dubia*	79
6	Ironbark	Heavy	*Gehyra dubia*	98
16	Ironbark	Heavy	*Gehyra dubia*	63
7	Box	Moderate	*Gehyra dubia*	55
11	Box	Moderate	*Gehyra dubia*	40
11a	Box	Moderate	*Gehyra dubia*	71
7a	Box	Moderate	*Gehyra dubia*	53
8	Ironbark	Moderate	*Gehyra dubia*	68
12	Ironbark	Moderate	*Gehyra dubia*	40
3	Box	Rotational	*Gehyra dubia*	51
13	Box	Rotational	*Gehyra dubia*	41
13a	Box	Rotational	*Gehyra dubia*	44
3a	Box	Rotational	*Gehyra dubia*	42
4	Ironbark	Rotational	*Gehyra dubia*	69
14	Ironbark	Rotational	*Gehyra dubia*	50
1	Box	Variable	*Gehyra dubia*	89
9	Box	Variable	*Gehyra dubia*	73
1a	Box	Variable	*Gehyra dubia*	64
9a	Box	Variable	*Gehyra dubia*	67
2	Ironbark	Variable	*Gehyra dubia*	91
10	Ironbark	Variable	*Gehyra dubia*	72
5	Box	Heavy	*Oedura castelnaui*	0
15	Box	Heavy	*Oedura castelnaui*	0

15a	Box	Heavy	*Oedura castelnaui*	7
5a	Box	Heavy	*Oedura castelnaui*	0
6	Ironbark	Heavy	*Oedura castelnaui*	1
16	Ironbark	Heavy	*Oedura castelnaui*	0
7	Box	Moderate	*Oedura castelnaui*	0
11	Box	Moderate	*Oedura castelnaui*	0
11a	Box	Moderate	*Oedura castelnaui*	16
7a	Box	Moderate	*Oedura castelnaui*	0
8	Ironbark	Moderate	*Oedura castelnaui*	6
12	Ironbark	Moderate	*Oedura castelnaui*	0
3	Box	Rotational	*Oedura castelnaui*	3
13	Box	Rotational	*Oedura castelnaui*	0
13a	Box	Rotational	*Oedura castelnaui*	0
3a	Box	Rotational	*Oedura castelnaui*	0
4	Ironbark	Rotational	*Oedura castelnaui*	9
14	Ironbark	Rotational	*Oedura castelnaui*	0
1	Box	Variable	*Oedura castelnaui*	1
9	Box	Variable	*Oedura castelnaui*	0
1a	Box	Variable	*Oedura castelnaui*	1
9a	Box	Variable	*Oedura castelnaui*	1
2	Ironbark	Variable	*Oedura castelnaui*	11
10	Ironbark	Variable	*Oedura castelnaui*	2
5	Box	Heavy	*Strophurus williamsi*	1
15	Box	Heavy	*Strophurus williamsi*	0
15a	Box	Heavy	*Strophurus williamsi*	0
5a	Box	Heavy	*Strophurus williamsi*	0
6	Ironbark	Heavy	*Strophurus williamsi*	0
16	Ironbark	Heavy	*Strophurus williamsi*	0
7	Box	Moderate	*Strophurus williamsi*	0
11	Box	Moderate	*Strophurus williamsi*	6
11a	Box	Moderate	*Strophurus williamsi*	7
7a	Box	Moderate	*Strophurus williamsi*	2
8	Ironbark	Moderate	*Strophurus williamsi*	1

12	Ironbark	Moderate	*Strophurus williamsi*	0
3	Box	Rotational	*Strophurus williamsi*	1
13	Box	Rotational	*Strophurus williamsi*	0
13a	Box	Rotational	*Strophurus williamsi*	3
3a	Box	Rotational	*Strophurus williamsi*	0
4	Ironbark	Rotational	*Strophurus williamsi*	0
14	Ironbark	Rotational	*Strophurus williamsi*	0
1	Box	Variable	*Strophurus williamsi*	0
9	Box	Variable	*Strophurus williamsi*	0
1a	Box	Variable	*Strophurus williamsi*	0
9a	Box	Variable	*Strophurus williamsi*	0
2	Ironbark	Variable	*Strophurus williamsi*	0
10	Ironbark	Variable	*Strophurus williamsi*	0