Title

The community wide effects of ecological release in White Sands lizards

Author

Noss, Clay Frederick

Publication Date

2022

Peer reviewed|Thesis/dissertation

The community wide effects of ecological release in White Sands lizards

By

Clay Frederick Noss

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor in Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Erica B. Rosenblum, Chair
Professor Mary E. Power
Professor Justin S. Brashares

Summer 2022

The community wide effects of ecological release in White Sands lizards

Abstract

The community wide effects of ecological release in White Sands lizards

by

Clay Frederick Noss

Doctor of Philosophy in Environmental Science, Policy, and Management
University of California, Berkeley

Professor Erica B. Rosenblum, Chair

A fundamental goal in ecology is understanding species interactions, such as predation and interspecific competition. Important insight into these processes is gained from examining systems where they have been relaxed. Reduction in these types of antagonistic interactions may lead to ecological release, a suite of changes that can include density compensation, higher intraspecific variation, and broader niche breadth. In the gypsum dune fields of White Sands, New Mexico, three species of lizards - *Aspidoscelis inornata*, *Holbrookia maculata* and *Sceloporus cowlesi* - have escaped most of their predators and interspecific competitors. White Sands lizards show multiple markers of ecological release. In this dissertation, I consider the community scale implications of this ecological release. In Chapter 2, I explore the relationship between trophic niche and community structure across an ecological gradient from White Sands to the surrounding desert scrub. I used stable isotopes to quantify three trophic niche metrics, including population niche width, degree of individual specialization and trophic position. There was substantial variation in all niche metrics across populations in all lizard species but broad patterns were generally similar between species and across years. Resource diversity, inter and intraspecific competition and predation all intersected to shape trophic niche. Individual specialization and population niche width were surprisingly decoupled, with specialization highest in low diversity habitats and population niche width highest at intermediate diversity. In Chapter 3 I tested for trophic cascades in White Sands. Intermediate predators like lizards should exert stronger trophic interactions after ecological release. However, prevailing theory predicts that top down control is relatively unimportant in desert ecosystems. Using exclosures, I experimentally manipulated the presence of lizards and measured the effects on arthropods and plants. Web building spider densities increased dramatically following lizard removal. At one sampling date, spider webs were closer to the ground in lizard exclosures. Across all or at specific dates, captures of all arthropods, Coleoptera, Collembola, Formicidae and other Hymenoptera were lower in lizard exclosures. On the last sampling date I found higher herbivory in exclosures. I found limited evidence that these shifts caused changes in plant biomass, abundance or reproductive effort. I hypothesize that high compensatory predation partially explains these results, and that ecologists need to consider top down forcing by carnivores in desert ecosystems. In Chapter 4, I test the hypothesis that a potential consequence of ecological release is higher mite ectoparasitism in White Sands lizards. I tested this hypothesis by quantifying ectoparasitism in four lizard species across habitats and years, and leveraged this dataset to test multiple other hypotheses for causes of variation in parasitism between populations and individuals. Contrary to my primary hypothesis, mite loading was lower in

White Sands than in the surrounding desert scrub across lizard species. I also found strong variation with species and year, with year effects dwarfing any other drivers of ectoparasitism. Consistent with other work, I found higher ectoparasitism on males than females and a positive relationship between body condition and ectoparasitism. Date, conspecific abundance, lizard abundance and squamate richness also had correlations with mite loading, with directionality varying by host species. My work demonstrates that the effects of ecological release are complex and multifaceted. Multiple ecological processes need to be considered in tandem in order to understand the consequences of shifts in species diversity and composition.

This dissertation is dedicated to the creatures of White Sands – how lucky I am to have spent time your presence.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I owe a substantial thanks to the undergraduate researchers I have been lucky to work with. I could always trust that these folks had my back during often tedious and difficult work, whether it was chasing the umpteenth whiptail through the baking desert, counting literally thousands of tiny springtails in the lab or dissecting muscle from <1 cm pieces of lizard tail. Their excitement and insights kept these efforts fresh for me over the years, and none of this would be possible without their work. Katharine Boyce – it was a particularly constructive that you were the first field tech I worked with. Your incredible organizational skills, attention to detail and insightful questions helped me grow tremendously as a field scientist. Tyler Cino – thank you for your hard work and great attitude, for sharing my love of the food of the Tularosa Basin, and for great company during our long drives. Allison Litmer – the best ally one could hope for the field, a rigorous and curious scientist who made the leap to join me in Alamogordo from across the country. Thank you for a great 2016 season, and I have been inspired following your work before and since we worked together. Yibing Yu – your ability to quickly master difficult skillsets as diverse as weighing isotopic samples or constructing sticky traps in the desert is amazing. Thank you in particular for leading during the intense lab efforts, I am so glad I had someone to trust during that time. Thank you also to Collin Bos, Shannon Buttimer, Molly Caldwell, Yujane Chen, Niko Frost, Jennifer Green, Hannah Howard, Analise Hober, Poojan Karnik, Nicole Kim, Seth LaRosa, Abriella Leeder, Aaron Luu, Aidan Maese-Czeropski, Madeline Moore, Tyler Moy, Linnea Norton, Kea Rutherford, Jessica Waller, Sam Wasserman and Jimmy Wehsener. Thank you to my sister-in-law Liz Kinkopf for help in the field.

Thank you to my advisor, Bree Rosenblum. Bree, thank you for the wisdom you've shared over these years. Your guidance and support, usually utterly practical yet unafraid of magic and mystery, has shaped me into not just a better scientist but a better person. I will carry your insights with me for life, and for this I am truly grateful. In particular I am thankful to be part of a community that Bree created and nurtured, the RoLab. I count many of my current and former lab mates among the most important people in my life. You are all inspiring scientists and I am so thankful for the fun we've had. Allie Byrne – whether it's digging perfect trenches or churning out beautiful papers, I am in awe of your ability to get things done while remaining so grounded. Andrew Rothstein – your joyful approach to work, life and community is something I strive for, thank you for your constant support. Alex Krohn – you're great in a million ways, but to me you will always be the uber-herpetologist, an inspiration for the love of reptiles. Karina Klonoski – thank you for always keeping it real, for your advice and for your support. Maddie Girard – I love the way you look at the world, happy to get weird but keeping the science excellent. Maggie Grundler – the wonder and love you have for nature always reminds me why we do what we do, I am so grateful to be a witness to your amazing work, and thank you for your patience as I try and bird alongside you. Molly Womack – it goes without saying that you are a scientist hero of mine, thank you for the hours of clear sighted advice, scientific and personal. Max Lambert – another scientist hero, I have never met anyone so intellectually unafraid yet practical, your support and advice, especially during the trying covid years, has been essential to keeping me moving forward. Thank you to all my other lab mates for everything, including Eveline Diepeveen, Alex Gunderson, Obed Hernandez-Gomez, Thomas Jenkinson, Telma Laurentino, Alex Mauro, Tom Poorten, Chris Martin, Simone des Roches and Sarah Wenner.

Thank you to the broader community at UC Berkeley, which truly lived up to its reputation for excellence. To my committee, Justin Brashares and Mary Power. Justin – thank

you for modeling excellence in teaching and research while being kind and supportive. Mary – thank you for always keeping the focus on natural history, the questions direct and clever yet broadly curious, and for being a model of how to keep a love of nature front and center. Thank you to the Center for Stable Isotope Biogeochemistry, in particular Stefania Mambelli for your advice and support. Thank you to Todd Dawson for the isotope advice and allowing me to use your equipment – this support was essential for completion of my work. Thank you to the Dawson lab, in particular Wendy Baxter and Chris Wong, for the advice and support. Thank you to Melanie Miller for your advice and demonstrating excellence for using and analyzing stable isotopes. Thank you to Jenny Hofmeister and Maya deVries for early advice on using stable isotopes and for sharing protocols. Thank you to Peter Oboyski for letting me borrow equipment and for advice on arthropod identification. Thank you to Kelsey Scheckel and Brian Whyte, and other folks in the Tsutsui lab, for helping me identify arthropods. Thank you to Drew Hart in the D-Lab for help me learn how to building simulations in R, your above and beyond support made my first chapter much stronger. Thank you to Rachel Baker, your R and general scientific advice was critical to moving my dissertation research forward. Thank you to Gregory Biging, in addition to reinforcing the fundamentals of sampling, an invaluable skill, I learned much from you in how to communicate statistics. Thank you to the community of the Museum of Vertebrate Zoology, I am so grateful to have been part of a community so centered on the joy of discovery and love of animals. Thank you to my PhD cohort, I had so much fun and learned so much from you all. In particular thank you to Kelsey Scheckel, Maggie Raboin and Matt Libbassi, our covid writing group was essential to keep me sane and moving forward. Thank you to the broader Department of Environmental, Science, Policy and Management, I am so thankful so many intelligent and compassionate people are invested in building a better future for all of life.

Thank you to the scientists and staff at White Sands National Park and White Sands Missile Range for facilitating my work. In particular thank you to David Bustos for insightful and wide ranging conversations on White Sands, your endless curiosity about this system despite your years of experience is inspiring. Thank you to Patrick Martinez for checking and repairing the lizard exclosures over two years – my second chapter could not have happened without you, I am eternally grateful. Thank you to Doug Burkett – for the advice, the endless knowledge of desert ecology and natural history, the fun, and for giving me something to aspire to as an amazing all around scientist and naturalist. Thank you to Eric Metzler, another endless source of knowledge and curiosity about White Sands, your advice and insights were invaluable.

Thank you to David Spiller and Thomas Schoener – you both took hours of your time to advise me on the promises and pitfalls of experimental investigations of lizards in food webs. My second chapter could not have happened without you. To Marcio Araujo, thank you for the multiple email consultations regarding the calculation of individual specialization from isotopes.

Thank you to my family, my mother Myra, my ecologist father Reed – the best naturalist I know, my siblings Max and April, my brother-in-law Armando and the little ones, Kai, Ren and Mae, for your love of nature. Needless to say I would not be nearly as obsessed with reptiles and amphibians if it wasn't for you all. I am so excited about our continuing adventures.

To Katherine Kinkopf, anthropology professor and scholar extraordinaire, and my wife. None of this would be possible without you – your heroic help in the field for 3 weeks, your patience teaching me R, the endless sharpening of scholarly inquiry. Hearing you type away in the other room, then coming in to breathlessly share your latest discoveries, is an endless source of joy. Thank you for everything, Katie.

Finally, to the lizards, arthropods, plants, gypsum, and all other components of White Sands, the Tularosa Basin, and the endless, infinite, beautifully perfect and terrible desert. I went to you to learn, and learn I did.

CHAPTER 1
INTRODUCTION

A fundamental goal in ecology is understanding species interactions like predation and interspecific competition. One avenue for understanding the ecological and evolutionary consequences of these interactions is to examine systems where they have been relaxed[1,2]. Ecological opportunity is the availability of novel resources, which can be a result of reduced interspecific competition or predation[2,3]. Following ecological opportunity, ecological release can include density compensation, higher intraspecific variation and increased resource and/or habitat breadth[2,3]. Ecological release is widely hypothesized to have important ecological and evolutionary implications and to the be an important generator of biological diversity[2,4]. Here, I leverage the escape of lizards from interspecific competitors and predators in White Sands to better understand the ecological consequences of ecological release.

Rising dramatically from the surrounding Chihuahuan desert scrub, White Sands is a 712 km^2 habitat island of gypsum sand dunes in south-central New Mexico[5]. The dune field is a mix of active, mobile dunes and interdunal areas where most of the vegetation and animals are found[5]. Out of the ~40 species of squamates found in the surrounding desert scrub, only three are abundant in White Sands, *Aspdidoscelis inornata*, *Sceloporus cowlesi* and *Holbrookia maculata*[6,7]. *S. cowlesi* and *H. maculata* are both in the family Phrynosomatidae and considered sit-and-wait predators, usually ambushing prey that come nearby[8]. *A. inornata* is in Teiidae and an active forager, relatively mobile and pursuing prey[8]. Famously, the White Sands lizards have convergently evolved blanched coloration[9] but all also show signs of ecological release[10]. Avian predators are also less abundant in White Sands, which in addition to snakes and other lizards are major predators of lizards in the region[8]. Investigation of *S. cowlesi* anti-predator behavior corroborates these shifts, with White Sands individuals being less wary than those in the desert scrub[11]. There are multiple lines of evidence that ecological release has followed ecological opportunity in White Sands lizards. With important differences between species, White Sands lizards show shifts in taxonomic composition of prey and broader dietary niches[10]. Changes in morphology (head and body size) and performance (bite force) accompany dietary shifts[10,12]. *S. cowlesi* in the surrounding desert scrub are found almost entirely on *Yucca elata*, but in White Sands other plants and the ground is used as well[6,13]. *S. cowlesi* also have more variable home range sizes in White Sands than on the ecotone with the desert scrub, indicative of a wider range of strategies and ecological release[13]. Community composition on the ecotone is intermediate between White Sands and the desert scrub, with predators and additional competitor species present and habitat structure relatively similar to the interior of the dunes[7,13]. My dissertation research further quantified ecological release in this system and considered some of its various ramifications, including for lizard diet, top-down forcing by lizards, and ectoparasitism.

In Chapter 2, I consider evidence for ecological release in lizard trophic niches and possible mechanisms behind any changes. Trophic niche is a fundamental descriptor of an organism's ecology, with profound implications for ecology, evolution and conservation[1,14]. Teasing apart the multiple dimensions of the trophic niche is essential to understanding these ramifications[15]. Important dimensions of the trophic niche include the extent of resources utilized by the entire population (population niche width[15]), individual specialization (differences between individuals in the same population[15]), and trophic position (the position on a food chain[16]). The relationship between these niche metrics provides insight into multiple ecological processes and the potentiality of ecological release for diversification[17,18]. These niche metrics

are known to be influenced by multiple processes, including inter and intraspecific competition[19,20], predation[21], resource diversity[17], with substantial variation over time[22] and with taxon[15]. Contrasting predictions from these multiple, interacting processes necessitates studies in systems like White Sands with multiple species occurring along an ecological gradient[23,24]. Over two years, I quantified trophic niche metrics (population niche width, individual specialization, and trophic position) using stomach contents and stable isotopes. I also measured community structure, including lizard abundance, conspecific abundance, lizard species richness, predator abundance, predator species richness and arthropod prey diversity. I found considerable variation in niche metrics across populations and habitats, but patterns were generally similar between species and years. My results are consistent with resource diversity, inter and intraspecific competition and predation jointly shaping trophic niche. Individual specialization and population niche width are surprisingly decoupled in this system. My work supports calls that multiple dimensions of trophic niche and community structure should be measured concurrently across multiple species and years, as analyzing these in isolation may be misleading[17,24].

I shift to an experimental approach in Chapter 3, testing for top-down forcing by White Sands lizards on arthropods and plants. Trophic cascades are permutations across at least two links in a food chain and are often described as ubiquitous[1,25]. There is a dearth of studies testing this claim in deserts, however[26]. Multiple theoretical frameworks and lines of evidence suggest that top-down control should be weak in deserts[27-30]. Importantly, some of the theories predicting weak cascades in deserts due to low primary productivity have been challenged[31]. Observational evidence and single link experiments (e.g. herbivores – plants) suggest that trophic cascades can occur in deserts[32,33]. The few rigorous experiments that have occurred in deserts have not found evidence of trophic cascades, although most of these were of short duration[26,34-36]. While ectotherms are predicted to have reduced per capita effects on lower trophic levels than endotherms[30,37], lizards are model organisms for demonstrating top down forcing in other ecosystems[38]. White Sands is a particularly compelling system to test for top down forcing by desert lizards because following ecological release they should exert stronger trophic interactions[39,40]. I experimentally manipulated lizard presence using lizard exclosures in White Sands and tested for effects on lower trophic levels. I found changes in densities of multiple arthropod taxa, spider microhabitat use, and herbivory. To my knowledge this was the first experimental demonstration of trophic cascades from a desert reptile and one of very few experimental confirmations of top-down forcing from desert carnivores[26,36]. In many ways this was an exploratory study, as connecting patterns to process often remained challenging and speculative even under my rigorous experimental approach. In other systems decades of research are still leading to better understanding of these complex interactions[38]. I conclude that ecologists need to consider top down forcing by carnivores in our understandings of desert ecosystems.

In Chapter 4 I examine rates of ectoparasitism in lizards and how it may vary with dramatic differences in lizard densities and diversity across habitats. Ectoparasitic mites (including ticks) can have broad health consequences for lizards including direct mortality and changes in behavior[41,42]. There can be substantial variation in ectoparasitism between and within species[43,44]. Abiotic conditions, especially temperature and moisture, can shapes ectoparasitism[45] and this partially drives strong seasonal and annual changes[46]. Host density can have contrasting effects on ectoparasitism, likely contingent on parasite strategy[47]. Similar to density, host diversity can strongly effect ectoparasitism in multiple directions, with species identity more important than diversity per se[48]. Within a population multiple processes contribute to variation in ectoparasite loading between individuals including sex[49], reproductive status[50], age[51], and

body condition[52]. I predicted that ectoparasitism would be relatively prevalent in White Sands due to high densities, low diversity, relatively cool and moist conditions, and reduced melanin production[53,54]. We sampled lizards and snakes across sites in White Sands, the surrounding desert scrub, and the ecotone between the two habitats and measured their ectoparasite loads over two years. Two distinct mites were found, one likely *Eutrombicula* sp. (found on all species and habitats) and the other an Ixodid tick (found only on *S. cowlesi*). Contrary to our hypothesis that high rates of parasitism would be a cost of ecological release in White Sands lizards, we found that mite loading was higher in the desert scrub. We also found effects of year, species, sex, and body condition, and correlations with conspecific and lizard abundance and lizard richness. I found that White Sands has a relative dearth of mite ectoparasites in addition to the known rarity of predators and reduced competitor richness.

Changes to species diversity over time and space can have profound consequences. My dissertation takes advantage of a natural experiment in White Sands to explore some of these consequences in tandem for multiple species across an ecological gradient.

CHAPTER 2
MULTIPLE DRIVERS OF TROPHIC NICHE STRUCTURE IN DESERT LIZARDS

2.1 ABSTRACT

Multiple ecological and evolutionary processes are intimately connected with a population's trophic niche width, trophic position and degree of individual dietary specialization. Individual specialization and population niche width are generally hypothesized to be positively related, with trophic position varying in tandem with changes in diet. Many processes shape trophic niche, including inter and intra-specific competition, predation and resource diversity, with influence varying with time and taxon. We used a combination of field surveys and stable isotope analyses to explore the relationship between trophic niche and community structure across an ecological gradient in four lizard species in White Sands, NM. While there was substantial variation in all niche metrics across populations in all lizard species, broader patterns were generally similar between species and years. Resource diversity, inter and intraspecific competition and predation all intersected to shape trophic niche. Individual specialization and population niche width were surprisingly decoupled, with specialization highest in low diversity habitats and population niche width highest at intermediate diversity. Trophic position and specialization were positively correlated. Our results highlight the need for measuring multiple components of community structure and trophic niche concurrently, as results may be misleading in isolation.

2.2 INTRODUCTION

An organism's trophic niche is a fundamental descriptor of its ecology, with profound significance for ecological patterns and processes, evolutionary dynamics, and conservation. Teasing apart various attributes of the niche, and what processes shape it, is critical to understanding these implications. For example, a population's niche width (or total niche width, 'TNW'), the extent of resources utilized by the entire population, indicates the breadth of interspecific interactions[15]. The degree of individual specialization (intra-populational niche variation, hereafter 'IS') shapes the strength of interspecific interactions and affects equilibrium dynamics for populations and communities[14,15,55]. Both TNW and IS provide the variation for natural selection to work with, shaping adaptive responses to natural and anthropogenic change[2]. Trophic position, the position of an organism on a food chain, has overlapping implications with TNW and IS, regulating processes like trophic cascades and bioaccumulation[16]. Niche width, IS and trophic position were historically assumed to be conserved between populations, and still are in certain contexts[15]. However, decades of empirical and theoretical work have demonstrated that within species and populations these metrics of trophic niche can indeed be labile[15,56].

A population's trophic niche can shift through a variety of processes, including through a number of ecological and evolutionary changes known as ecological release[57]. Ecological release can follow ecological opportunity, variously defined but used here as an availability of novel resources[2-4,58]. Resources can become available ecologically or evolutionarily, through the colonization of a new habitat, escape from interspecific antagonists (e.g. predators, competitors), and/or an evolutionary innovation[2]. The resulting ecological release can include density compensation (resulting in presumably higher intraspecific competition) and broader TNWs[59]. Population niche width can expand in two main ways[15]. On one hand, individuals may increase

their niche widths, resulting in a population of relative generalists ('parallel release')[60]. Alternatively, the niche variation hypothesis posits that individuals maintain relatively narrow niches and the increase in TNW is the result of a greater degree of IS[18]. Support for niche expansion following ecological release, and for the niche variation hypothesis, is mixed[2,3,17,60,61]. Trophic position can be assumed to change with TNW and IS if predators target different trophic levels[10]. A well-known example is the global expansion of mesopredator niches following top carnivore extinctions[40]. Trophic position may also theoretically influence the degree to which the other niche metrics are flexible[56,62]. Svanbäck et al. (2015) note that trophic cascade theory predicts that the relative importance of predation, inter and intraspecific competition should all vary with trophic level[27,56,62-64]. Examining multiple aspects of trophic niche jointly should help illuminate when and how trophic niches shift following ecological opportunity.

Trophic niche is clearly shaped by multiple interacting ecological and evolutionary processes that make generalizations even under the powerful ecological release framework difficult[3]. Studies that simply compare mainland to island populations, those in different habitats, or indigenous vs invasive populations, are typical but are limited in their power to link specific mechanisms to resultant niche shifts[22]. A promising direction is isolating more specific processes so we can understand how they influence trophic niche both in isolation and in aggregate[2,3]. Early work on trophic niche lability focused on the role of inter and intra-specific competition, and these process are still central to our understandings of trophic niche[2,18,20]. Interspecific competition generally constrains TNW and limits IS[22,65]. Intra-specific competition is often assumed to expand TNW and increase IS[2]. However in a recent review, Jones and Post (2016) found that greater intraspecific competition decreased TNW and IS in as many cases as it increased them[19]. Predation is another process that can have contrasting effects on trophic niche[21]. Ecological release and some evolutionary theory has predicted stabilizing selection from predation, constraining TNW and IS[2,66]. However predation can also drive negative frequency dependent selection, driving more differences between individuals of the same species[21,67]. Resource diversity has also been long recognized to facilitate trophic niche shifts, with empirical and theoretical support for increased diversity promoting larger TNW and IS[2,17,20,22,68]. Generalizations can further be challenging given that each of the described processes can vary with season, year, and taxon studied[15,22,23].

Contrasting predictions arising from the multiple, interacting processes that shape trophic niches necessitate studies in systems with multiple species occurring across an ecological gradient[3,17,23,24]. The White Sands (WS), a 712 km^2 habitat island of gypsum sand dunes in south-central New Mexico, and the surrounding Chihuahuan desert scrub (DS) provides such a gradient with multiple sympatric species. Out of the diverse suite of squamates found in the surrounding DS (~40 species) only three are abundant in WS, *Aspidoscelis inornata, Sceloporus cowlesi* and *Holbrookia maculata*[6,7]. White Sands also has reduced diversity and abundance of avian predators[6,13], which in addition to snakes and other lizards are major predators of lizards in the region[8]. The ecological opportunity in WS, specifically a reduction in predator and interspecific competitor richness, is accompanied by multiple lines of evidence of ecological release. With important differences between species, WS lizards generally show shifts in taxonomic composition of diet including more hard-bodied prey, possibly broadened TNW and increased variance in trophic position[10]. White Sands lizards have morphological (head and body size) and performance shifts (bite force) that corroborate these shifts[10,12]. In addition, *S. cowlesi* has broadened microhabitat use and more variable home range size in WS[6,13]. There is evidence that the community composition at the ecotone (ECO) between DS and WS is intermediate, with

similar habitat structure to the WS interior but a higher richness of predators and competitors[7,13]. Trophic niche dynamics remain unexplored in the ecotone, and it may represent an opportunity to tease apart which ecological processes are contributing to trophic niche shifts in WS lizards.

Here, we measured dimensions of the realized niche – TNW, IS, and trophic position – in multiple lizard species across multiple WS, DS and ecotone sites over two years. We used carbon ($\partial^{13}C/\partial^{12}C$) and nitrogen ($\partial^{15}N/\partial^{14}N$) stable isotopes ratios to quantify trophic niche, which provide long term averages of diet. Carbon isotopes are useful for indicating which primary producers and consumers predators are eating, whereas nitrogen is particularly useful for quantifying trophic position[69]. We also characterized community structure at each site, broadly sampling the reptile and arthropod communities for competitors, predators and prey. We predict that (1) our results will confirm that WS provides ecological opportunity through lower predator and competitor richness for some lizards species, with intermediate opportunity in ecotone sites, (2) TNW and IS will be higher in WS relative to DS sites, with intermediate values in the ecotone, (3) shifts in trophic position will accompany other changes in diet and (4) variation between sites in community structure will allow us to tease apart the relative contribution of different community characteristics (predation, inter and intraspecific competition, resource diversity) to any trophic niche shifts.

2.3 METHODS

Field surveys

We surveyed multiple WS, DS and ecotone sites for reptiles, arthropods and plants in summer 2015 and 2016. A pool of sites were selected in accordance with White Sands National Monument and White Sands Missile Range regulations that ensured sites (1) were not near areas of high visitor use, (2) not near sensitive archaeological resources and (3) would not interfere with NPS or military operations. This resulted in about 2 sites per habitat per year.

Reptiles were captured using the standard technique of drift fences with funnel and bucket traps[70]. Fences were constructed from aluminum flashing and were 15.2 meters long, 40 cm high and buried 10 cm. Pitfall traps (19 liter paint buckets) were located at both ends of the fence, and 2 funnel traps (wire mesh bags with a funneled entrance) facing opposite directions were placed along each side of the fence. Half of the fences were kept open at a time for alternating 72 hour periods (1 per habitat) and checked daily. Reptiles were also captured by hand or noose in time and area constrained searches within 250 m of the center of the drift fences[71]. At one site, DS4, lizards were solely captured by constrained search due to restrictions imposed by the US Military. The arthropod community was also characterized at each site by recording individuals captured in pitfall and funnel traps[70]. The relative size of arthropods was recorded in order to distinguish potential prey from arthropods that are likely too large to be prey (this was mostly tenebrionid beetles)[72]. We sampled plant tissue from four 3.1 m^2 plots, each located 10 meters in every cardinal direction from the center of each site (fence) at each year. We haphazardly sampled living leaf and stem tissue from every plant species located within each plot. Plant samples were frozen until further preparation for isotopic analysis.

Lizard diet was measured only for species with adequate sample sizes, which included *A. inornata* (ASP), *H. maculata* (HOL), *S. cowlesi* (SCE) and *Uta stansburiana* (UTA). Tail tips (the distal ~1cm of tail) were collected and frozen from all lizards captured for stable isotope analysis. Tissue was not collected from lizards with regenerated tails. Lizard stomach content

samples were collected through the standard technique of stomach flushing[73]. Lizards were induced to open their jaws, which were kept open with a plastic ring. A 75 mm x 16 g curved stainless steel dosing cannula (Harvard Apparatus, Holliston, MA, USA) attached to a 5 mL plastic syringe was then carefully inserted into the digestive tract. Stomach contents were then flushed out with tap water and later frozen for taxonomic identification and stable isotope analysis. If after two rinses no stomach contents were recovered, we assumed the lizard's stomach was empty. All lizards were marked with a Sharpie to ensure that recaptures were not processed twice. Stomach contents were not collected in 2016 in order to save time and maximize sample sizes for lizard isotopes. Stomach content ratios used in subsequent IS estimations were therefore assumed to be the same between years and in two cases between the most nearby sites.

Isotopic Analysis

We measured $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios in lizards, their arthropod prey recovered through stomach flushing, and plants. Muscle tissue was dissected from lizard tail tips, in order to account for variation in isotopic turnover between tissue types and variation between species in the proportion of tail tips that are muscle[74]. Muscle samples were freeze dried then homogenized with a Mini–BeadBeater-16 (BioSpec) in 2 ml XXTuff vials (BioSpec) with stainless steel ball bearings. Very small dried samples (< 3 mg) were not homogenized, since recovery of 1.5 mg of tissue wasn't guaranteed. A subset of muscle samples, representing every combination of sex, species and site used in further analyses (n = 68), were selected for delipification to account for potential bias in isotope signatures[75]. We extracted lipids by mixing a 2:1 chloroform:methanol solution with the powdered muscle, agitating for 1 hour, centrifuging, then removing supernatant[76]. This process was repeated twice, then samples were dried in a dessicator for 24 hours. We tested for an effect of delipification on carbon and nitrogen ratios and variances using paired t-tests and F tests. There was a significant shift in carbon ratios due to delipification, from a mean of -17.9 to -16.8 ($t_{67} = 9.62$, $p < 0.0001$) and no significant shift in nitrogen ratios ($t_{67} = 1.28$, $p = 0.21$). Because delipification had no effect on sample variance for carbon ($F_{67} = 0.98$, $p = 0.92$) or nitrogen ($F_{67} = 0.98$, $p = 0.92$) correction was not needed for further analyses.

Stomach contents were separated taxonomically before being prepared for stable isotope analysis. Whole arthropods and fragments were sorted by morphospecies, then identified to order (family in the case of Formicidae). If there was uncertainty as to whether specimens belonged to the same morphospecies, they were assumed to be distinct. Specimens were then rinsed with deionized water, stored individually in microcentrifuge tubes, and freeze dried. Like lizard samples, arthropod specimens were homogenized if their dry mass exceeded 3 mg and kept whole if not. Plant specimens were oven dried at 60° C for 48 hours then homogenized in the same manner animal specimens, except 7 ml Polypropylene vials were used (BioSpec).

Freeze dried lizard and arthropod samples were weighed to 1.8 mg, and plants to 4 mg, into tin capsules (5 x 9 mm, Costech Analytical Technologies). Samples were analyzed at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley and at the University of California Davis Stable Isotope Facility. Berkeley's long-term precision for C and N is ±0.1% and ±0.2%, respectively and Davis' is ±0.2% and ±0.3%,. Both facilities analyzed samples via elemental analyzer/continuous flow isotope ration mass spectrometry; Berkeley using a CHNOS Elemental Analyzer (model: Vario ISOTOPE cube; Elemntar, Hanau, Germany)

and an IsoPrime 100 mass spectrometer (Isoprime Ltd, Cheadle, UK) and Davis using a PDZ Europa ANCA-GSL elemental analyzer and a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The same reference materials were run in both facilities to ensure that results were directly comparable.

Before using isotopic data to calculate measures of dietary niche (see below), carbon and nitrogen values for each lizard species/site/year (hereafter 'population') were screened for outliers. Values were removed for all subsequent analyses if deemed extreme outliers through the quartile method[77,78]. Mean isotopic ratios within each arthropod taxon at each site were used in subsequent analyses. In a subset of cases, the mass of arthropod prey was not high enough to estimate isotopic ratios. We used empirical plant and arthropod isotopes to construct linear models of the relationship between mean plant and mean arthropod isotopic ratios, across sites for each arthropod taxon[79-81]. These models were then used to predict specific arthropod taxon isotopic ratios for sites where empirical values were lacking.

Measure of population niche width

We quantified the TNW for each population using standardized Bayesian ellipse area (SEA_B, R package "SIAR")[24,82-85]. Standardized ellipse area (SEA) is essentially a standard deviation measure in two dimensions, here carbon and nitrogen isotopic ratios[82]. Using a Bayesian approach in SIAR generates a distribution of SEA_B estimates, for each population, accounting for uncertainty arising from the sampling process[82]. We then selected the mode SEA_B from these distributions for downstream analyses. Although uncertainty decreases with larger sample sizes, SEA_B mode is not directionally biased from small sample size[82]. We therefore selected a minimum sample size of 5 for estimation of SEA_B, so that these results were directly comparable to measures of IS and trophic position (see below).

Measure of individual specialization

We quantified the degree of IS for each population for both nitrogen and carbon isotopes. Our measure of IS was the average proportional similarity index (PS_i), a measure of the overlap between an individual's diet and the population diet[86]. The PS_i is a function of p_{ij}, the proportion of the *j*th resource category in individual *i*'s diet, and q_j, the proportion of the *j*th resource category in the population's diet (**Eqn. 1**).

$$PS_i = 1 - 0.5 \Sigma \mid p_{ij} - q_j \mid \qquad \textbf{Eqn. 2.1}$$

Average PS_i values close to 1 reflect a population with little IS, whereas average PS_i values closer to 0 reflect populations with a relatively high degree of IS[86].

We quantified the average PS_i for each population using a method developed by Araujo et al. (2007) that allows PS_i to be estimated from predator and prey isotopic signatures[87]. Significantly, distinct populations can be directly compared using this approach because variation in isotopic baselines is accounted for[23,87]. We recreated Araujo et al.'s C program VarIso 1.0 as a function in R, "VarIsoR", to facilitate sensitivity analyses and reproducibility. VarIsoR produces nearly identical results as VarIso 1.0 ($t_{16} = 0.05$, $p = 0.96$). The function first creates a multinomial probability distribution based on the population diet vector, the proportion of various taxa (by dry mass) in the population's stomach contents. The diet of individuals is

then simulated by giving each individual *s* random draws from the population diet vector. If *s* = 1, dietary specialization is maximized because each individual only consumes one resource type. As *s* increases, each individual's diet vector converges with the population diet vector. Each individual's isotopic signature is then simulated using empirically derived prey isotope signatures. This then allows for the population isotopic variance ($Var\delta_i$) and proportional similarity index, PS_i, to be estimated. These steps are then repeated for 100 replicate populations for each of 57 values of s (ranging from 1 to 1000 in increasing increments). The relationship between PS_i and $Var\delta_i$ is then modelled with a logistic regression, which allows the estimation of PS_i using the empirical $Var\delta_i$. This marks the only departure from Araujo et al.'s method, which modeled this relationship with a quadratic regression. We compared the quadratic and logistic regression estimates of PS_i and found general agreement, with the logistic approach having a better fit especially at high levels of $Var\delta_i$. Finally, we multiplied carbon and nitrogen PS_i for a two dimensional metric of IS ('NC PS_i') that could be directly compared to our two dimensional measure of TNW, SEA_B.

Our VarIsoR function also allowed us to explore the influence of sample size on estimates of PS_i through bootstrapping. Specifically, our sample size for lizards with recovered stomach contents varied, with consistently higher sample sizes in WS populations. We subsampled, without replacement, individuals from every WS population from which stomach contents were recovered, generating new population diet vectors. Keeping all other inputs constant, we independently ran VarIsoR 1000 times each for subsample sizes of 1, 2, 3, 4 and 5. We then used t-tests (or Shapiro-Wilk tests) to test for a difference between the empirical estimates of PS_i and simulation means and medians. We also tested for the effect of sample size on our estimates of isotopic variance, a key input in the estimation of PS_i. We subsampled, with replacement, carbon and nitrogen isotopes from each population with $n > 4$. This process was repeated 1000 times for sample sizes 2 to 25, and the standard deviation of variance estimates calculated at each sample size. We then plotted the relationship between sample size and mean and standard deviation of variance estimates to identify a minimum sample size. Bootstrapping revealed no relationship between the sample size of lizards with recoverable stomach contents and mean C or N PS_i estimates, although low sample sizes resulted in high variances in estimates (Table 2.5, Fig 2.21, 2.22). Because sample sizes were limited and we found no directional bias, we set a minimum sample size of 1 for lizards with recovered stomach contents per study population. We also found no relationship between isotope sample size and our estimate of isotopic variance (Figs 2.23, 2.24). Bootstrapping also revealed that isotopic variance estimates became more precise at $n = 5$ for both nitrogen and carbon, so this was selected as a minimum sample size (Figs 2.25, 2.26).

Measure of trophic position

We use a standard method of estimating the trophic position (TP) of individual lizards as where λ is the trophic position of the basal resource (1), $\partial^{15}N_{consumer}$ is directly measured for each lizard, $\partial^{15}N_{basal}$ is averaged across plant samples for each site and Δ_n is the trophic fractionization of $\partial^{15}N$ (how the isotopic ratio changes between trophic levels; **Eqn. 2**)[16].

$$TP = \lambda + (\partial^{15}N_{consumer} - \partial^{15}N_{basal}) / \Delta_n \qquad \textbf{Eqn. 2}$$

We used Δ_n = 3.4%, commonly used in food chain studies, including those of lizards[10,88-90]. We used the mean trophic position within population for subsequent analyses. We estimated the effect of sample size on mean trophic position through the same process as for isotopic variance (see above). Bootstrapping revealed no directional relationship between mean trophic position sample size (Fig 2.27). We found that mean estimates became more precise at n = 5, so this was used as a minimum sample size per population (Fig 2.28).

Statistical Analyses

We investigated how community structure varied across habitat (WS, DS and ECO) using generalized linear models (GLMs; using R 4.0.3, 'lm' function in package stats version 3.6.2[91]). Community characteristics for each site and year included lizard relative abundance (pooled across all species), conspecific relative abundance (for each lizard species), lizard richness, predator relative abundance (terrestrial predators of lizards), predator richness, and arthropod diversity (Shannon's diversity of Orders[92]). Quantification of community structure was not possible at site DS4, so this was excluded from downstream analyses that included these metrics. The same validation process was used for all models in this study and included checking residual normality with Shapiro-Wilk tests, plotting residuals versus fitted values and qq-plots[93]. We tested for an effect of sex or age class on carbon and nitrogen isotopic ratios for each population with linear models (LMs).

We explored the relationship between our four niche metrics (SEA_B, carbon and nitrogen PS_i, and trophic position) and explanatory variables (site, habitat, lizard species, year and community structure) using four main approaches. *First*, we constructed individual LMs for every combination of niche metric and explanatory variable. We used GLMs (Gamma distribution) for SEA_B because these were better supported following model validation. *Second*, we ran linear mixed models (LMMs, GLMMs for SEA_B; 'lmer' and 'glmer' functions in package lme4 version 27.1[94]) which included site as a random effect paired with each other explanatory variable as fixed effects. To help interpret the results from the first two approaches, we used chi square tests, ANOVAs and spearman rank correlations to detect collinearity amongst fixed effects[93,95]. *Third*, the combined effect of explanatory variables on niche metrics were tested for using LMMs, again with site as a random effect. For this third step we performed automated model selection using the 'dredge' function in package 'MuMIn' version 1.43.17[96], which evaluated every combination of fixed effects in modeling the niche metrics. These models were evaluated based on AICc, with models with $\Delta_i < 2$ considered having substantial support[97]. Before running dredge we used a backward selection process to identify multicollinearity with variance inflation factors (VIFs)[77]. We calculated VIFs for using the function 'vif' in the package 'car'[98], removing fixed effects until all VIFs were below 5[93]. The results of the above ANOVAs and chi-square tests were used to assess categorical variables before using dredge. *Fourth*, we used LMs (GLMs for SEA_B) to assess relationships for every combination of niche metrics and explanatory variables for each species individually.

The four approaches used here are complimentary. In general, we were not as interested in the effect of study site as we were in other explanatory variables. Mixed models allowed us to minimize variance associated with site, making our results more generalizable to the study area and lowering error[77]. However the number of levels per site varied between 1 and 6, so in some cases mixed models may be overly conservative[77]. The additional step of automated model selection using AICc allowed us to test the predictive power of our explanatory variables in

relation to each other[93]. The fourth step allowed us to assess patterns within species and compare these results to those in the overall lizard community. Only linear models were useful for this fourth approach because the number of levels per site was much more limited when data were subset by species[93]. If relationships between niche metrics and explanatory variables were robust with multiple approaches we had more confidence in the results.

2.4 RESULTS

We captured 487 lizards and snakes across two summers (n = 466 of 4 focal species), 135 of which were stomach flushed (n = 98 stomach contents recovered, 92 of which had identifiable specimens). We directly measured the isotopic ratios of 74 stomach content specimens, and used regressions to estimate ratios for 65 specimens. We measured isotopic ratios for 447 lizards, excluding 8 outliers from carbon analyses and 4 from nitrogen analyses.

We found evidence for isotopic niche partitioning by sex or age class in just two populations. At site DS1 in 2015, the mean N15 ratios for *U. stansburiana* were 18.24 ± 1.63 for juveniles, 17.30 ± 0.54 for males and 17.14 ± 0.74 for females ($F_{2, 31} = 3.325$, $p = 0.049$; Tukey HSD test M - F $p = 0.93$, J-F $p = 0.07$, J-M $p = 0.09$). We did not find evidence for niche partitioning from C13 isotopes in 2015 ($F_{2, 29} = 3.33$, $p = 0.69$) or for N15 partitioning in 2016 ($t_{4.4} = -1.10$, $p = 0.33$), although no juveniles were captured in 2016. At site WS2 in 2016 the mean C13 ratio for *H. maculata* was -19.76 ± 0.99 for males and -20.94 ± 0.97 for females ($t_{7.51} = 2.29$, $p = 0.05$). At this site we did not find evidence for niche partitioning for N15 isotopes in 2016 ($t_{17.98} = 1.56$, $p = 0.14$) or for C13 isotopes in 2015, although in 2015 we only sampled 2 females.

Community Structure

Lizard relative abundance, pooled across all species, was higher in WS relative to other habitats (Table 2.1; Tukey HSD test WS - DS $p = 0.02$, WS – ECO $p = 0.002$, DS-ECO $p = 0.29$). Conspecific relative abundance, pooled across all species, was higher in WS relative to ecotonal sites (Table 2.1; Tukey HSD test WS - DS $p = 0.19$, WS – ECO $p < 0.001$, DS – ECO $p = 0.11$). *A. inornata* relative abundance was higher in WS relative to other habitats ($F_{2,8} = 14.84$, $p = 0.002$; Tukey HSD test WS – DS $p = 0.004$, WS-ECO $p = 0.004$). *S. cowlesi* also had higher relative abundance in WS relative to ECO, and was absent from sites where standardized trapping was possible in DS ($F_{1,6} = 25.45$, $p = 0.008$). We found higher *U. stansburiana* relative abundance in DS relative to ECO sites, with none caught in WS, but this difference was not statistically significant ($F_{1,4} = 1.49$, $p = 0.29$). We also found a trend for higher *H. maculata* relative abundance in WS relative to ECO, with no individuals caught at DS sites ($F_{1,4} = 4.38$, $p = 0.11$). We found no predators in WS and intermediate levels on the ecotone, but these differences were not statistically significant for predator abundance or richness (Table 2.1). We found no difference in lizard species richness between habitats (Table 2.1). Arthropod diversity varied with habitat, with less diversity in WS than DS, and a trend for less diversity in WS relative to ECO (Table 2.1; Tukey HSD test WS - DS $p = 0.07$, WS-ECO $p = 0.11$, ECO-DS $p = 0.94$). We found broad collinearity between explanatory variables (Table 2.6). Backward selection of VIFs resulted in all explanatory variables being dropped besides species, arthropod diversity (VIF = 2.22), predator abundance (VIF = 3.3) conspecific abundance (VIF = 1.59) and lizard richness (VIF = 3.41) for use in the full dredge models.

Population niche width

The range of SEA_B estimates for each population varied, but were generally broader for those in ecotonal habitats than WS or DS (Figs 2.1-2.4, 2.6). The modes of the SEA_B estimates were not normally distributed (Fig 2.6; Shapiro Wilk test, $W = 0.74$, $p < 0.001$), so a Gamma distribution was used for downstream analyses[93]. One *S. cowlesi* site in 2016 was a high outlier (Fig 2.3; site ECO4 in 2016), but we chose to include it in analyses because model validation was still acceptable and we had no ecological basis for removal. Table captions include descriptions of the few occurrences where removing this outlier shifted results. Using GLMs and GLMMs we found multiple significant relationships between continuous explanatory variable and SEA_B modes (Table 2.2). Using GLMs we found that SEA_B varied between all habitats (Table 2.2; Fig 2.6; Tukey HSD test WS-DS $p = 0.06$, WS-ECO $p < 0.001$, DS-ECO $p = 0.01$). Using GLMMs we found that SEA_B varied with habitat (Table 2.2; Fig 2.6; Tukey HSD test WS-DS $p = 0.03$, WS-ECO $p < 0.001$, DS-ECO $p = 0.003$) and species (Table 2.2; Fig 2.5; Tukey HSD test ASP-HOL $p = 0.004$, ASP-SCE $p = 0.01$, ASP-UTA $p < 0.001$, HOL-SCE $p < 0.001$, HOL-UTA $p < 0.001$, SCE-UTA $p = 0.001$). Model ranking with dredge revealed four models with $\Delta_i < 2$, all included species as a fixed effect with conspecific abundance and arthropod diversity absent, included separately, and together (Table 2.3).

Linear models subset by species revealed that SEA_B varied with habitat for *A. inornata* (Fig 2.6; Table 2.7; Tukey HSD test WS-DS $p = 0.95$, WS-ECO $p < 0.001$, DS-ECO $p < 0.001$), *H. maculata* (Fig 2.6; Table 2.8; WS-ECO $p = 0.02$) and *S. cowlesi* (Fig 2.6; Table 2.9; WS-DS $p = 1$, WS-ECO $p = 0.02$, ECO-DS $p = 0.05$). For *H. maculata*, we found a negative relationship between SEA_B and lizard abundance (Fig 2.8) and a positive relationship between SEA_B and lizard richness (Fig 2.9) , predator abundance (Fig 2.10) predator richness (Fig 2.11), and arthropod diversity (Fig 2.7; Table 2.8). For *S. cowlesi*, we found a positive relationship between SEA_B and lizard richness (Fig 2.9; Table 2.9). For *U. stansburiana* we found a positive relationship between arthropod diversity and SEA_B (Fig 2.7; Table 2.10).

Individual specialization

We found a range of carbon PS_i estimates (Fig 2.6), normally distributed (Shapiro-Wilk, $W = 0.98$, $p = 0.76$). Using LMs, we found that C PS_i varied with site and between all habitats (Table 2.2; Fig 2.6; Tukey HSD test WS-DS $p < 0.0001$, WS-ECO $p = 0.003$, DS-ECO $p = 0.02$). There was a trend for C PS_i to vary with species, but pairwise comparisons revealed no significant differences (Table 2.2; Fig 2.5; Tukey HSD test ASP-HOL $p = 0.28$, ASP-SCE $p = 0.28$, ASP-UTA $p = 0.96$, HOL-SCE $p = 0.99$, HOL-UTA $p = 0.22$, SCE-UTA $p = 0.22$). We found relationships between C PSi and lizard abundance, predator abundance, predator richness and arthropod diversity (Table 2.2). When LMMs were used we found that C PS_i only varied between all habitats (Fig 2.6; Tukey HSD test WS-DS $p < 0.0001$, WS-ECO $p < 0.0001$, DS-ECO $p = 0.01$), but not any other community metric (Table 2.2). Model ranking with dredge revealed one model with $\Delta_i < 2$, which included no fixed effects and just site as a random effect (Table 2.3).

Linear models subset by species revealed that C PSi varied with habitat for *A. inornata* (Table 2.7; Fig 2.6; Tukey HSD test WS-DS $p = 0.002$, WS-ECO $p = 0.29$, DS-ECO $p = 0.02$), and *S. cowlesi* (Table 2.9; Fig 2.6; WS-DS $p = 0.04$, WS-ECO $p = 0.03$, ECO-DS $p = 0.92$). For *H. maculata* we found a negative relationship between C PSi and conspecific abundance (Fig

2.12; Table 2.8). For *S. cowlesi* we found a positive relationship between C PSi and lizard richness (Fig 2.9; Table 2.9). For *U. stansburiana* we found a negative relationship between C PSi and arthropod diversity (Fig 2.7; Table 2.10).

We found a range of nitrogen PS_i estimates (Fig 2.6), normally distributed (Shapiro-Wilk, $W = 0.94$, $p = 0.16$). Using LMs, we found a trends for N PS_i to vary with site and conspecific abundance, and significant relationships with lizard abundance, predator abundance and arthropod diversity (Table 2.2). When LMMs were used we found no significant relationships between N PS_i and any community metrics (Table 2.2). Model ranking with dredge revealed one model with $\Delta_i < 2$, which included no fixed effects and just site as a random effect (Table 2.3). For *A. inornata* linear models revealed a positive relationship between N PSi and lizard abundance (Fig 2.8) and negative relationships with predator abundance (Fig 2.10), predator richness (Fig 2.11) and arthropod diversity (Fig 2.7; Table 2.7).

Trophic position

We found a range of trophic position within and between populations, sites and years (Figs 2.6, 2.13-2.16). Mean trophic positions were normally distributed (Shapiro-Wilk, $W = 0.94$, $p = 0.16$). Using LMs, we found that trophic position varied with site and with habitat (Table 2.2; Fig 2.6; Tukey HSD test WS-DS $p = 0.03$, WS-ECO $p = 0.16$, DS-ECO $p = 0.87$). Trophic position varied with species (Table 2.2; Fig 2.5; Tukey HSD test ASP-HOL $p = 0.13$, ASP-SCE $p = 0.08$, ASP-UTA $p = 0.99$, HOL-SCE $p = 0.99$, HOL-UTA $p = 0.25$, SCE-UTA $p = 0.18$). Linear models and LMMs revealed correlations between trophic position and multiple community characters (Table 2.2). When LMMs were used we found that trophic position still varied with species (Table 2.2; Fig 2.5; Tukey HSD test ASP-HOL $p < 0.001$, ASP-SCE $p < 0.001$, ASP-UTA $p = 0.83$, HOL-SCE $p = 0.95$, HOL-UTA $p = 0.09$, SCE-UTA $p = 0.02$). Model ranking with dredge revealed one model with $\Delta_i < 2$, which included species, arthropod diversity and site as a random effect (Table 2.3). For *A. inornata* LMs revealed negative relationships between trophic position and lizard richness (Fig 2.9), predator abundance (Fig 2.10), predator richness (Fig 2.11) and arthropod diversity (Fig 2.7; Table 2.7). We also found a negative relationship between trophic position and arthropod diversity for *U. stansburiana* (Fig 2.7; Table 2.10).

Relationships between niche metrics

Using LMs, we found that most niche metrics were not correlated with each other when all species were pooled (Figs 2.17-2.20; Table 2.4). Including all species, trophic position was negatively correlated with carbon PS_i (Fig 2.19; Table 2.4) and we found a negative trend between trophic position and SEA_B (Fig 2.20; Table 2.4). Models subset by species revealed negative correlations between trophic position and C PSi and NC PSi for *S. cowlesi* (Table 2.9). For *U. stansburiana* we found a negative relationship between SEA_B and trophic position, a negative relationship between C PSi and SEA_B, and a positive relationship between C PSi and trophic position (Table 2.10).

2.5 DISCUSSION

Few studies have paired quantification of several dimensions of trophic niche, across multiple species, with in depth field surveys of community structure. Here, we found dramatic variation in TNW, degree of IS and mean trophic position within all species at a fine spatial scale (Fig. 2.6). While there was mixed support for our predictions, patterns were generally similar across all four species and between years. *First*, we a identified clear differences between habitats in community structure, with increases in overall lizard abundance and conspecific abundance in WS correlated with declines in lizard richness and predators. These clear markers of ecological opportunity and release are complicated by the parallel decline in arthropod diversity in WS. *Second*, while we did find a strong effect of habitat on TNW and IS, patterns did not always fit our predictions or prevailing theory. *Third* we found a negative relationships between mean trophic position and carbon PSi. *Fourth* while strong collinearity complicates our understanding of mechanisms, our results are consistent with multiple processes shaping trophic niche.

Our study adds to a growing body of evidence that an expanded TNW is not necessarily the result of greater IS. Across all species found in multiple habitats, TNW was highest at ECO sites, with WS and DS minimally differentiated. While carbon IS was highest in WS, intermediate in ECO, and lowest in DS, nitrogen IS did not vary with habitat. Population niche width was therefore not correlated with C PSi, N PSi, or CxN PSi. This striking result is counter to our predictions and the longstanding niche variation hypothesis, that IS and TNW should be positively correlated[18]. An exception was *U. stansburiana*, in which we found the predicted positive relationship between IS and TNW (Table 2.10). This was the only species with sampling restricted to one habitat. It may be that the relationship between IS and TNW is clearer within habitats because the contrasting effects of disparate processes on trophic niche are less pronounced. Mirabasso et al. (2020) found a clear IS/TNW relationship in salamanders when only single species sites were considered, but the relationship disappeared in more diverse communities[99]. However, restricting our analyses to within habitats did not reveal clear IS/TNW relationships across all species or within additional species. Species traits, such as the nature of any functional tradeoffs in foraging, may also modulate the relationship between IS and TNW[23]. The disparate IS and TNW results, along with the lack of relationship between C and N PSi (Table 2.4; Fig 2.18), underline the importance of quantifying multiple dimensions of trophic niche[17,23,100].

In our system broad TNWs could be driven by parallel release, or expansion of individual niche widths, rather than greater IS[60]. For example, Costa et al. 2019 found that in expanded TNW in *Leptodactylus* frogs were the result of individuals becoming relative generalists[17]. Numerous evolutionary and ecological models predict parallel release, broadly suggesting that individuals' capacity to consume novel prey types are less limited by functional trade-offs[101-103]. Another possibility is that TNWs can be relatively impervious to shifts in individual niche widths. Bolnick et al. (2010) reported that expansion of three-spine stickleback (*Gasterosteus aculeatus*) individual niches was not necessarily accompanied by TNW expansion, because IS declined concurrently ('individual release hypothesis')[60]. Decoupled shifts like this could explain why in WS habitats we saw a high degree of IS and narrow TNWs. These hypotheses, that individual niche widths are higher outside of WS, do contrast with previous stomach content data from this system. Des Roches et al. 2015 found that individuals of all 3 WS species had higher niche widths than DS individuals (morphospecies richness in *S. cowlesi* and *A. inornata*,

diversity of arthropod orders in *H. macualata*)[10]. This discrepancy may be methodological (e.g. Des Roches et al. only targeted males and measured to morphospecies level) and/or temporal, as trophic niche can shift strongly over time[22,104]. It is also possible that our different approaches in quantifying TNW and IS obscured any general relationship. Specifically, our measure of IS, PSi, controls for variance in prey isotopic ratios, whereas our measure of TNW, SEAB, does not. However, we found no relationship between baseline variance in prey isotopes and habitat. While we did not quantify individual niche widths, future studies should do so in order to better clarify the relationship between IS and TNW.

Contrary to our prediction, we found dramatically higher TNWs in ECO sites within and across all species. While this result doesn't include 2 ECO sites with *U. stansburiana* due to their limited sample sizes, one of the sites had by far the highest TNW estimate while the other was within the range of DS estimates (SEA_B modes = 9.66, 2.11). While ours was the first investigation of dietary niche on the ecotone, our prediction that TNW would be highest in WS was predicated on prior work demonstrating pronounced ecological opportunity and release in WS[10]. For example, Des Roches et al. (2015) found higher $\partial^{13}C$ variance in WS *S. cowlesi* and higher $\partial^{15}N$ variance in WS *H. maculata*, relative to DS populations. Because SEA_B incorporates both nitrogen and carbon, and is correlated with but distinct from variance, it is not especially surprising that our conclusions are distinct[82,100]. Our community composition data generally corroborate and extend previous work, demonstrating that declines in reptile diversity and increases in abundance in WS corresponded with declines in arthropod diversity (Table 2.1). Ecotonal sites may have the highest ecological opportunity because they represent an ideal balance – less natural enemies than DS habitats and higher resource diversity than WS (Table 2.1). Low lizard densities suggest that inter and intraspecific competition are also lowest on the ecotone. As resources become available, individuals are likely foraging more broadly[17]. Individual specialization, as opposed to strict parallel release, also contributed to the high TNW as carbon IS was intermediate on the ecotone. It may be that TNWs are frequently maximized when antagonistic interactions and resources availability are intermediate[19]. Eloranta et al. (2021) found that European whitefish (*Coregonus lavaretus*) TNWs were highest at medium levels of heterospecific fish abundance[24]. They hypothesize that this is partly because when competitor abundance is lower, resource diversity is also low[24]. More studies should explore niche dynamics on ecotones between more and less diverse ecosystems, as these sites may be important for diversification[105].

High carbon IS in WS, with intermediate and low values on the ecotone and DS, respectively, matched our predictions and prior work in this system. *S. cowlesi* has greater variance in microhabitat use in WS than DS (ecotone intermediate), and greater variance in WS home range size than the ecotone[6]. Our field notes support this, with *S. cowlesi* individuals much more reliant on yucca outside of the WS interior. Habitat and diet are highly correlated in lizards, so differences in habitat use could explain the high IS in WS[106]. Future work should compare habitat use between habitats in additional species in this system. *A. inornata* and *H. maculata* have larger heads and bite force in WS[12]. While this has been shown to broaden TNW it could independently increase IS by allowing individuals to more easily focus on components of the TNW[20]. For example, while *H. maculata* WS and DS populations don't differ in the mean proportion stomach contents that are hard bodied prey (usually Hymenoptera and Coleoptera), WS individuals are more variable[12].As with the expanded TNW on the ecotone, it is likely that the high IS in WS is due the interaction of multiple community characters. The generally high density of conspecifics in WS likely translates to strong intraspecific competition, increasing

variation in traits like habitat use or prey selection[22]. It is likely that the rarity of lizard predators in WS facilitates this variation indirectly via density compensation[22]. A direct link between predation and high IS in WS is difficult to establish because TNW is constrained, meaning lizards aren't using 'novel' resources that are also found in DS. This could be due to the relatively low arthropod diversity in WS. As discussed above, there are multiple theoretical reasons why IS and TNW may be decoupled. Lizards in WS may represent cases of 'ultra partitioning' (sensu Sjodin et al. 2018), where high IS is accompanied by low individual niche width[103]. To our knowledge this is the first case of ultra-partitioning reported in the literature, although not all studies quantify both IS and TNW. Future work should quantify TNW, IS and individual niche widths as ultra-partitioning may be a more common phenomena than appreciated, especially in depauperate systems. The high IS in WS has multiple ecological and evolutionary implications. Heightened IS following ecological release in depauperate systems has long been theorized to contribute to the generation of biological diversity[2]. High IS may also modulate trophic cascades as prey experience stronger or weaker effects from a subset of predators[107]. These dynamics may be especially important in WS, where lizards have high densities and likely function as important predators for many taxa.

We found a positive correlation between carbon IS and trophic position (Table 2.4; Fig 2.17). Svanbäck et al. (2015) extended trophic cascade theory to predict the degree of IS based on trophic position. They note that in four trophic level systems (plants – herbivores – intermediate predators – top predators) competition should be relatively important for regulating top predators and herbivores, and predation more so for intermediate predators[27,62]. If competition is primarily intraspecific, we then expect more IS in top predators and herbivores (and the converse from primarily interspecific competition). Intermediate predators may then be hypothesized to have less IS due to constraining predation. Our results are consistent with intraspecific competition playing a larger role in regulating lizard populations at higher trophic levels. In populations at lower trophic levels, predation may be more important, constraining IS. Indeed, we found a negative relationship between trophic level and predator richness and abundance (Table 2.2; Figs 2.10, 2.11). This interpretation comes with important caveats. Trophic levels are abstractions, theoretically useful but real food webs are made up of multiple, dynamic, interlocking chains[108]. The metric used here – population mean trophic level – does reflect differences in diet and food web structure between populations[16]. However, given the trophic diversity of lizard prey it is unclear whether strength of limiting factor (and therefore IS) should vary with trophic position. It is possible in our system variation in both IS and trophic position with habitat (Fig 2.6) is driving a correlation between these niche metrics.

Echoing existing theory, we found multiple lines of evidence that resource diversity shapes trophic niche. Across modeling approaches, arthropod diversity had a positive relationship with TNW (Table 2.2). Within species, this pattern was mirrored in *H. maculata* and *U. stansburiana,* with a trend for *S. cowlesi*. This pattern makes intuitive sense, and has been found in multiple systems[17,22,68]. We also found a negative relationship between trophic position and arthropod diversity (Fig 2.7), a pattern also significant within *A. inornata* and *U. stansburiana* (Tables 2.7, 2.10). It may be that the lizards generally prefer prey at lower trophic levels, and when diversity is higher they are able to target them. In WS, where trophic levels are generally higher, the presumably high competition could force lizards to more fully exploit the limited diversity. Interestingly, arthropod abundance (which we did not include in models) varied inversely with diversity and was generally higher in WS and intermediate on the ecotone. This could explain why carbon IS increased in less diverse sites (only the LM was significant) – with

the high abundances, it could be easier for individuals to specialize on a subset of prey[22]. While few studies have disentangled the effects of diversity and abundance on trophic niche, Sánchez-Hernández et al. (2021) found that brown trout (*Salmo trutta*) TNW and IS increased with prey diversity but not abundance. However both the diversity and abundance differences between habitats were driven by high Hymenoptera captures in WS (almost entirely Formicidae). When Hymenoptera are excluded, mean abundance is slightly lower in WS than DS or the ecotone and diversity is similar between habitats . Still, it is unlikely that variation in Hymenoptera abundance explain all of the dietary shifts between habitats. We found Hymenoptera prey in most population's stomach contents and Des Roches et al. (2016) only document higher Hymenoptera consumption in WS *H. maculata*[10]. Future work should strive for higher taxonomic resolution when measuring the effect of resource diversity on trophic niche, as shifts in composition rather than diversity per se are likely important[68].

Understanding variation in trophic niche between and within species and populations is a major goal of ecology. We found substantial differences in IS, TNW and trophic position in four species of desert lizards in a relatively small area. These patterns were generally conserved between species and years. Resource diversity, inter and intraspecific competition and predation intersect to shape trophic niche. As a consequence, we found that IS and TNW can be surprisingly decoupled. Future work should take care to measure community structure along with multiple trophic niche metrics, as these patterns can be misleading in isolation.

Acknowledgements

We thank Katharine Boyce, Tyler Cino, Allison Litmer and Seth LaRosa for help with fieldwork. We thank Yibing Yu, Sam Wasserman, Yujane Chen, Aaron Luu, Molly Caldwell, Jennifer Green, Tyler Moy, Hannah Howard and Jessica Waller for help with lab work. Thanks to the Rosenblum lab for valuable feedback on the manuscript. Funding was provided by the National Science Foundation, the American Society of Ichthyologists and Herpetologists, the Philomathia Foundation, UC Berkeley's Department of Environmental Science, Policy, and Management, and the Museum of Vertebrate Zoology. All animals were handled in accordance with New Mexico Department of Game and Fish Scientific Collecting Permit (authorization number 3184) and under the University of California, Berkeley, Institutional Animal Care and Use protocol #AUP-2014-11-6857.

Table 2.1. Means ± standard deviations of community characteristics across habitats with results of GLMs testing for differences (Gamma family for arthropod diversity, Poisson for all others). Sample sizes (n) denote site by year sampling events (2 sites White Sands, 4 for the ecotone and 3 for desert scrub).

	Mean ± SD					
	White Sands n = 4	Ecotone n = 4	Desert Scrub n = 4	F	df	*p*
Lizard abundance	43.25 ± 10.9	7.50 ± 5.5	19.00 ± 12.4	13.27	2, 9	< 0.001
Conspecific abundance	14.42 ± 7.67	2.55 ± 2.44	9.00 ± 8.07	9.29	2, 28	< 0.001
Lizard richness	3.00 ± 0	3.75 ± 0.50	3.5 ± 1.73	0.54	2, 9	0.6
Predator abundance	0 ± 0	1.25 ± 0.96	2 ± 2.16	2.19	2, 9	0.17
Predator richness	0 ± 0	0.75 ± 0.50	1.5 ± 1.73	2.08	2, 9	0.18
Arthropod diversity	0.63 ± 0.24	1.29 ± 0.56	1.39 ± 0.38	4.04	2, 9	0.06

Table 2.2. Results of linear models (LMs) and linear mixed models (LMMs; Site included as a random effect) exploring the relationship between niche metrics and explanatory variables. Generalized LMs and LMMs (Gamma family) were used for SEA_B mode. Non – significant relationships are denoted by '-'. Values are coefficients. An inverse link was used for the SEA_B models, so coefficients were changed to their additive inverse for simpler interpretation. Results of post-hoc tests for categorical variables (Site, Habitat, Species, Year) are in main text.. Significance is represented with p values, with * indicating p <0.1 (trends), ** indicating p < 0.05, *** indicating p < 0.01 and **** indicating p < 0.001.When the SEA_B outlier was removed (*S. cowlesi* site ECO4, 2016) the GLM results changed, with predator abundance shifting to a stronger positive relationship (Est = 0.06, p = 0.02) as did predator richness (F = 0.06, p = 0.05). See Table 2.11 and 2.12 for F values, degrees of freedom and specific p values.

	Population Niche Width (SEA_B mode)		Carbon Specialization (PSi)		Nitrogen Specialization (PSi)		Trophic Position	
	GLM	GLMM	LM	LMM	LM	LMM	LM	LMM
Site	**		****		*		****	
Habitat	****	****	****	****	-	-	**	-
Species	-	**	*	-	-	-	**	****
Year	-	-	-	-	-	-	-	-
Lizard abundance	-0.01***	-0.01***	-0.006**	-	0.005**	-	0.01**	-
Conspecific abundance	-	0.01**	-	-	0.007*	-	-	-0.02**
Lizard richness	0.09**	-	-	-	-	-	-0.28****	-0.22*
Predator abundance	-	-	0.06**	-	-	-	-0.20****	-0.18***
Predator richness	-	-	0.08*	-	-	-	-0.27****	-0.25***
Arthropod diversity	0.38***	0.38***	0.19**	-	-0.15**	-	-0.54***	-0.58**

Table 2.3. Best performing models ($\Delta_i < 2$) after automated model selection using function dredge in package MuMin[96], which explored every combination of site (random effect) and explanatory variables (fixed effects) after screening for multicollinearity (species, arthropod diversity, predator abundance, conspecific abundance and lizard richness). Linear mixed models were used for PSi C, PSi N and trophic position, whereas generalized linear mixed models were used for SEA_B (family = Gamma). An inverse link was used for the SEA_B models, so negative coefficients indicate positive relationships.

Niche metric	ΔAICc	Intercept				Conspecific Abundance				Arthropod Diversity				Species
		Est.	SE	t	p	Est.	SE	t	p	Est.	SE	t	p	
SEA_B	0	0.65	0.13	5.15	<0.001	-0.01	0.01	-2.57	0.01	-	-	-	-	+
	1.20	0.79	0.14	6.65	<0.001	-	-	-	-	-0.27	0.12	-2.35	0.02	+
	1.38	0.52	0.09	5.78	<0.001	-	-	-	-	-	-	-	-	+
	1.59	0.89	0.18	5.02	<0.001	-0.01	0.01	-2.19	0.03	-0.26	0.15	-1.74	0.08	+
PSi C	0	0.59	0.07	8.73	<0.001	-	-	-	-	-	-	-	-	-
PSi N	0	0.56	0.05	11.24	<0.001	-	-	-	-	-	-	-	-	-
Trophic Position	0	2.86	0.22	13.04	<0.001	-	-	-	-	-0.50	0.16	-3.20	0.01	+

Table 2.4. Results of linear models exploring relationships between niche metrics, across all species (GLMs for SEA_B). An inverse link was used for the SEA_B models, so coefficients were changed to their additive inverse for simpler interpretation. Dropping the SEA_B outlier shifted one relationship, making the correlation between trophic position and SEA_B stronger (Est = -0.29, SE = 0.07, p = 0.002).

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	Est	SE	p	Est	SE	p	Est	SE	p	Est	SE	p
SEA_B	-	-	-	-	-	-	-	-	-	-	-	-
Carbon PSi	0.20	0.28	0.49	-	-	-	-	-	-	-	-	-
Nitrogen PSi	-0.19	0.35	0.59	-0.11	0.26	0.67	-	-	-	-	-	-
Trophic Position	-0.20	0.12	0.09	-0.22	0.10	0.04	0.03	0.09	0.77	-	-	-
Nitrogen X Carbon PSi	0.15	0.41	0.72	-	-	-	-	-	-	-0.08	0.07	0.31

Table 2.5. The effect sample size, of individuals with recoverable stomach contents, on estimates of PS_i. Six populations (3 species from 2 sites) each were subsampled 1000 times each to generate distributions of PS_i. Medians and means were then taken from these distributions, and then these statistics were compared against the empirical PS_is using t-tests (X^2 test used for nitrogen sample size of 1). Mean (± SD) refers to the average of differences between statistics summarizing simulated distributions (mean or median) and the empirical PS_i. Mean absolute difference (± SD) refers to average of absolute differences between simulation statistics and empirical PSi. The variance in prey nitrogen isotopic ratios from site WS1 was relatively low, resulting in ~5% of simulated values to fall below 0, these values were culled from these analyses.

		Comparison of means					Comparison of medians				
Isotope	Subsample Size	Mean difference	Mean absolute difference	t	df	*p*	Mean difference	Mean absolute difference	t	df	*p*
N	1	-0.014 ± 0.198	0.158 ± 0.098	0.190	9.985	0.853	0.008 ± 0.233	0.162 ± 0.162	$X^2 = 5$	5.000	0.416
N	2	0.067 ± 0.134	0.121 ± 0.076	1.039	8.982	0.326	0.024 ± 0.115	0.079 ± 0.079	0.353	9.625	0.732
N	3	0.063 ± 0.100	0.089 ± 0.072	1.027	8.238	0.334	0.029 ± 0.090	0.060 ± 0.060	0.446	9.113	0.666
N	4	0.044 ± 0.073	0.060 ± 0.057	0.716	8.433	0.493	0.029 ± 0.082	0.053 ± 0.053	0.448	9.065	0.665
N	5	0.032 ± 0.059	0.047 ± 0.045	0.505	8.664	0.626	0.018 ± 0.062	0.040 ± 0.040	0.283	9.244	0.784
C	1	0.010 ± 0.195	0.155 ± 0.097	0.084	6.316	0.936	-0.004 ± 0.212	0.147 ± 0.138	0.035	6.485	0.973
C	2	0.091 ± 0.133	0.124 ± 0.095	1.005	7.418	0.347	0.048 ± 0.173	0.129 ± 0.112	0.515	7.273	0.622
C	3	0.080 ± 0.098	0.087 ± 0.090	1.041	8.443	0.327	0.049 ± 0.090	0.063 ± 0.080	0.729	9.318	0.484
C	4	0.058 ± 0.089	0.068 ± 0.080	0.801	8.873	0.444	0.039 ± 0.079	0.055 ± 0.067	0.603	9.641	0.560
C	5	0.042 ± 0.071	0.049 ± 0.066	0.625	9.409	0.547	0.023 ± 0.057	0.040 ± 0.044	0.385	9.970	0.709

Table 2.6. Multicollinearity amongst explanatory variables. Chi square tests were used for categorical – categorical comparisons (values are $\chi 2$ statistics), ANOVAs for categorical – continuous comparisons (values are F statistics), and spearman rank correlations for continuous – continuous comparisons (values are ρ). Although these results are considered when interpreting model output (see Discussion), variance inflation factors (VIFs) were used to detect multicollinearity when including multiple predictor variables for dredge (cutoff VIF < 5). The VIF method resulted in arthropod diversity (VIF =2.22), predator abundance (VIF = 3.3), conspecific abundance (VIF = 1.59) and lizard richness (VIF = 3.41) being used in the full dredge model. The degree of collinearity is denoted with p values, with * indicating $p < 0.05$, ** indicating $p < 0.01$ and *** indicating $p < 0.001$.

	Habitat	Year	Species	Lizard abundance	Conspecific abundance	Lizard richness	Predator abundance	Predator richness	Arthropod diversity
Habitat	-	-	-	-	-	-	-	-	-
Year	4.5	-	-	-	-	-	-	-	-
Species	13.33*	0	-	-	-	-	-	-	-
Lizard abundance	13.27***	13.52**	0.28	-	-	-	-	-	-
Conspecific abundance	9.29**	5.99*	1.47	0.69***	-	-	-	-	-
Lizard richness	0.54	7.11*	0.09	-0.73***	-0.65***	-	-	-	-
Predator abundance	2.19	4.07	1.54	-0.71***	-0.41*	0.59**	-	-	-
Predator richness	2.08	2.93	1.54	-0.71***	-0.41*	0.59**	1***	-	-
Arthropod diversity	4.05	4.97	0.51	-0.91***	-0.69***	0.67***	0.61**	0.61**	-

Table 2.7. Results of linear models exploring the relationship between *A. inornata* niche metrics and explanatory variables. Generalized linear models (Gamma family) were used for SEA_B mode.

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Habitat	40.84	2, 6	<0.001	16.45	2, 7	0.002	2.00	2, 6	0.22	0.84	2, 6	0.48
Year	0.94	1, 7	0.36	0.12	1, 8	0.76	1.49	1, 7	0.26	1.05	1, 7	0.34
Lizard abundance	3.43	1, 7	0.11	0.76	1, 8	0.41	8.03	1, 7	0.03	3.44	1, 7	0.11
Conspecific abundance	1.26	1, 7	0.29	2.39	1, 8	0.16	5.25	1, 7	0.06	2.25	1, 7	0.18
Lizard richness	0.94	1, 7	0.37	0.51	1, 8	0.49	3.07	1, 7	0.12	19.51	1, 7	0.003
Predator abundance	0.07	1, 7	0.80	2.93	1, 8	0.13	14.67	1, 7	0.007	9.09	1, 7	0.02
Predator richness	0.07	1, 7	0.80	2.87	1, 8	0.13	7.23	1, 7	0.03	11.78	1, 7	0.01
Arthropod diversity	3.03	1, 7	0.13	1.09	1, 8	0.33	5.99	1, 7	0.04	8.03	1, 7	0.03
SEA	-	-	-	-	-	-	-	-	-	-	-	-
Carbon PSi	0.37	1, 7	0.56	-	-	-	-	-	-	-	-	-
Nitrogen PSi	0.83	1, 7	0.39	0.81	1, 7	0.39	-	-	-	-	-	-
Trophic Position	1.53	1, 7	0.26	0.39	1, 7	0.55	2.11	1, 7	0.19	-	-	-
N X C PSi	0.76	1, 7	0.41	-	-	-	-	-	-	0.46	1, 7	0.52

Table 2.8. Results of linear models exploring the relationship between *H. maculata* niche metrics and explanatory variables. Generalized linear models (Gamma family) were used for SEA_B mode.

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Habitat	15.70	1, 4	0.02	2.86	1, 4	0.17	0.90	1, 4	0.39	1.18	1, 4	0.34
Year	0.86	1, 4	0.41	0.03	1, 4	0.87	0.01	1, 4	0.92	0.53	1, 4	0.51
Lizard abundance	11.04	1, 4	0.03	4.01	1, 4	0.12	2.07	1, 4	0.22	0.17	1, 4	0.70
Conspecific abundance	3.54	1, 4	0.13	14.33	1, 4	0.02	1.29	1, 4	0.32	0.01	1, 4	0.92
Lizard richness	15.70	1, 4	0.02	2.86	1, 4	0.17	0.90	1, 4	0.39	1.18	1, 4	0.34
Predator abundance	17.37	1, 4	0.01	0.71	1, 4	0.45	4.79	1, 4	0.09	3.57	1, 4	0.13
Predator richness	17.37	1, 4	0.01	0.71	1, 4	0.45	4.79	1, 4	0.09	3.57	1, 4	0.13
Arthropod diversity	23.34	1, 4	0.009	7.13	1, 4	0.06	2.85	1, 4	0.17	0.52	1, 4	0.51
SEA	-	-	-	-	-	-	-	-	-	-	-	-
Carbon PSi	2.24	1, 4	0.21	-	-	-	-	-	-	-	-	-
Nitrogen PSi	4.37	1, 4	0.11	1.19	1, 4	0.34	-	-	-	-	-	-
Trophic Position	1.81	1, 4	0.25	0.02	1, 4	0.91	0.007	1, 4	0.94	-	-	-
N X C PSi	0.003	1, 4	0.96	-	-	-	-	-	-	0.13	1, 4	0.74

Table 2.9. Results of linear models exploring the relationship between *S. cowlesi* niche metrics and explanatory variables. Generalized linear models (Gamma family) were used for SEA_B mode.

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Habitat	13.5	2, 4	0.02	12.92	2, 4	0.02	1.32	2, 4	0.36	1.70	2, 4	0.29
Year	0.99	1, 5	0.37	1.17	1, 5	0.33	<0.001	1, 5	0.99	1.00	1, 5	0.36
Lizard abundance	6.06	1, 4	0.07	2.96	1, 4	0.16	0.71	1, 4	0.45	0.83	1, 4	0.41
Conspecific abundance	5.41	1, 4	0.09	2.53	1, 4	0.19	0.05	1, 4	0.83	1.55	1, 4	0.28
Lizard richness	25.2	1, 4	0.007	18.31	1, 4	0.01	0.01	1, 4	0.92	2.96	1, 4	0.16
Predator abundance	0.44	1, 4	0.55	4.94	1, 4	0.09	0.04	1, 4	0.84	6.59	1, 4	0.06
Predator richness	0.44	1, 4	0.55	4.94	1, 4	0.09	0.04	1, 4	0.84	6.59	1, 4	0.06
Arthropod diversity	5.49	1, 4	0.08	4.94	1, 4	0.09	0.23	1, 4	0.65	1.86	1, 4	0.24
SEA	-	-	-	-	-	-	-	-	-	-	-	-
Carbon PSi	2.03	1, 5	0.21	-	-	-	-	-	-	-	-	-
Nitrogen PSi	0.04	1, 5	0.85	2.78	1, 5	0.16	-	-	-	-	-	-
Trophic Position	0.98	1, 5	0.37	13.12	1, 5	0.02	2.83	1, 5	0.15	-	-	-
N X C PSi	0.30	1, 5	0.61	-	-	-	-	-	-	8.15	1, 5	0.04

Table 2.10. Results of linear models exploring the relationship between *U. stansburiana* niche metrics and explanatory variables. Generalized linear models (Gamma family) were used for SEA_B mode. *U. stansburiana* only had sufficient sample sizes for calculation of niche metrics in dark soils habitats, so cross habitat analyses were not possible.

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Habitat	-	-	-	-	-	-	-	-	-	-	-	-
Year	0.001	1, 2	0.98	0.36	1, 3	0.59	0.05	1, 2	0.85	0.004	1, 2	0.96
Lizard abundance	0.61	1, 1	0.58	6.36	1, 2	0.13	5.64	1, 1	0.25	0.52	1, 1	0.60
Conspecific abundance	0.02	1, 1	0.91	1.33	1, 2	0.37	76.69	1, 1	0.07	0.01	1, 1	0.93
Lizard richness	1.39	1, 1	0.45	3.04	1, 2	0.22	2.09	1, 1	0.39	1.19	1, 1	0.47
Predator abundance	0.71	1, 1	0.55	1.15	1, 2	0.39	4.55	1, 1	0.28	0.61	1, 1	0.58
Predator richness	1.39	1, 1	0.45	1.07	1, 2	0.41	2.09	1, 1	0.39	1.19	1, 1	0.47
Arthropod diversity	1229	1, 1	0.02	27.89	1, 2	0.03	0.09	1, 1	0.82	223.6	1, 1	0.04
SEA	-	-	-	-	-	-	-	-	-	-	-	-
Carbon PSi	5.65	1, 2	0.05	-	-	-	-	-	-	-	-	-
Nitrogen PSi	0.09	1, 2	0.79	0.49	1, 2	0.56	-	-	-	-	-	-
Trophic Position	6.14	1, 2	0.005	19.48	1, 2	0.05	0.16	1, 2	0.73	-	-	-
N X C PSi	3.19	1, 2	0.22	-	-	-	-	-	-	2.82	1, 2	0.26

Table 2.11. Results of linear models exploring the relationship between niche metrics and explanatory variables. Generalized linear models (Gamma family) were used for SEA_B mode. When the SEA_B outlier was removed (*S. cowlesi* site ECO4, 2016) predator abundance shifted to a stronger positive relationship (F = 6.04, p = 0.02) as did predator richness (F = 4.34, p = 0.05). For coefficients see Table 2.2.

	Population Niche Width (SEA_B mode)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Site	3.88	6, 19	0.012	6.72	7, 20	<0.001	2.49	6, 19	0.06	9.76	6,19	<0.001
Habitat	11.68	2, 23	<0.001	24.3	2, 25	<0.001	0.86	2, 23	0.44	4.10	2, 23	0.03
Species	1.26	3, 22	0.31	2.44	3, 24	0.09	0.24	3, 22	0.87	3.48	3, 22	0.03
Year	2.52	1, 22	0.13	0.35	1, 26	0.56	0.39	1, 24	0.54	1.35	1, 24	0.26
Lizard abundance	11.53	1, 22	0.003	5.62	1, 24	0.08	7.15	1, 22	0.01	5.24	1, 22	0.03
Conspecific abundance	1.93	1, 22	0.18	0.61	1, 24	0.44	3.63	1, 22	0.07	0.09	1, 22	0.77
Lizard richness	5.71	1, 22	0.03	0.66	1, 24	0.43	1.22	1, 22	0.28	16.27	1, 22	<0.001
Predator abundance	1.47	1, 22	0.24	4.55	1, 24	0.04	2.96	1, 22	0.10	23.26	1, 22	<0.001
Predator richness	1.12	1, 22	0.30	3.44	1, 24	0.08	1.77	1, 22	0.20	26.42	1, 22	<0.001
Arthropod diversity	12.44	1, 22	0.002	5.66	1, 24	0.03	5.57	1, 22	0.03	13.61	1, 22	0.001

Table 2.12. Results of linear mixed models exploring the relationship between niche parameters and explanatory variables with Site included as a random effect. Generalized linear mixed models (Gamma family) were used for SEA_B mode. When the SEA_B outlier was removed (*S. cowlesi* site ECO4, 2016) the overall effect of habitat became less strong (F = 7.79, p = 0.11; Tukey HSD test WS-DS p = 0.05, WS-ECO p = 0.002, ECO-DS p = 0.34). Degrees of freedom were calculated using the 'mixed' function in package afex[160]. For coefficients see Table 2.2.

	Population Niche Width (SEA)			Carbon Specialization (PSi)			Nitrogen Specialization (PSi)			Trophic Position		
	F	df	p	F	df	p	F	df	p	F	df	p
Habitat	16.44	2, 23	<0.001	24.3	2, 25	<0.001	0.37	2, 4.09	0.71	0.92	2, 3.37	0.47
Species	9.35	3, 17.29	0.03	1.35	3, 18.73	0.29	0.29	3, 19.77	0.83	11.71	3, 16.42	<0.001
Year	0.01	1, 21.38	0.91	0.03	1, 23.15	0.86	0.17	1, 23	0.69	0.08	1, 18.86	0.78
Lizard abundance	9.51	1, 5.04	0.01	1.17	1, 10.17	0.30	3.51	1, 5.69	0.11	0.43	1, 12.65	0.52
Conspecific abundance	3.78	1, 20.32	0.03	0.003	1, 22.45	0.96	1.59	1, 21.99	0.22	5.69	1, 17.79	0.03
Lizard richness	1.69	1, 5.85	0.29	0.43	1, 9.3	0.53	0.76	1, 7.02	0.41	5.57	1, 4.63	0.07
Predator abundance	0.21	1, 8.09	0.71	1.42	1, 11.06	0.26	1.67	1, 8.45	0.23	15.77	1, 8.16	0.004
Predator richness	0.40	1, 6.32	0.60	1.15	1, 8.31	0.31	0.95	1, 7.01	0.36	17.03	1, 8.04	0.003
Arthropod diversity	11.47	1, 4.81	0.003	0.95	1, 10.64	0.35	2.42	1, 6.26	0.17	6.74	1, 10.33	0.03

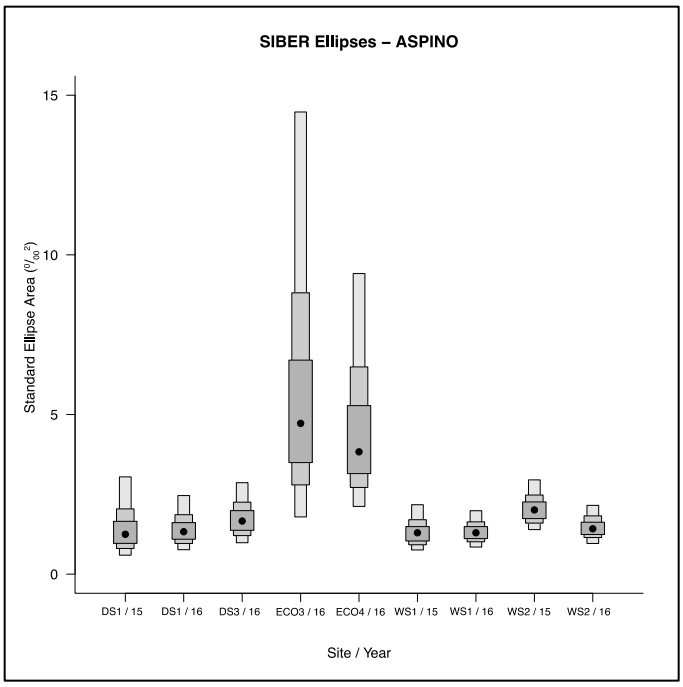

Fig 2.1. Estimates of SEA_B for *A. inornata* by site and year. Mode is indicated with black dots and box shading shows 50%, 75% and 95% credible intervals from dark to light grey.

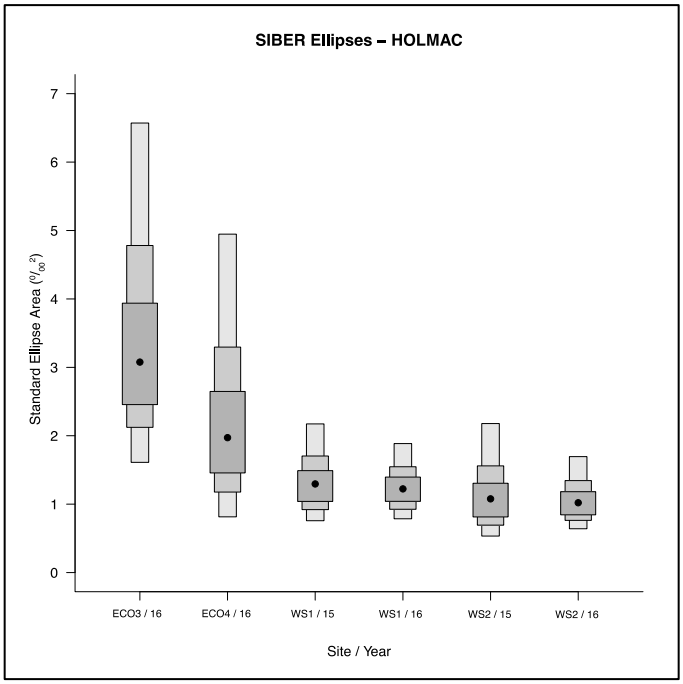

Fig 2.2. Estimates of SEA_B for *H. maculata* by site and year. Mode is indicated with black dots and box shading shows 50%, 75% and 95% credible intervals from dark to light grey.

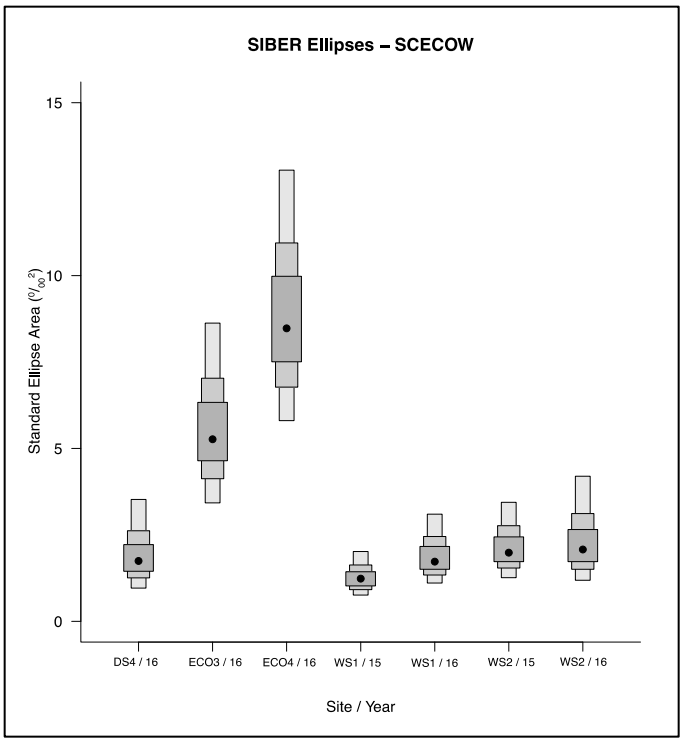

Fig 2.3. Estimates of SEA_B for *S. cowlesi* by site and year. Mode is indicated with black dots and box shading shows 50%, 75% and 95% credible intervals from dark to light grey.

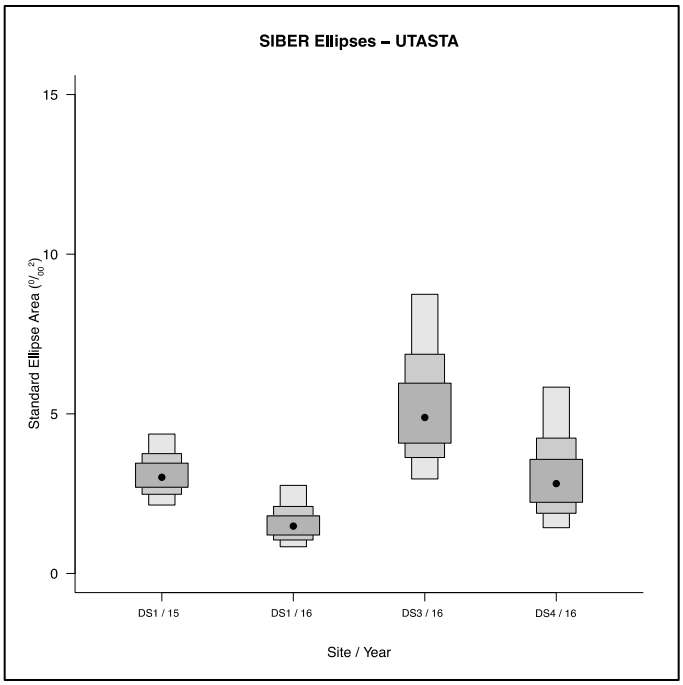

Fig 2.4. Estimates of SEA_B for *U. stansburiana* by site and year. Mode is indicated with black dots and box shading shows 50%, 75% and 95% credible intervals from dark to light grey.

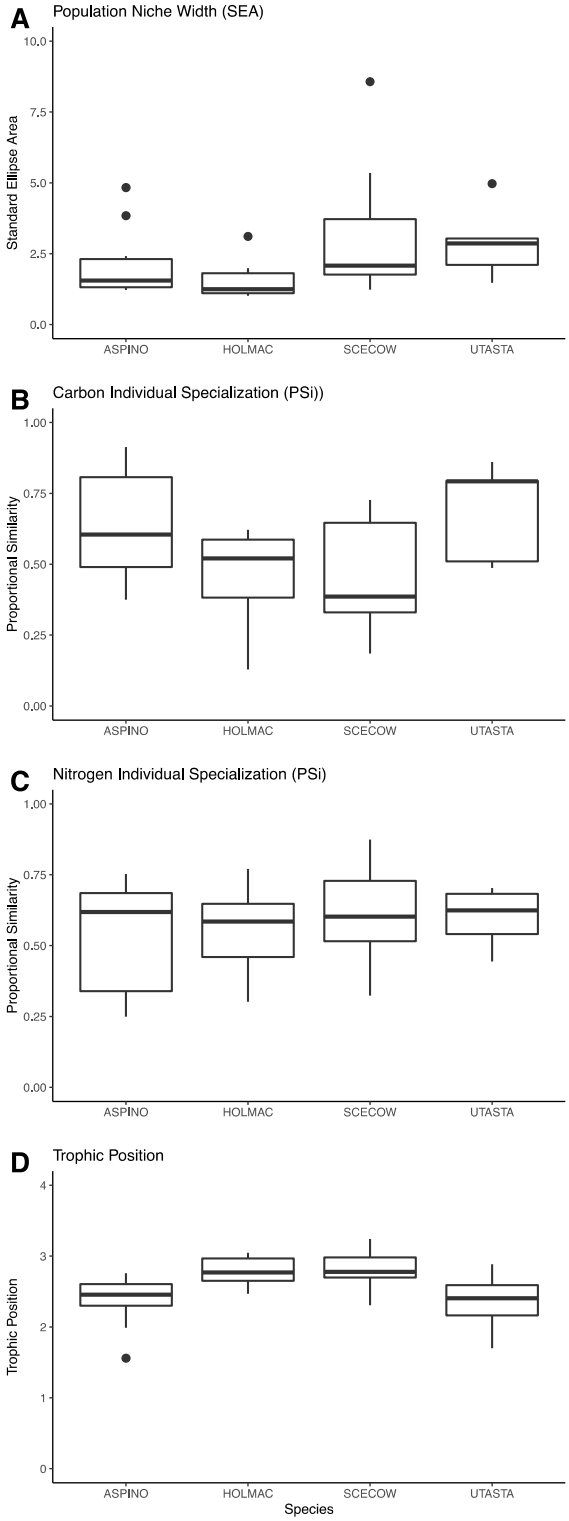

Fig 2.5. Relationship between niche metrics and species. First and third quartiles are marked with lower and upper hinges of the box. Whiskers extend no further than ± 1.5 * inter-quartile range, with data beyond that plotted individually.

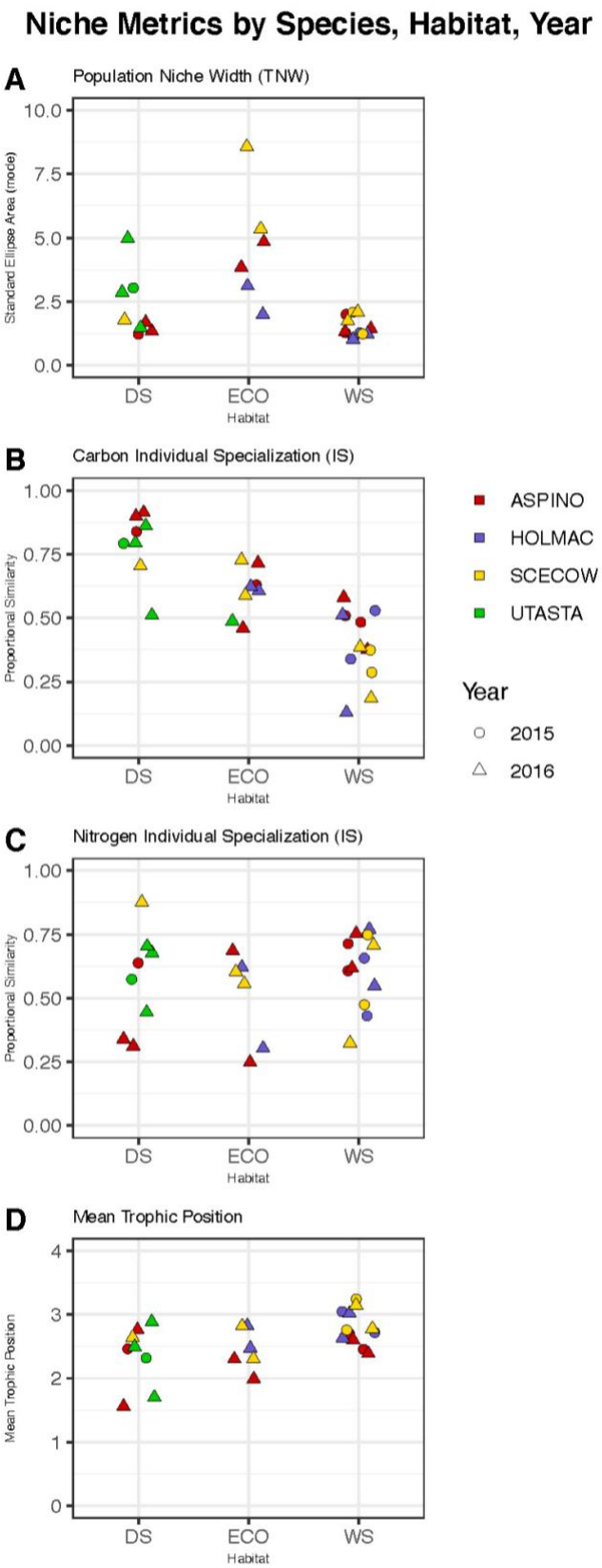

Fig 2.6. Niche metrics by species, habitat and year. Minimal jittering was used to reduce overlap

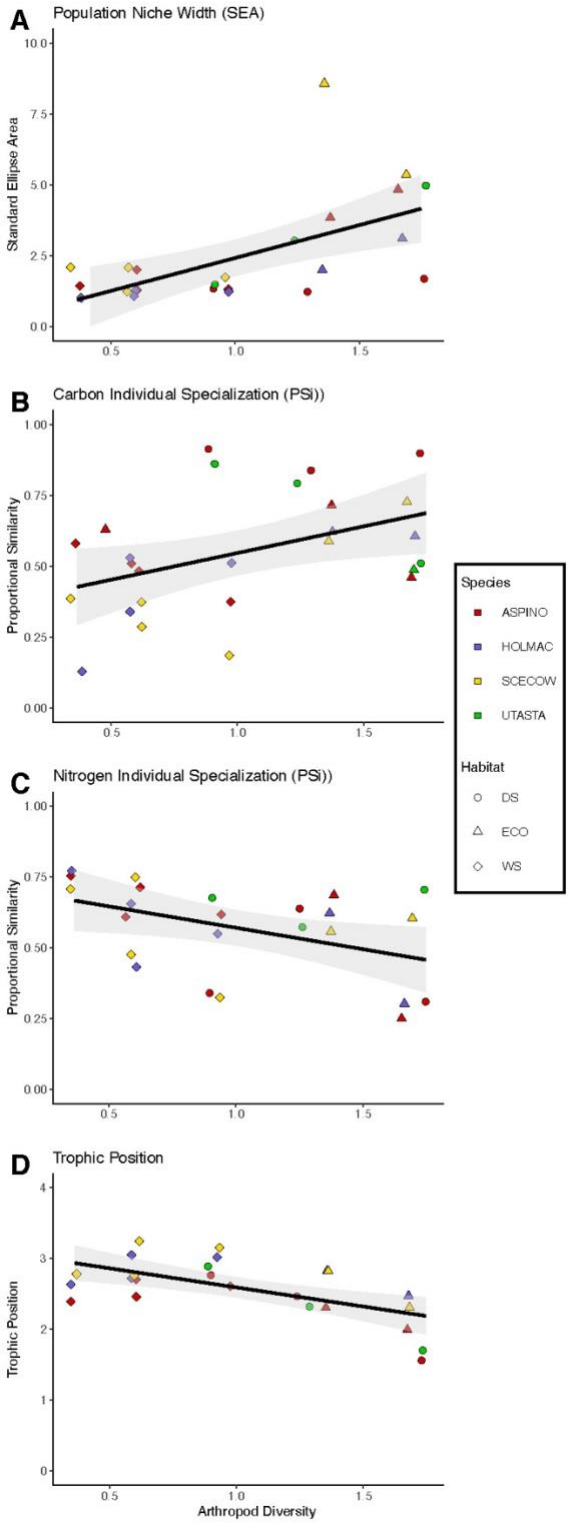

Fig 2.7. Relationship between niche metrics and arthropod diversity (Shannon's diversity index of Orders). Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

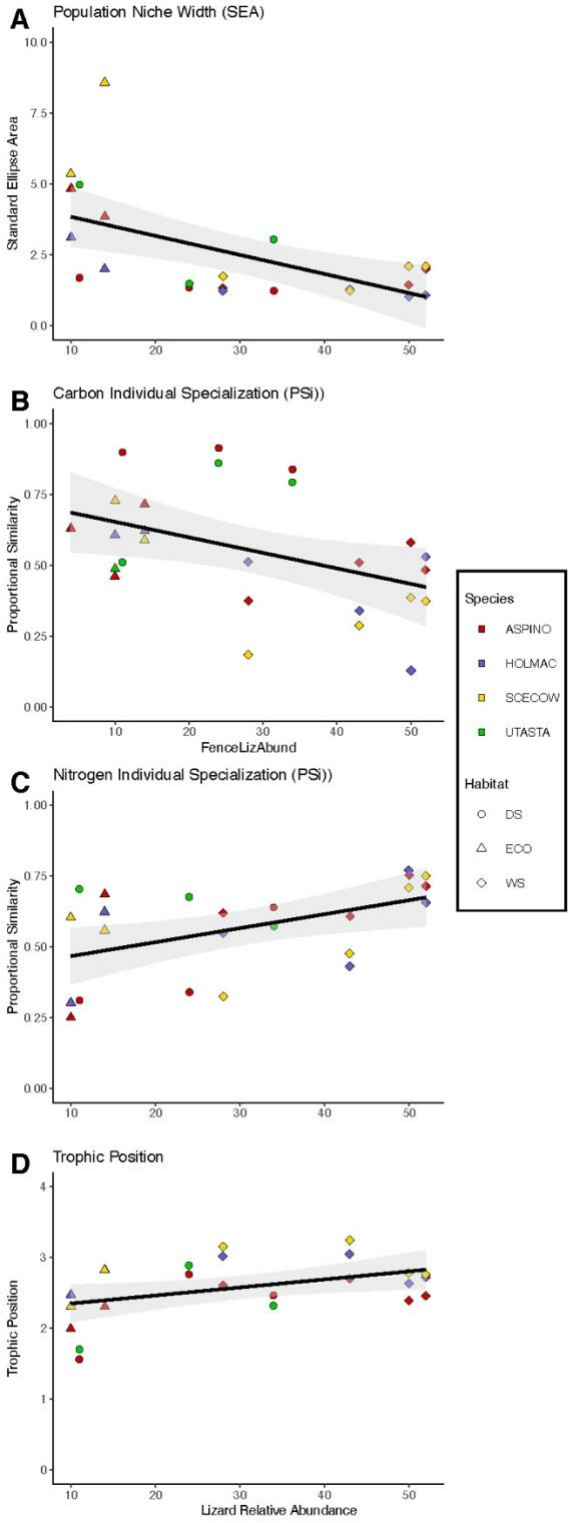

Fig 2.8. Relationship between niche metrics and lizard relative abundance. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

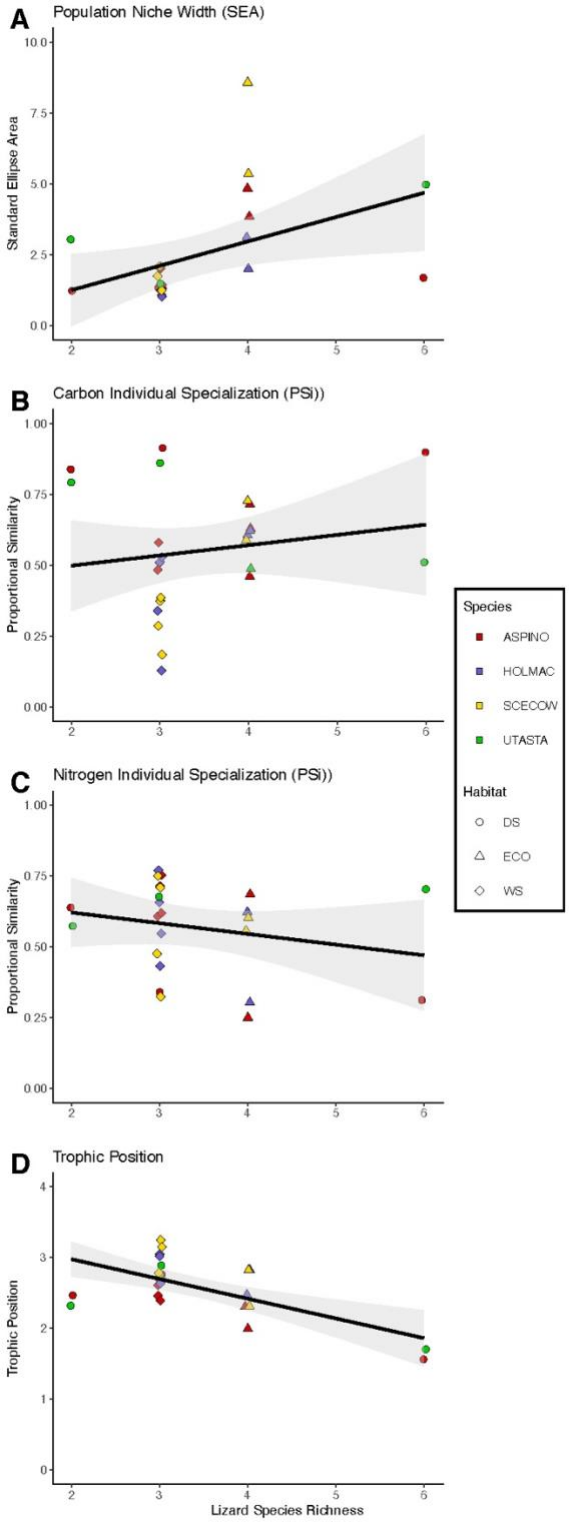

Fig 2.9. Relationship between niche metrics and lizard species richness. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

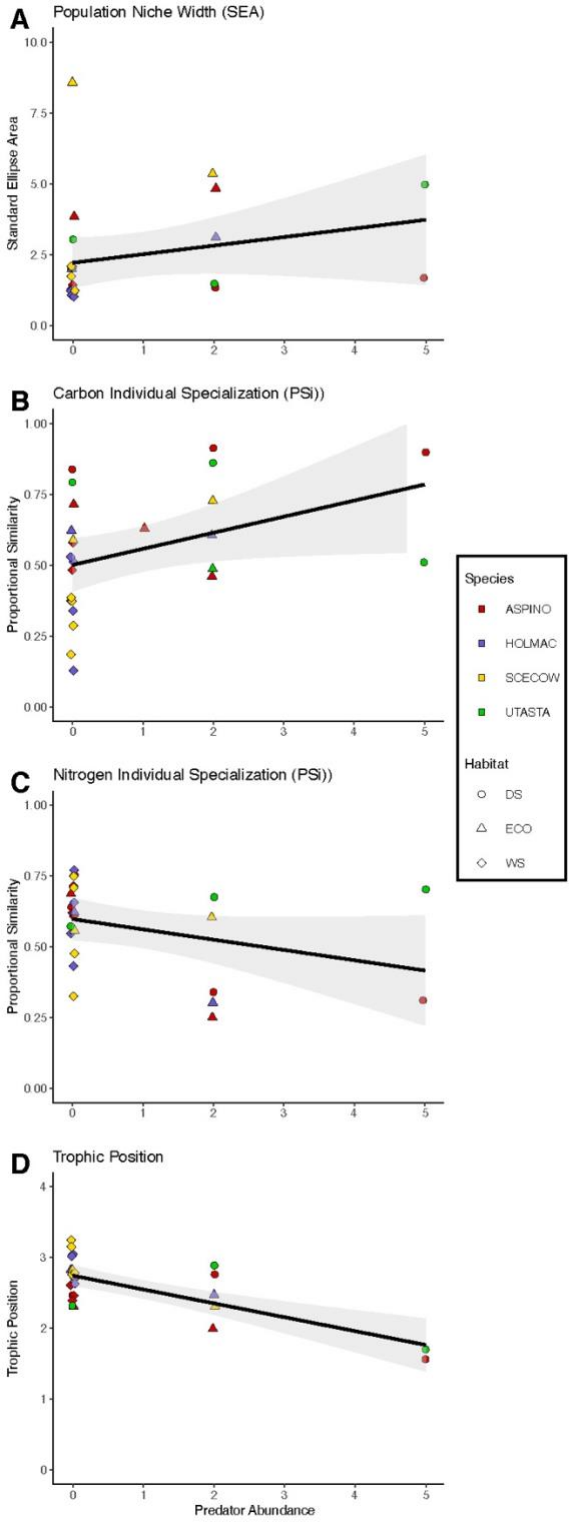

Fig 2.10. Relationship between niche metrics and predator relative abundance. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

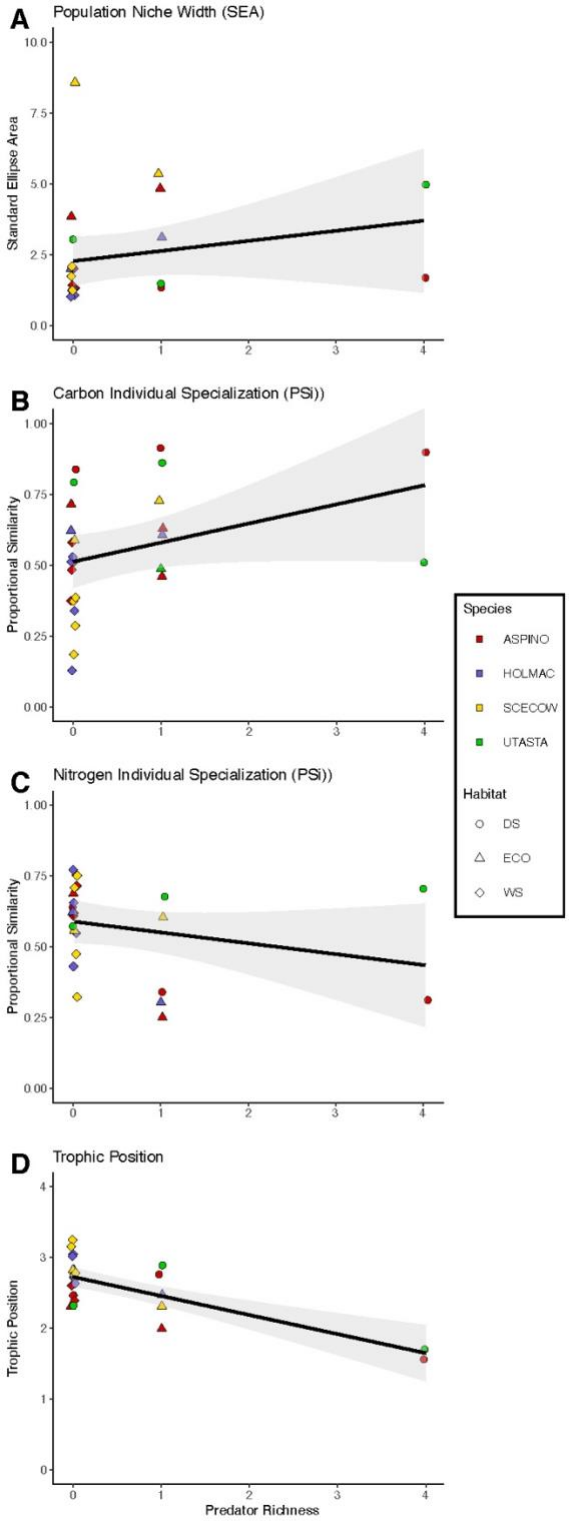

Fig 2.11. Relationship between niche metrics and predator richness. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

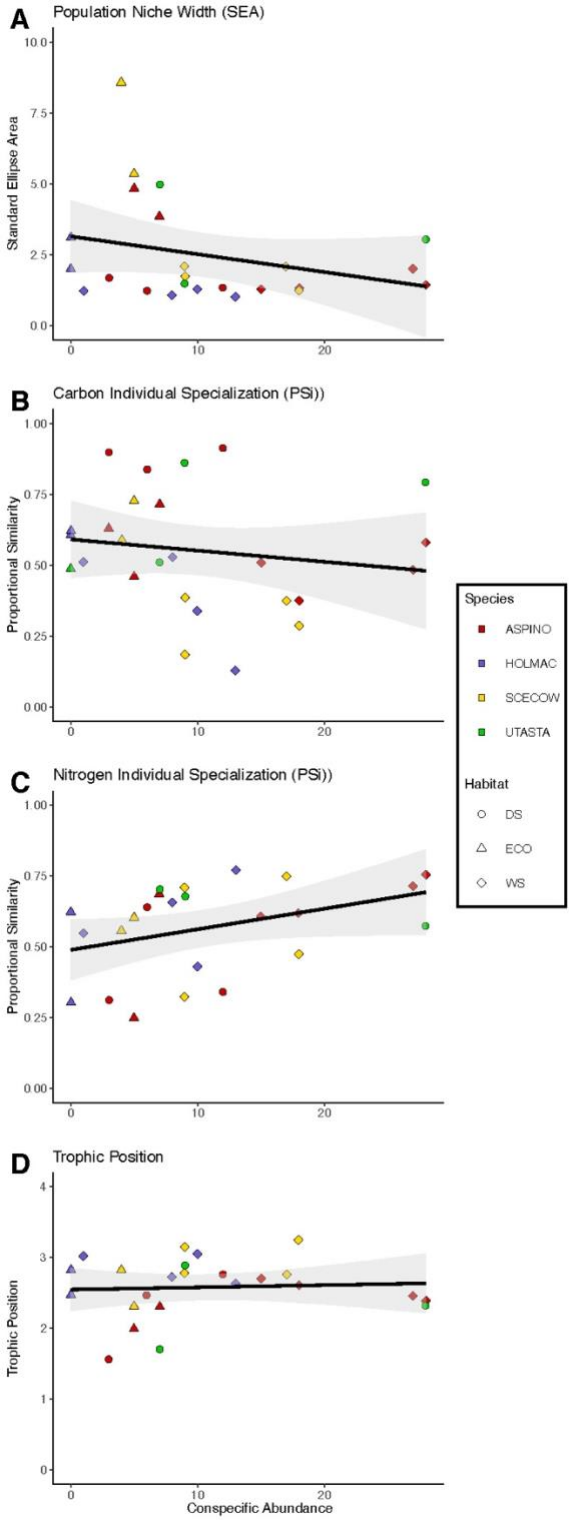

Fig 2.12. Relationship between niche metrics and conspecific abundance. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

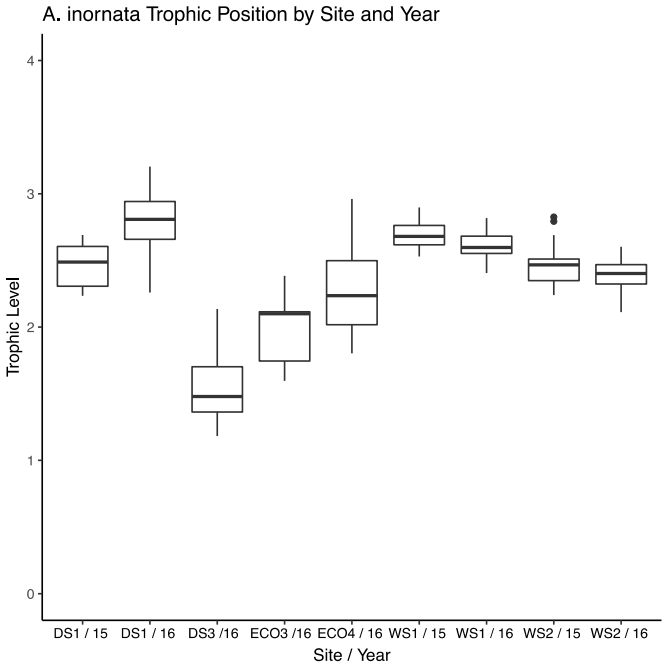

Fig 2.13. *A. inornata* trophic level across individuals by site and year. First and third quartiles are marked with lower and upper hinges of the box. Whiskers extend no further than ± 1.5 * inter-quartile range, with data beyond that plotted individually.

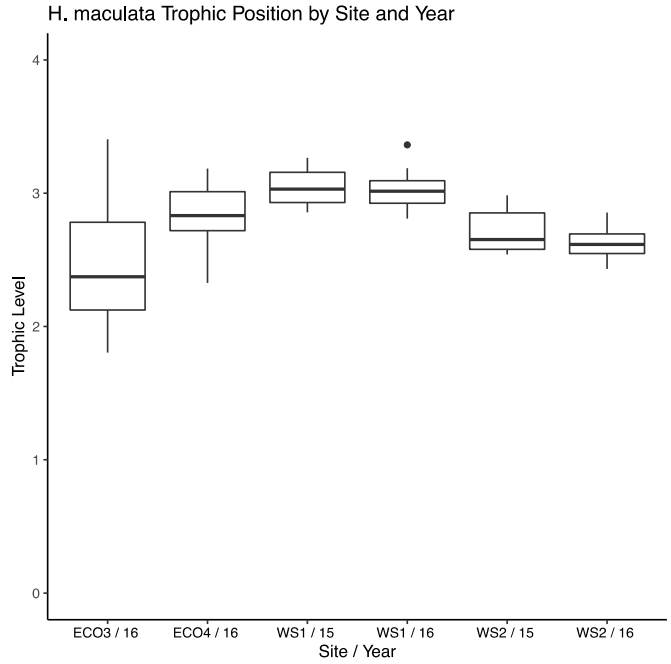

Fig 2.14. *H. maculata* trophic level across individuals by site and year. First and third quartiles are marked with lower and upper hinges of the box. Whiskers extend no further than ± 1.5 * inter-quartile range, with data beyond that plotted individually.

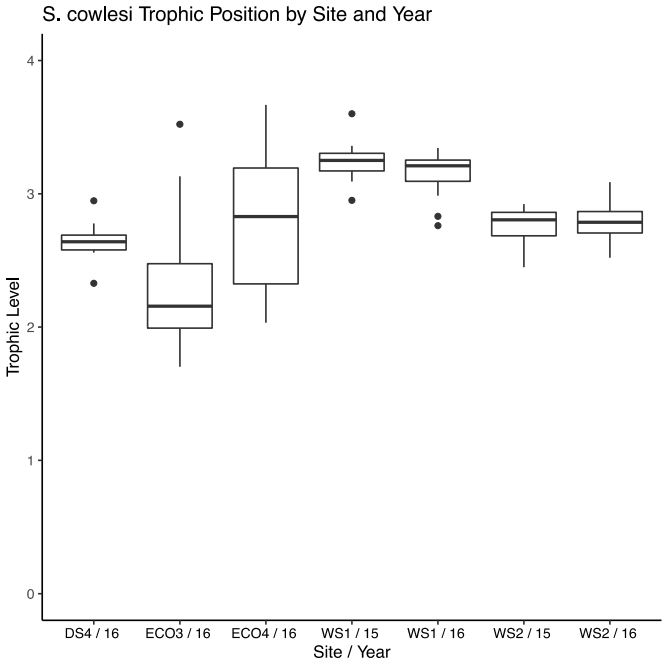

Fig 2.15. *S. cowlesi* trophic level across individuals by site and year. First and third quartiles are marked with lower and upper hinges of the box. Whiskers extend no further than ± 1.5 * inter-quartile range, with data beyond that plotted individually.

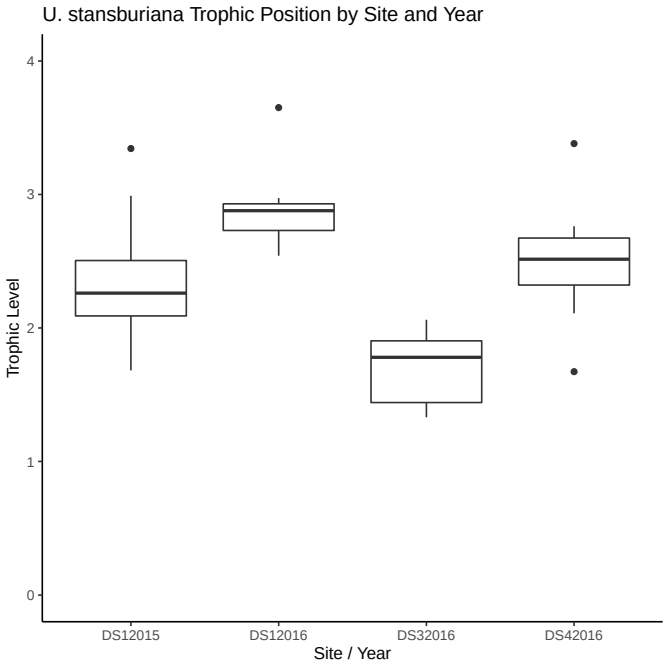

Fig 2.16. *U. stansburiana* trophic level across individuals by site and year. First and third quartiles are marked with lower and upper hinges of the box. Whiskers extend no further than ± 1.5 * inter-quartile range, with data beyond that plotted individually.

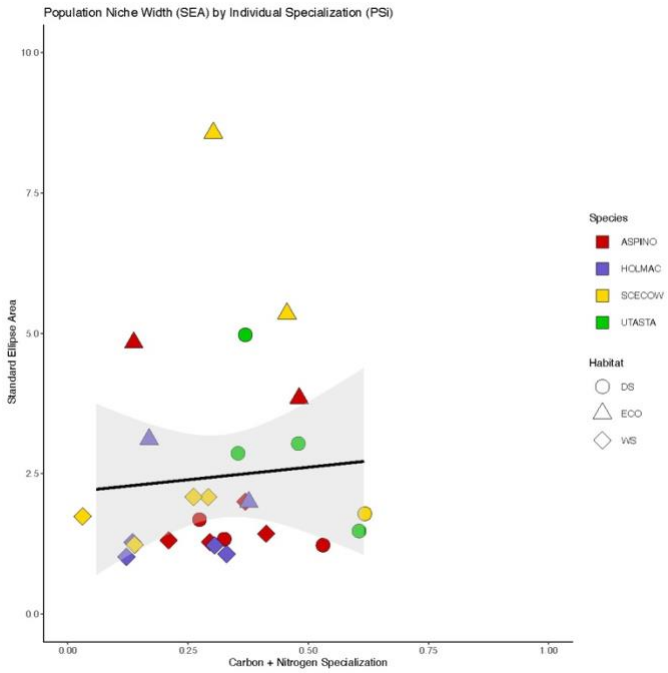

Fig 2.17. Relationship between population niche width (SEA_B mode) and nitrogen by carbon individual specialization (PS_i). Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

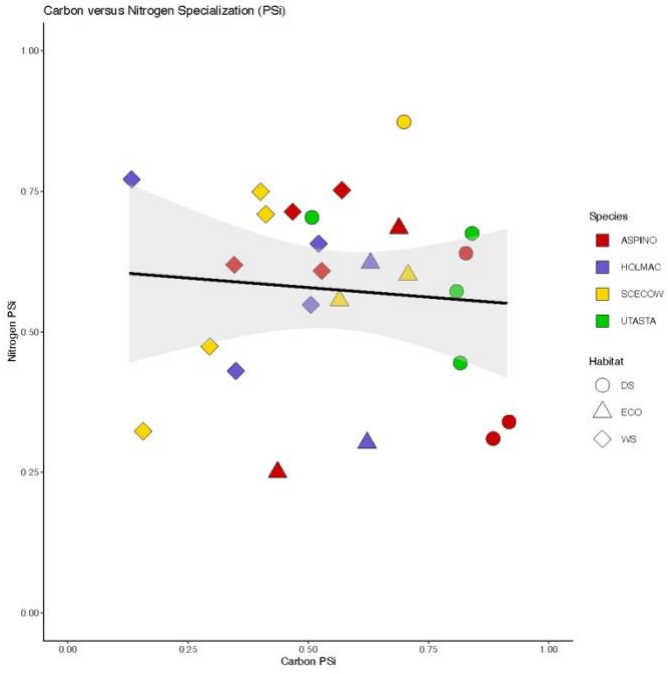

Fig 2.18. Relationship between carbon individual specialization (PS_i) and nitrogen individual specialization (PS_i). Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

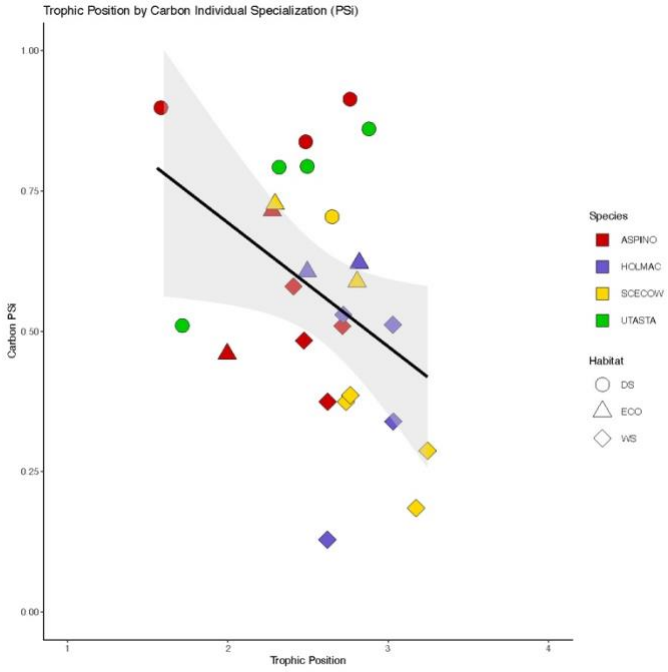

Fig 2.19. Relationship between carbon individual specialization (PS_i) and mean trophic position. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

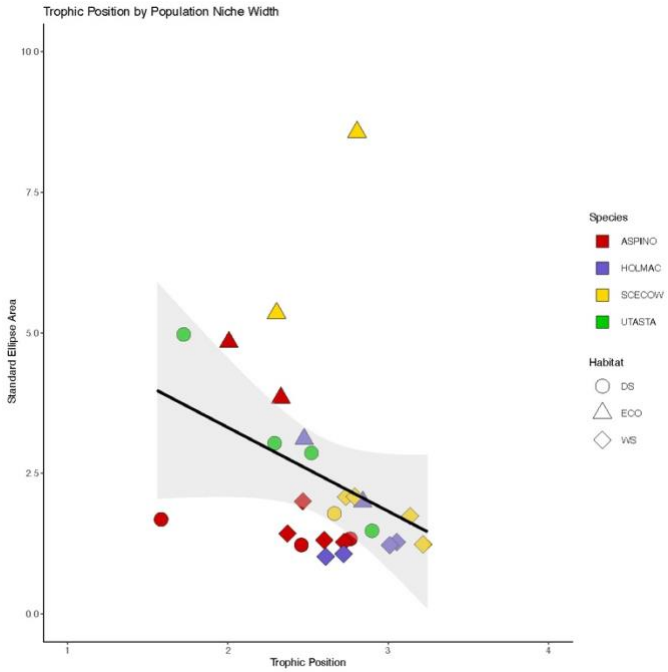

Fig 2.20. Relationship between population niche width (SEA_B mode) and mean trophic position. Shading represents the standard error of the estimate. Minimal jittering was used to reduce point overlap.

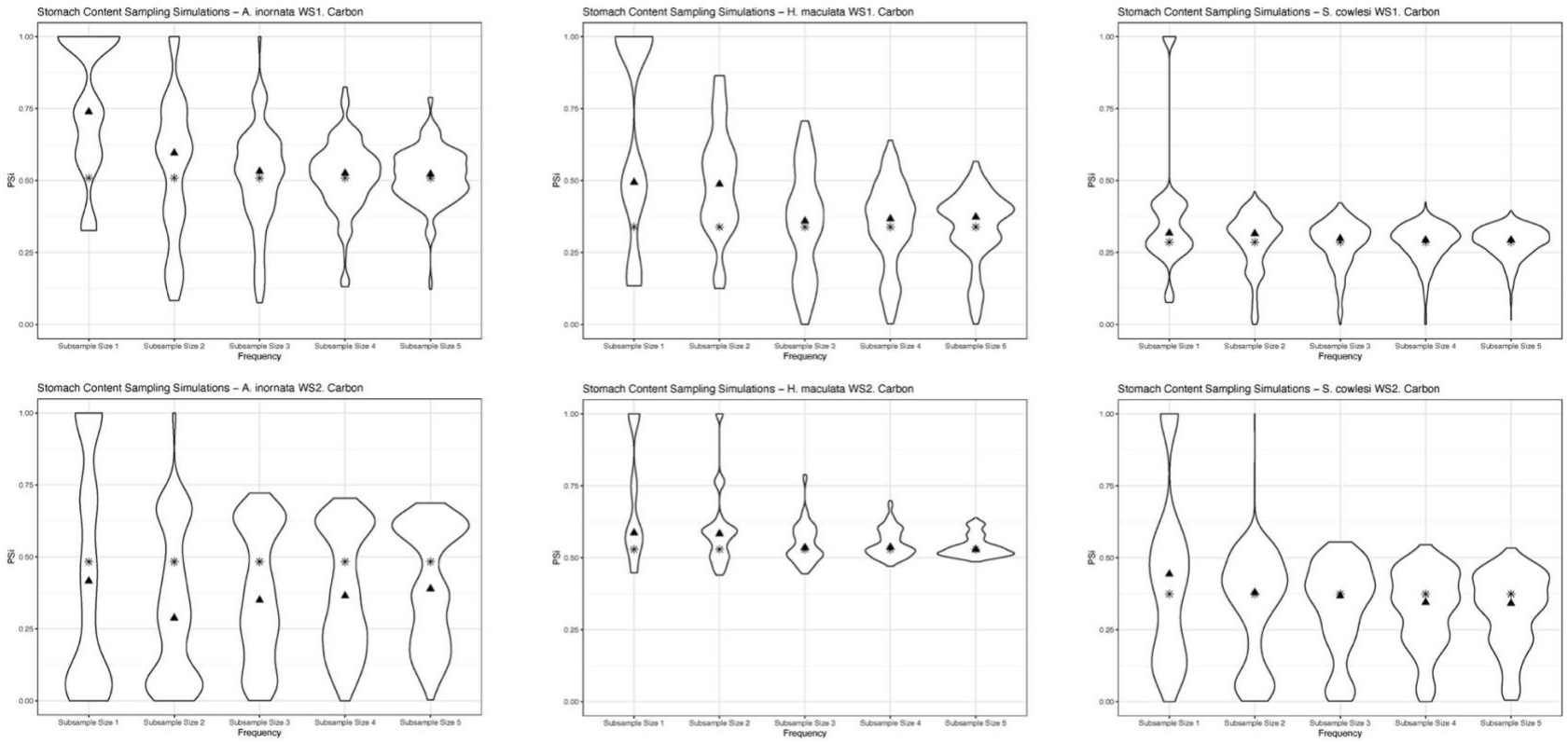

Fig 2.21. Violin plots depicting the effect of sample size of lizards with recoverable stomach contents and C PSi. We simulated 1000 PSi estimates for each sample size, sampling without replacement. Triangles represent the mode of simulated values and asterisks indicate the empirical PSi, based on the full sample size. While there was a large variance in estimates from low sample sizes, there was no consistent directional bias. See Table 2.5 for results of tests for directional bias.

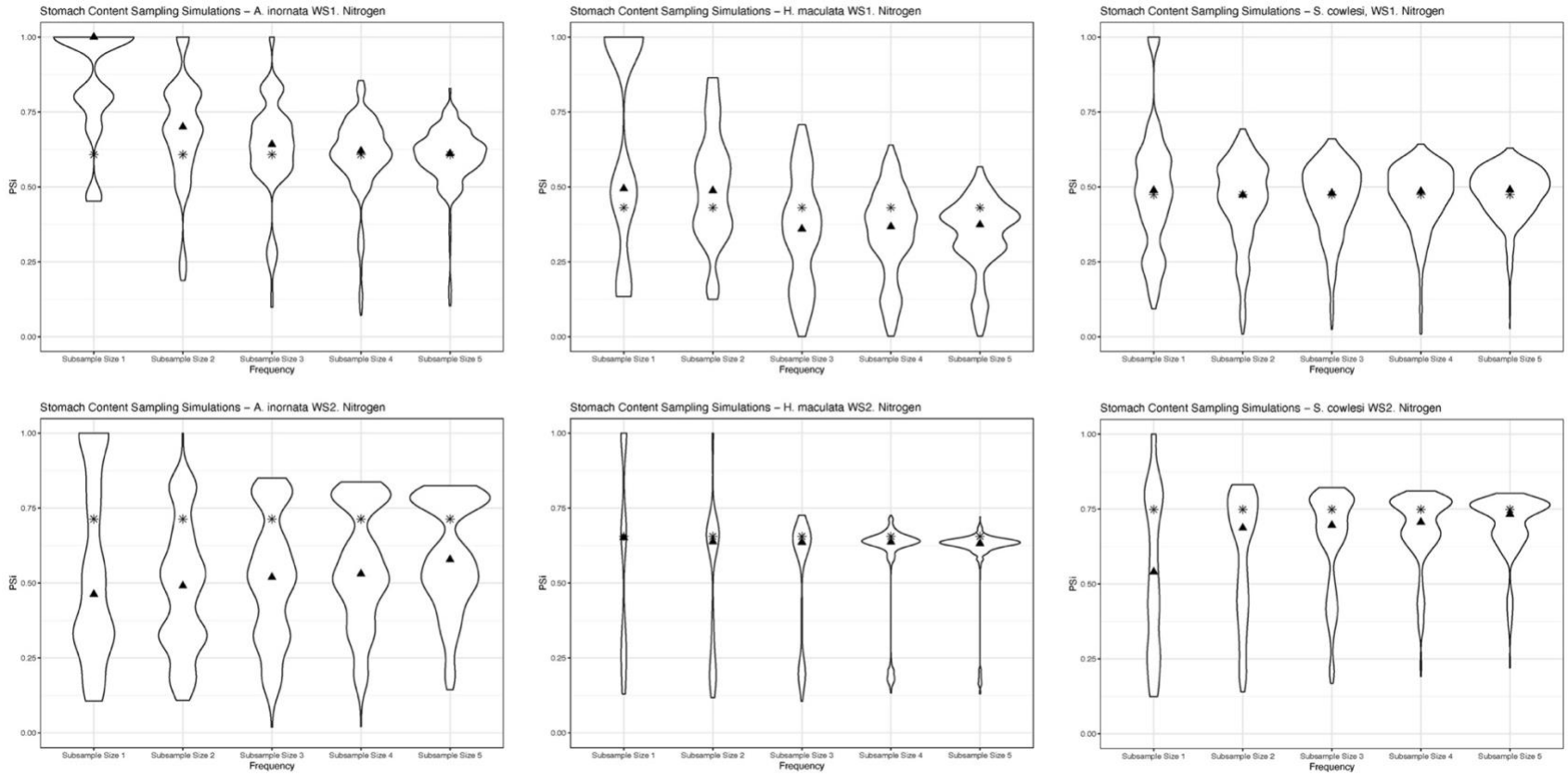

Fig 2.22. Violin plots depicting the effect of sample size of lizards with recoverable stomach contents and C PSi. We simulated 1000 PSi estimates for each sample size, sampling without replacement. Triangles represent the mode of simulated values and asterisks indicate the empirical PSi, based on the full sample size. While there was a large variance in estimates from low sample sizes, there was no consistent directional bias. See Table 2.5 for results of tests for directional bias.

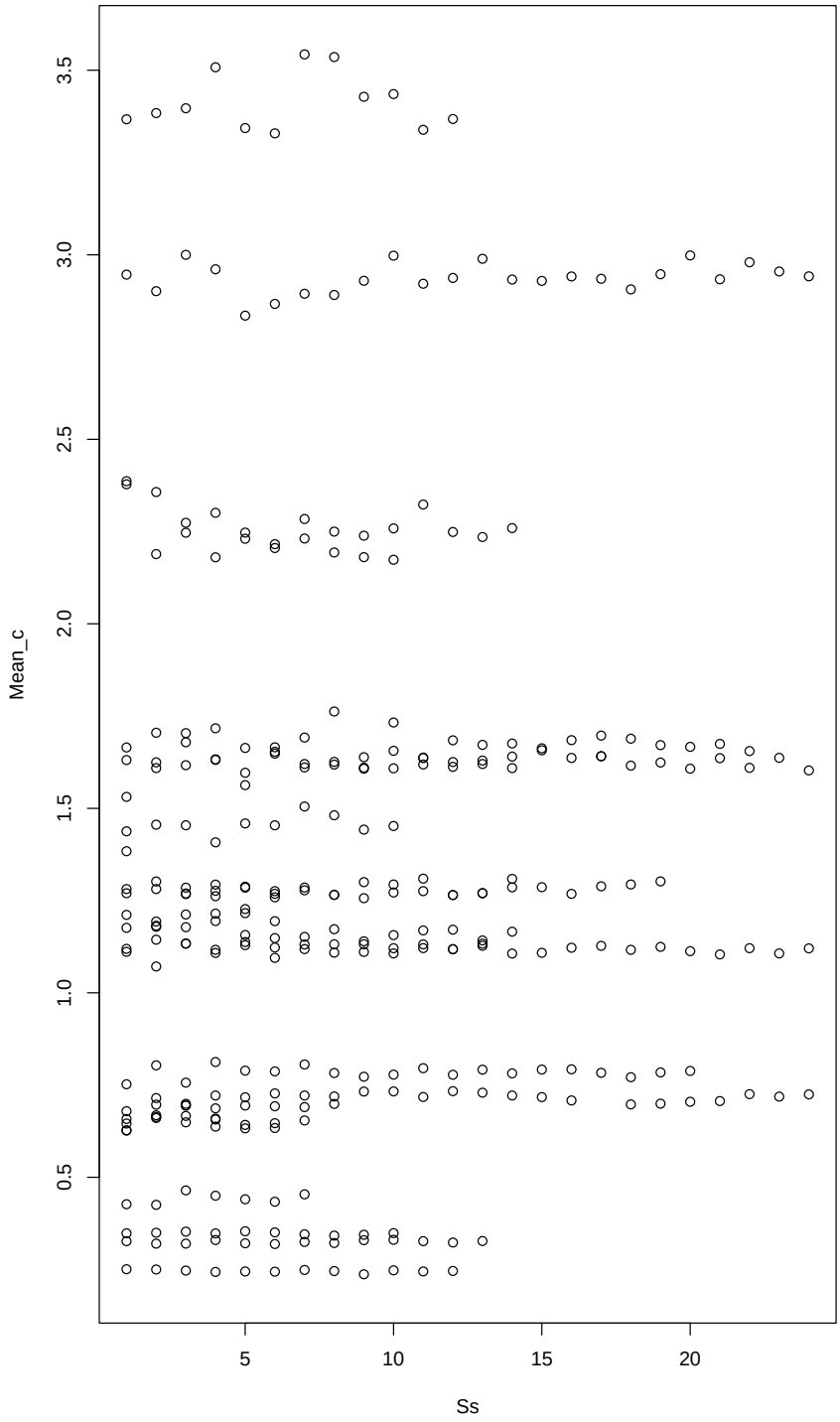

Fig 2.23. Relationship between sample size (Ss) and mean carbon isotopic variance (Mean_c). We subsampled, with replacement, carbon and nitrogen isotopes from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 25. The mean variance estimate was plotted against sample size to test for any directional bias of sample size on variance estimates.

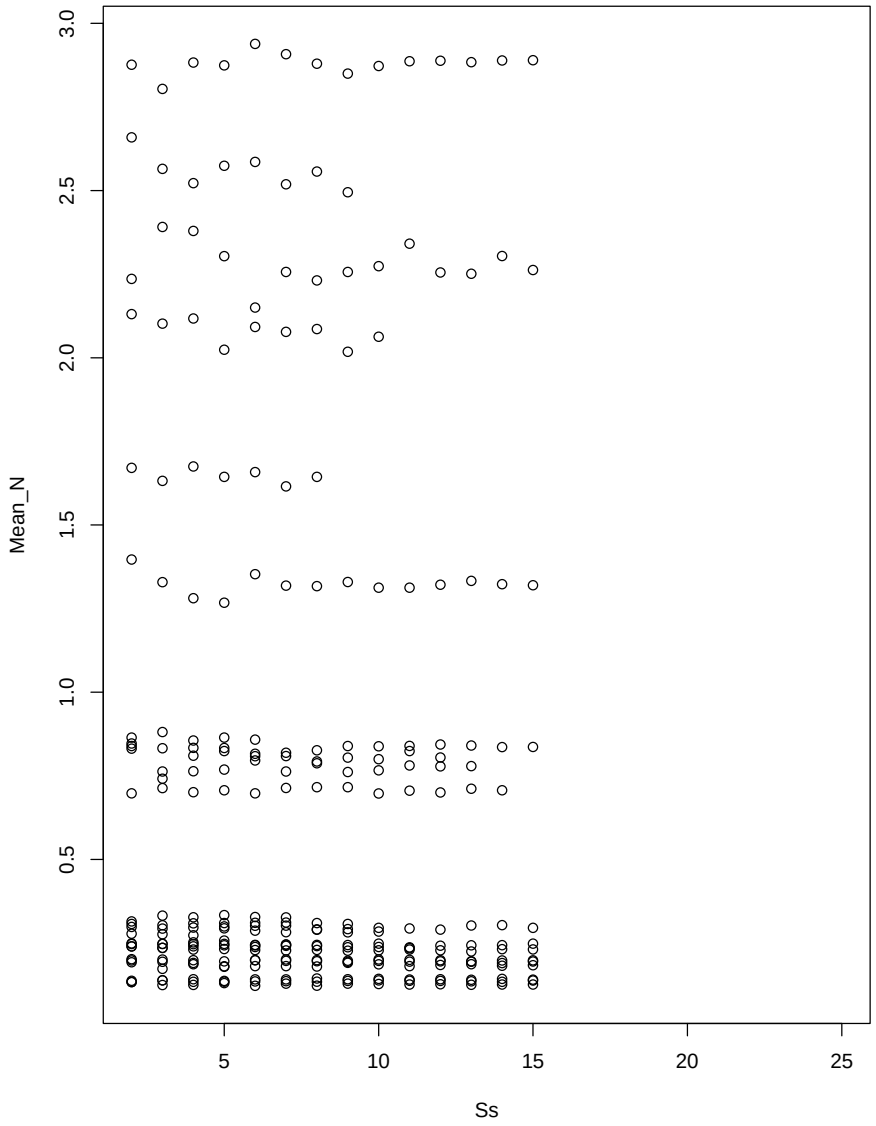

Fig 2.24. Relationship between sample size (Ss) and mean nitrogen isotopic variance (Mean_N). We subsampled, with replacement, carbon and nitrogen isotopes from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 15. The mean variance estimate was plotted against sample size to test for any directional bias of sample size on variance estimates.

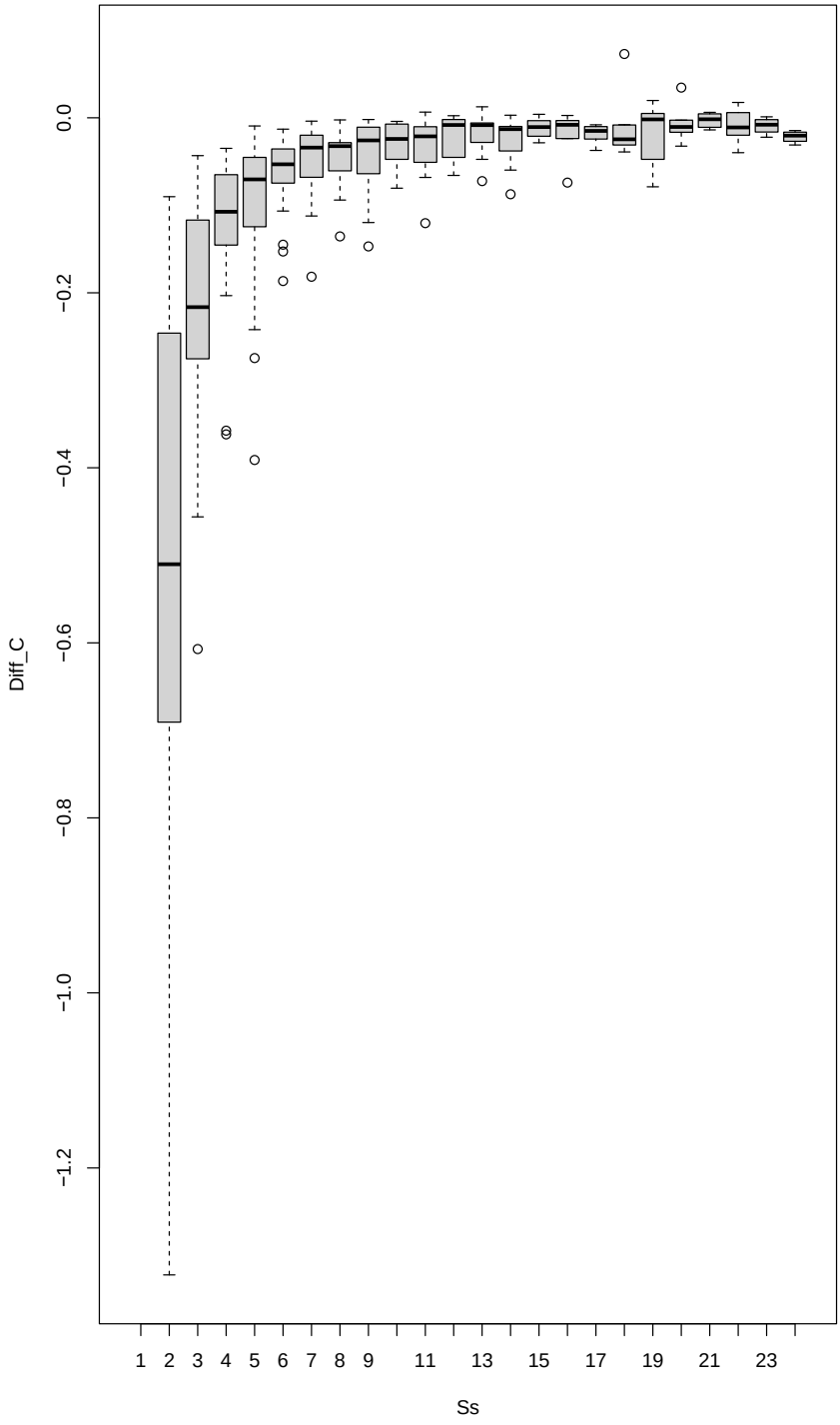

Fig 2.25. Relationship between sample size (Ss) and precision of carbon isotopic variance estimate, the change in the standard deviation of simulated variances as sample size increases by 1 (Diff_C). We subsampled, with replacement, carbon and nitrogen isotopes from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 25. Boxplots are pooled across populations.

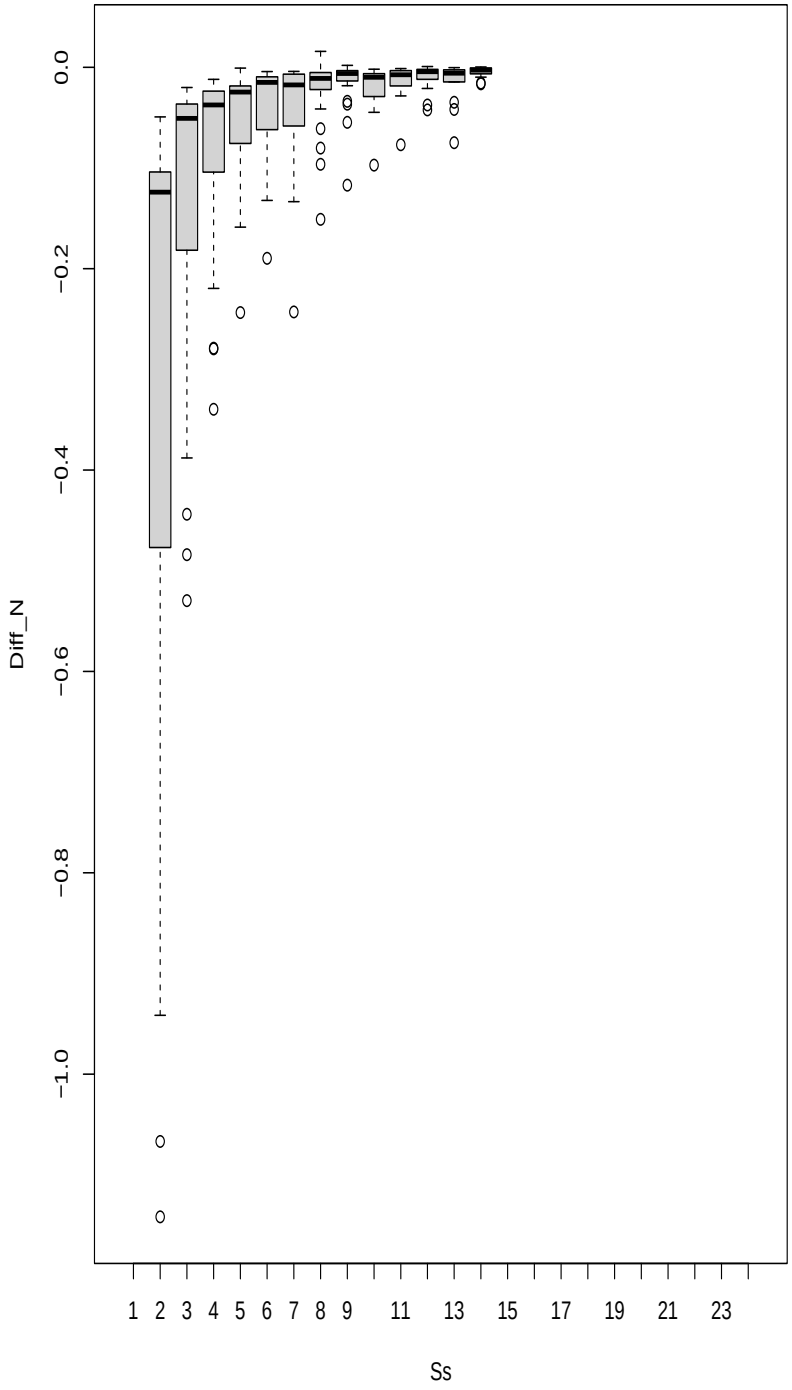

Fig 2.26. Relationship between sample size (Ss) and precision of nitrogen isotopic variance estimate, the change in the standard deviation of simulated variances as sample size increases by 1 (Diff_N). We subsampled, with replacement, carbon and nitrogen isotopes from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 15. Boxplots are pooled across populations.

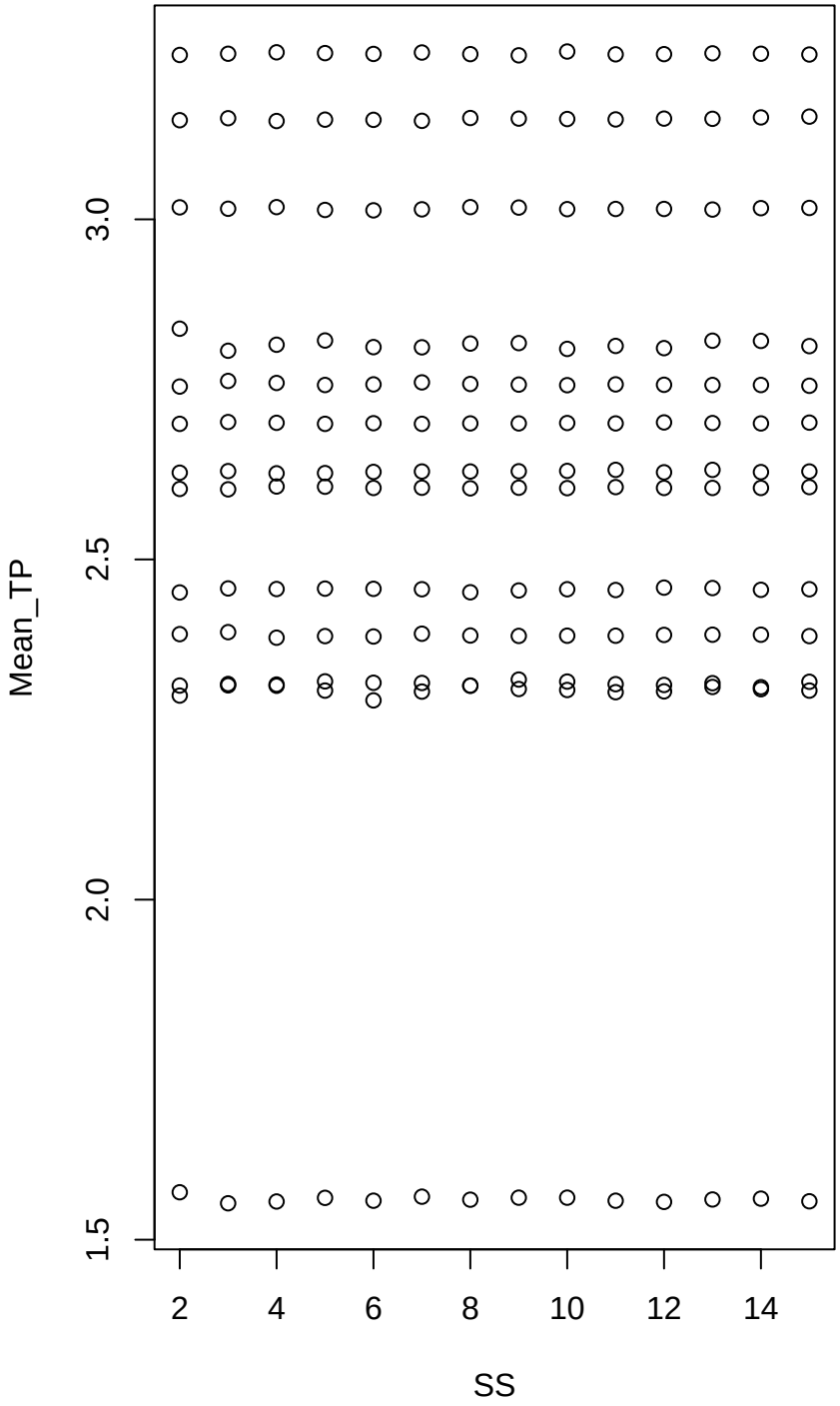

Fig 2.27. Relationship between sample size (SS) and mean trophic level estimate (Mean_TP). We subsampled, with replacement, trophic levels from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 15. The mean trophic level estimate was plotted against sample size to test for any directional bias of sample size on mean trophic level estimates.

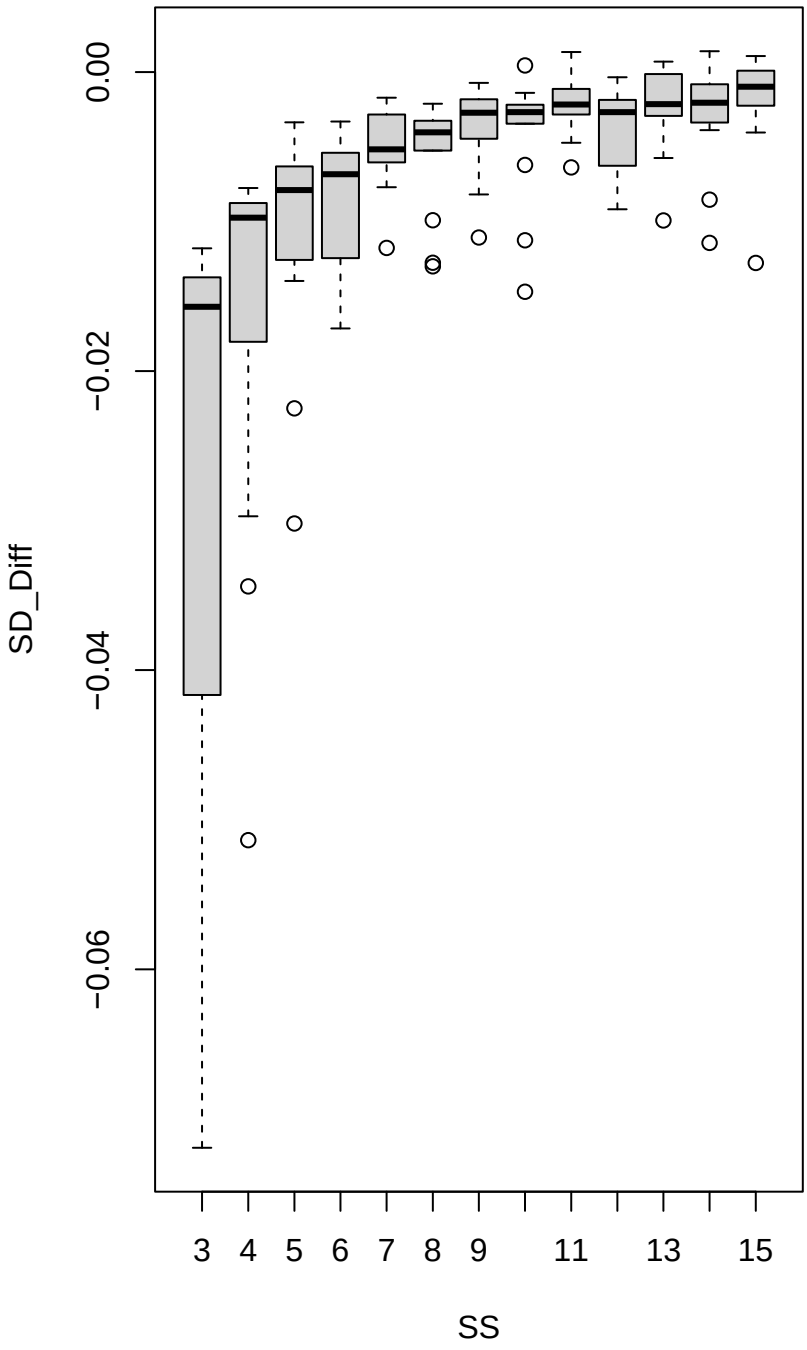

Fig 2.28. Relationship between sample size (SS) and precision of mean trophic position estimate, the change in the standard deviation of simulated means as sample size increases by 1 (SD_Diff). We subsampled, with replacement, trophic levels from each study population with n > 4. This process was repeated 1000 times each for sample sizes 2 to 15. Boxplots are pooled across populations.

CHAPTER 3
TROPHIC CASCADES IN THE DESERT? AN EXPERIMENTAL TEST IN WHITE SANDS

3.1 ABSTRACT

Trophic cascades are often described as ubiquitous, although there is a serious lack of data from many ecosystems testing this. This is especially true for deserts. There are multiple reasons that trophic cascades may not occur in deserts, including water limitation and prevalence of ectotherms. We experimentally manipulated the presence of lizards in a desert community, White Sands, and measured response variables associated with arthropods and plants for two years. Ten by ten meter plots were used as either lizard exclosures, partial fence controls or no fence controls (n = 6 per treatment). We found that desert lizards exert top down forcing on arthropods that cascades to herbivory. Web building spider densities increased dramatically following lizard removal. At one sampling date, spider webs were closer to the ground in lizard exclosures. Across all or at specific dates, captures of all arthropods, Coleoptera, Collembola, Formicidae and other Hymenoptera were lower in lizard exclosures. We hypothesize that high compensatory predation explain these results. On our last sampling date we found higher herbivory in exclosures. We found limited evidence that these shifts caused changes in plant biomass, abundance or reproductive effort. We conclude that ecologists need to consider top down forcing by carnivores in our understandings of desert ecosystems.

3.2 INTRODUCTION

The direct and indirect role of predation in structuring many ecological patterns and processes has long been recognized. Trophic cascades are permutations across at least two links in a food chain[109]. They are most frequently invoked when there are shifts in the primary trophic level (autotrophs) caused by changes at least two trophic levels above plants. Trophic cascades have been found to be extremely important across many ecosystems globally, with the effects of predation branching into processes as disparate as atmospheric carbon influx and wildfire[25]. Historically, ecologists have debated the importance of these sorts of 'top-down' processes versus those that are 'bottom-up' (changes in the primary trophic level, often driven by abiotic factors)[110]. Today there is relative consensus that both directions are relevant, with the relative strength of either varying spatially and temporally. However, although trophic cascades are often described as ubiquitous[1,25], there is still a serious lack of data testing this hypothesis in many ecosystems, including deserts[26,111]. Drylands cover 41% of the terrestrial surface[112], and are undergoing particularly severe global change[113]. Even though it may be safe to assume that both top down and bottom up forcing occur, it is critical to have a detailed understanding of these processes[110].

An early extension of trophic cascade theory, the exploitation ecosystems hypothesis (EEH), proposed that the strength of top-down control by predators should increase in more productive habitats[27,114,115]. In relatively resource poor ecosystems, including deserts, plant and herbivore biomass were predicted to be insufficient to support a third functional trophic level of predators. At higher productivity predators could eventually be supported but herbivore biomass would stay constant even if productivity increased, as herbivore biomass is now limited by predation[27,114]. This thinking paired well with that of early desert ecology, which argued that desert communities are mostly structured through bottom-up processes because they are severely

water limited[28]. Indeed this is still a prevailing paradigm, as decades of research have documented the relative importance of precipitation for ecosystem processes in drylands[104,116-122]. Biological activity is understood to be highly correlated with pulses of precipitation followed by periods of relative dormancy (the 'pulse-reserve' and 'pulse dynamics' paradigms[118,123]). This temporally heterogenous water availability also contributes to the substantial investment of many desert plants in physical and chemical defenses, which would attenuate any trophic cascade[26,29,124,125]. Trophic cascades may also be density dependent, and it may be that in desert ecosystems many consumers don't reach high enough abundances to shape lower trophic levels[111,126]. Finally, a relatively high proportion of desert animals are ectotherms[127], whose low metabolic rates relative to endotherms potentially limit any consumptive effects[30,37,114].

Given these reasons, it is perhaps unsurprising that arid ecosystems have historically been neglected in the search for trophic cascades[1]. However, there is evidence that top-down control can occur in deserts. Multiple studies have not found a positive relationship between productivity and trophic cascade strength, a key prediction of the EEH[31,128-130]. In a reanalysis of the EEH, Oksanen and Oksanen (2000) argue that some deserts are functionally three-trophic level systems because the conversion of primary to secondary production is highly efficient[114]. Underpinning these theoretical shifts has been the ample evidence of biotic links in deserts[131-135]. Desert food webs are not simple, and do indeed support a huge variety of interacting predators, omnivores and herbivores[136]. The prominence of macro-detritivorous arthropods in desert food webs, coupled with primarily ectothermic predators, may further explain their ecological efficiency[127,136]. Moisture limitation can also drive higher rates of predation and herbivory, as consumers seek food that contains water[111]. In the western Chihuahuan desert the interaction strength between spiders, crickets and leaf material was much stronger in dry than wet conditions[137]. Observations even support trophic cascades in deserts. For example, dingoes have been demonstrated to have impacts across lower trophic levels in Australian drylands, with their impact even extending to geomorphological processes[129,138-140] (but see Castle et al. 2022 and references therein[34]).

The existing evidence for trophic cascades in arid ecosystems is mostly theoretical and observational. Careful experimentation is key for conclusively demonstrating trophic cascades given the complexity of the multiple, interacting processes[34,38,114,141]. While experiments exploring single links (e.g. granivores and plants) in desert food chains are classics in ecology[32,33], very few have extended across more than two trophic levels[26]. Those that have did not find evidence of strong trophic cascades, although experiments have generally been of short duration[26,34-36,142]. While these experimental results may show an absence of top-down forcing in drylands, they may also reflect the heterogenous nature of trophic cascades in these systems. Ecological processes in drylands vary strongly over multiple spatial and temporal scales relative to other ecosystems[111,119,143]. Single link experiments, which have been longer in duration, have confirmed that relationships can vary strongly between seasons, years and decades[33]. To our knowledge no studies have experimentally investigated trophic cascades induced from a dominant group of desert vertebrates, lizards.

In general, ectotherms are expected to have a reduced per capita effect on lower trophic levels than endotherms due to their lower metabolisms[30,37]. This distinction is partially why the EEH was reformulated to focus on top-down regulation by endotherms[114]. Nevertheless, lizards are model organisms in our understanding of top down effects[38]. Pioneering and continuing work in the Caribbean has demonstrated that lizards have strong and multifaceted effects on lower trophic levels, including spiders, herbivorous arthropods, plants and other lizard species[38,90,144-

[149]. Similar to other taxa, we do have observational evidence that suggests biotic interactions involving desert lizards can be important[39,150,151]. But in general data involving the trophic role of desert lizards, especially insectivores, are seriously lacking.

Here, we fill this gap by experimentally manipulating the presence of lizards in White Sands, New Mexico and measuring response variables associated with arthropods and plants. White Sands is well suited for an experimental investigation of top-down forcing by lizards. Three lizard species are found in White Sands *Aspidoscelis inornata, Sceloporus cowlesi, Holbrookia maculata*. These lizards are in a dramatically different ecological context in White Sands relative to the surrounding desert scrub, having escaped most of their competitors and vertebrate predators[7,13]. Correlated with the change in richness White Sands lizards have undergone ecological release, including increases in density and broadened microhabitat use[6]. Intermediate predators like lizards exert stronger trophic interactions when released from predation[39,40,151]. Furthermore, relatively depauperate systems like White Sands should have less reticulate food webs, which may strengthen trophic cascades[152] (but see Borer et al. 2005[30]). Although speculative, White Sands may also have relatively high primary productivity, as the water table in the gypsum dune field is much more shallow than the surrounding desert scrub (~0.3-0.9 m below surface of interdune[153]). Multiple studies have also detailed the trophic niche of White Sands lizards, increasing our ability to deduce mechanisms behind any patterns (Table 3.1).

We predict that direct links between lizards in White Sands and arthropod prey are stronger than indirect links with other arthropods or plants[38]. This means that in general, arthropod taxa should increase in proportion to the degree to which they are consumed if lizards are removed, with an overall increase in arthropod densities (Table 3.1). Due to the trophic diversity of lizard prey at White Sands, we then expect any impacts on plants to be muted as any indirect effects of lizards are compensated for by increased predatory arthropods[108,136]. We also predict that the prevalence of bottom up processes, especially precipitation, in structuring the community should attenuate top down control[26,28]. Alternatively, lizards may have a relatively strong impact on herbivores, so their absence could indirectly cause higher herbivory and more likely affect plant growth and performance[38]. Another alternative hypothesis is that lizards have a disproportionate impact on carnivorous arthropods, so their absence should indirectly depress herbivores and possibly aid plants[38]. It is also likely that any direct or indirect effects of lizard removal should change with season and year, consistent with other trophic cascade studies[38] and reflective of the heterogenous nature of deserts[33,119].

3.3 METHODS

Study site and experimental design

Our study site was within the gypsum dunes of White Sands National Park in the northern Chihuahuan desert (New Mexico, USA), which manages a portion of the 712 km^2 dunefield. White Sands is a desert, with the majority of precipitation (mean annual precipitation ~ 228 mm) falling during the June-September monsoon season[5]. Our experiment took places in an interdune situated between active dunes, where the majority of vegetation in the barachanoid dunefield is found[5]. To facilitate interpreting results, we selected an interdune where previous observational food web work occurred, including characterization the ecological community and lizard dietary ecology. Previous surveys found that all three White Sands lizard species are

abundant in this interdune. The dominant vegetation is the grass alkali sacaton (*Sporobolus airodes,* hereafter 'sacaton'), with Trans-pecos false clapdaisy (*Pseudoclappia arenaria,* hereafter 'clapdaisy'), James' sea-heath (*Frankenia jamesii*), purple sand verbena (*Abronia angustifolia*), Torrey's jointfir (*Ephedra torreyana*), and soaptree yucca (*Yucca elata*) also abundant ('Chihuahuan gypsophilous grassland', National Vegetation Classification Standard[5]).

We manipulated the presence or absence of lizards using fenced exclosures (Fig 3.1) paired with two control treatments - partial fence ('partial') and no fence ('control'). The experiment was initiated in June 2017 and data collected intermittently until June 2019. We systematically selected 6 sites ('arrays') within the interdune from a grid of sites at least 10 meters apart. Sites were selected only if the soil was stabilized by vegetation, as shifting sands would cause logistical and visitor safety issues. This resulted in 5 arrays arranged N-S, with 1 array to the west, all at least 10 m from each other. Arrays were broadly similar in vegetation structure and composition. We systematically applied one of three treatments to adjacent west-east 10x10 m plots within each array. One plot, the exclosure, was enclosed in fencing and all lizards removed. Another plot, the partial treatment, had the same fence but with seven 1 m gaps and lizards were not removed. The partial treatment was to help control for any fence effects on arthropods or plants, independent of lizard removal[147]. A third treatment, the control, had no fence. For logistical reasons the partial treatment was always situated between the control and exclosure, while the other treatments alternated between the east and west side of the array. Construction occurred between 5/20 and 5/30 2017. Fences were made with aluminum flashing reinforced with rebar and were 20 cm tall and buried 20 cm. We cut one 50x7.5cm screened (0.64 cm hardware cloth) openings in each side of exclosures to facilitate movement of terrestrial arthropods but not lizards. Multiple arthropods were observed using screened openings during the experiment, including harvester ants (*Pogonomyrmex* sp.) carrying seeds.

Lizards were initially removed from exclosures using a combination of funnel traps (wire mesh bags with a funnel entrance) and visual surveys. While fences generally obstructed lizards, there were instances when they entered exclosures if fences were damaged or vegetation blew against fences. Throughout the duration of the experiment NPS personnel checked exclosures every ~2 weeks, conducting necessary repairs and removing lizards with visual surveys and funnel traps (set for >24 hrs). Exclosures were also designed so that lizards could exit them relatively easily. Rebar, which lizards could climb, was on the inside of the fence. Additionally, while overhanging or nearby vegetation outside of fences was trimmed, vegetation inside exclosures was not to facilitate lizard exit. Standardized 10 minute surveys over the course of the experiment revealed that exclosures effectively limited lizard densities (mean lizard per plot ± std error; Exclosures 0±0, Partials 0.8±0.35, Controls 1.03±0.46 ; Poisson GLM $F_{2,87}$= 7.53, $p < 0.001$).

We assumed that abiotic conditions and primary production did not vary substantially between plots and arrays, and that any differences between arrays could be modeled as random effects. We tested for an effect of fencing on temperature in August 2018 with data loggers (Thermochron iButtons, DS1922L-F50, Maxim Integrated Products) recording temperature every 15 minutes for 72 hours. We placed 2 data loggers in every plot in 3 arrays, one in the center of the plot (5 m from edges) and another in the southeast corner, 2 m from edges. Just including partial and full exclosures, we found no difference in temperatures near or far from fences (paired t-tests; mean temperature $t_4 = -0.13$, $p = 0.90$; maximum temperature $t_4 = -0.71$, $p = 0.52$; mean daily max $t_4 = 0.38$, $p = 0.72$). We also found no difference between treatments in

temperature (ANOVAs ; mean temperature $F_{2,15} = 0.77$, $p = 0.48$; maximum temperature $F_{2,15} = 0.32$, $p = 0.73$; or mean daily max $F_{2, 15} = 0.15$, $p = 0.86$).

The five years leading up to this study were relatively "normal" in terms of precipitation, with regionally dry conditions (moderate drought) in 2016[154]. The beginning of the study (2017) was also a relatively normal year (258.6 mm rain at White Sands weather station ; Fig 3.32) with most falling in the preceding winter and summer monsoon. Although 2018 was drier throughout the region[154], White Sands was generally similar to 2017 in yearly total (274.1 mm), but the 2017-2018 winter was relatively dry. Then 2019 was generally similar to previous years, with a wetter May than previous years before the experiment was terminated in June.

Arthropod sampling

We sampled arthropods in every plot using a combination of pitfall and sticky traps at the beginning of the experiment as a baseline (June 2017; for logistical reasons samples collected 1 week after fence construction) and in 6 sampling events over two years (August 2017, November 2017, March 2018, June 2018, August 2018 and June 2019). Pitfall traps, which primarily target ground dwelling arthropods[70], were made from 530 ml plastic cups (depth = 117 mm, brim diameter = 92 mm) buried with the top flush to the ground. Each cup had 150 ml of water and 1 ml of soap, with a 12x12 mm piece of hardware cloth just in the water to prevent vertebrates from drowning. Four pitfalls were placed in each plot (n = 72 total), each 3 m from the corner and ~30 cm from vegetation. Pitfalls were deployed for 72 hours and checked daily to replenish water, and were only deployed when weather permitted (e.g. no storms). Specimens were then transferred to 70% EtOH and stored until they were counted and sorted to Order (family for Formicidae and Cicadellidae, class for some Arachnida and Chilopoda) in the lab.

Sticky traps were 22x28 cm pieces of plastic sheeting placed 14 cm off the ground, attached between two wooden stakes[155]. The north side of each trap was coated with Tanglefoot Tangle-Trap Sticky Coating. Traps (n = 4 per plot, 72 per sampling event) were located ~1 m from pitfall traps, 30 cm from vegetation, and stakes were kept in the same location for the duration of the experiment[155,156]. Sticky traps were deployed for 24 hours within the same period as pitfall trapping. After deployment traps were covered in cellophane and stored at -20° C until specimens were taxonomically sorted and counted.

Mean captures per trap were analyzed in downstream analyses, with some taxa excluded from taxon specific analyses if they had too few captures (from pitfalls - Blattodea, Chilopoda, Ephemeroptera, Isoptera, Leipdoptera, Orthoptera, Neuroptera, Thysanoptera, from sticky traps - Blattodea, Ephemeroptera, Lepidoptera, Neuroptera, Odonata, Orthoptera, Plecoptera, Trichoptera from sticky traps). Solifugae and Opiliones were sorted, but were lumped with 'Arachnida' (excluding Araneae) analyses of pitfall data because captures were low. All taxa, including unknowns, were included in analyses of 'all' captures for both trap types.

Because web-building spiders were not captured using pitfall or sticky traps, we initiated surveys for web building spiders in June 2018 and collected these data for the remainder of the study. Every plot was broken into 5 2m wide strips and the same observer (C. Noss) would search each strip for 1.5 minutes, recording all spiders seen and the height of any webs (lowest point of a frame thread). The timer was paused when recording data. If a spider's web was connected to fencing they were noted but not included in downstream analyses, although this was rare. All arboreal spiders seen were recorded, but search effort was concentrated towards web building spiders because they were easier to find. At least three species were recorded, with the vast majority *Metepeira* sp.. Densities (counts per plot) were used in downstream analyses.

Vegetation sampling

We used multiple approaches to quantify any effect of lizard exclusion on plant growth and performance. While there was some redundancy in methods (specifically sacaton and clapdaisy reproduction were measured using two methods) they were generally complementary. No plant data were collected within 1 m of plot edges to minimize potential fence effects. First, we counted individual plants in a grid of 25 1x1 meter quadrats placed in every plot. Plants were deemed individuals if stems were >10 cm from stems of the same species, and for aggregating species (e.g. sacaton) 10x10 cm patches were counted as individuals. Only plants rooted within the quadrat were counted. Counts per plot were used in analyses. Whether or not an individual was reproducing or not was also recorded, and the proportion of individuals reproductive per plot used in analyses. Plot wide plant community quadrats were collected three times – June 2017 (onset of experiment), June 2018 and June 2019. Six species were common enough for further analyses, including *A. angustifolia*, *E. torreyana*, *F. jamesii*, *P. arenaria* (clapdaisy), *S. airoides* (sacaton) and *Y. elata*.

Second, we monitored growth and biomass (indirectly) of the dominant vegetation, alkali sacaton, using the point-intercept method in repeated measure quadrats ('sacaton quadrats')[157]. Plots were broken up into 64 m^2 sections (the first 1 m from plot edges were excluded), and random sections sequentially chosen until there was one in each plot quarter that contained sacaton. A 0.25 m^2 quadrat was then established at each section for monitoring throughout the experiment. We dropped a pin every 2.5 cm in a 10x10 grid across the quadrat (n = 100 pts per quadrat), using a frame made from PVC pipe and hardware cloth for standardization. We recorded every species that touched the pin at any point, and recorded bare ground and dead vegetation as well. Reproductive effort (count of panicles) was also recorded. Point intercept data were collected in June 2017, August 2017, June 2018, August 2018 and June 2019. Counts of hits of live sacaton and counts of panicles were further analyzed.

Third, we monitored individual 'focal clapdaisies' (*P. arenaria*) throughout the experiment for herbivory, growth, and reproduction. Clapdaisies were chosen because relative to other species their succulent leaves allowed relatively straightforward quantification of herbivory, and they were found in every plot. Every individual clapdaisy in each plot was enumerated, and then four per plot were randomly chosen for monitoring (two plots had <4 clapdaisy total). Reproductive effort was quantified with counts of reproductive structures, e.g. individual radiate heads. We measured herbivory by visually estimating the percentage of individual leaf volume removed in 25% bins, but ended up simplifying to proportion of leaves with damage, per plant, for analyses[158,159]. An individual stem was randomly selected, and all leaves scored. Additional stems were selected until a minimum of 30 leaves per plant were scored. Width of plant base (where main stem entered ground) and height were also measured at every sampling event. Clapdaisy data were collected at all sampling events besides March 2018, when all leaves were senescent (November 2017 data were excluded from reproduction analysis due to zero reproduction). Basal width and height were included in models as fixed effects (see *Statistical analyses*).

Statistical analyses

We tested for an effect of treatment (lizard exclosures, partial fence, or control) on arthropods and plants using linear mixed models (LMMs) and generalized mixed models (GLMMS, Program R, version 4.0.3[91], 'lmer' and 'glmer' functions in package lme4 version 27.1[94]). For all response variables, we first ran a model across all dates (excluding June 2017), including treatment, date and a date*treatment interaction as fixed effects. Nested random effects were included, including array (n=6) and plot (n=3 per array) and further if sampling occurred at a finer scale than plot level (e.g. arthropod traps, sacaton quadrats, focal clapdaisies, all n=4 per plot)[93]. We then ran a similar model for each date individually, necessarily dropping the finest scale random effect. For LMMs, we used the 'anova' function in base R to calculate p values and degrees of freedom to test for importance of fixed effects. For GLMMs, we estimated degrees of freedom and p values for fixed effects using the 'mixed' function in the package 'afex' (method = Satterthwaite)[160]. We performed post-hoc Tukey tests for differences between treatments using the function 'glht' from the package 'multcomp'[161]. All models were tested for performance using the 'DHARMa' package, which facilitates inspection of residuals and performs diagnostic tests (K-S tests, dispersion tests, outlier tests)[162]. If models did not pass validation, we first tried a different distribution family in the mixed model[93]. This resulted in focal clapdaisy herbivory and plant reproduction proportions being switched from binomial to Gaussian families. One model needed further refinement, the June 2018 analysis of all pitfall captures, which was switched to Gaussian family and then array dropped as a random effect. The aforementioned refinements resulted in no significant changes to F or p values, and did not change any conclusions. Spider counts (surveys), sacaton quadrat panicle counts, and focal clapdaisy reproduction were analyzed under Poisson distribution, and spider web heights, sacaton quadrat point intercepts and focal clapdaisy herbivory under Gaussian (other distributions can be found in table captions).

3.4 RESULTS

Arthropod sampling

All arthropod and plant results are summarized in Table 3.2. We collected 45,210 arthropods representing at least 17 orders (n = 33,862 from pitfalls, including 18,556 Collembola and n = 11,348 from sticky traps). Pitfall and sticky trap captures varied strongly with date for all taxa, with wide seasonal fluctuations (Tables 3.3 , 3.4). Lumping across all dates and taxa we found a fence effect that decreased pitfall arthropod captures in partial and exclosure plots ($F_{2, 10}$ = 9.8, p = 0.009 ; Tukey HSD E-C p <0.001, P-C p =0.008, P-E p = 0.28 ; Table 3.3; Fig 3.2). This effect was not apparent in individual date models, and for two dates (June and August 2018) exclosures had fewer pitfall captures than partial treatment (Table 3.3 ; Fig 3.2). For individual taxa, exclosures had fewer pitfall captures than control and/or partial plots across dates (Collembola [Fig 3.6], Formicidae [Fig 3.8], Hymenoptera [Fig 3.10]) and at individual dates (Araneae [Fig 3.4], Coleoptera [Fig 3.5], Collembola [Fig 3.6], Formicidae [Fig 3.8], Hymenoptera [Fig 3.10] ; Table 3.3). Subsetting by taxa also revealed fence effects across dates and/or at individual dates (all [Fig 3.2], Araneae [Fig 3.4], Coleoptera [Fig 3.5] ; Diptera [Fig 3.7] ; Table 3.3).

Sticky trap captures did not vary with treatment across all taxa and dates ($F_{2, 10}$ = 1.8, p = 0.28) but exclosures did have fewer captures in August 2018 (Fig 3.11; Table 3.4). For

individual taxa, the only treatment effects across all dates was a trend for higher Cicadellidae captures in control plots relative to partial plots (Fig 3.13, Table 3.4). Exclosures had fewer captures than control and/or partial plots at other individual dates for Cicadellidae (Fig 3.13), Diptera (Fig 3.15), Hymenoptera (Fig 3.17) and Thysanoptera (Fig 3.19; Table 3.4). At the onset of the experiment (June 2017) there was a trend for lower captures in exclosures relative to other treatments for Cicadellidae (Fig 3.13; Table 3.4) and for higher captures in controls relative to other treatments (fence effects) for Hymenoptera (Fig 3.17; Table 3.4).

Spider surveys revealed that exclosures had higher spider densities than control or partial plots when lumped across all dates ($F_{2, 10} = 11.75$, $p = 0.002$; Tukey HSD E-C $p < 0.001$, P-C $p = 0.91$, P-E $p = 0.002$; Table 3.2 ; Fig 3.20), that densities varied significantly with date ($F_{2, 30} = 10.47$, $p < 0.001$) and no significant date by treatment interaction ($F_{4, 30} = 1.16$, $p = 0.35$). When subset by date we found that exclosures had higher densities than other treatments in June 2018 ($F_{2, 10} = 10.32$, $p = 0.005$; Tukey HSD E-C $p = 0.001$, P-C $p = 0.91$, P-E $p = 0.002$), June 2019 ($F_{2, 10} = 4.99$, $p = 0.003$; Tukey HSD E-C $p = 0.009$, P-C $p = 0.51$, P-E $p = 0.09$) but not August 2018 ($F_{2, 10} = 1.45$, $p = 0.23$). We found no effect of treatment on spider web height when lumping across all dates ($F_{2, 10} = 1.53$, $p = 0.26$; Table 3.2; Fig 3.21), variation with date ($F_{2, 304} = 2.41$, $p = 0.05$) and date by treatment interactions ($F_{4, 292} = 2.41$, $p = 0.05$). When subset by date web height was lower in exclosures than other treatments in August 2018 ($F_{2, 103} = 10.05$, $p = 0.001$; Tukey HSD E-C $p = 0.002$, P-C $p = 0.99$, P-E $p < 0.001$) but there were no differences in June 2018 ($F = 0.90$, $p = 0.41$) or June 2019 ($F = 0.03$, $p = 0.97$).

Vegetation sampling

There was limited evidence for an effect of lizard exclusion on plant counts or reproduction. Lumping across June 2018 and June 2019, we found that *E. torreyana* counts were higher in the partial treatment than exclosures ($F_{2, 10} = 3.2$, $p = 0.25$; Tukey HSD E-C $p = 0.73$, P-C $p = 0.15$, P-E $p = 0.03$; Table 3.5; Fig 3.24), with no differences in June 2017, and higher values in partial treatments thereafter. *E. torreyana* reproduction was higher in exclosures than partial plots when lumping across dates ($F_{2, 13} = 2.9$, $p = 0.09$; Tukey HSD E-C $p = 0.20$, P-C $p = 0.94$, P-E $p = 0.09$; Table 3.5; Fig 3.24) and for individual dates there was more reproduction in exclosures than control plots in June 2019. While there was no overall treatment effect for *A. angustifolia*, we found that counts were lower in the exclosures at the onset of the experiment, then controls had more than partials in June 2018, and then there were no differences by June 2019 (Table 3.24; Fig 3.22). The *A. angustifolia* results corresponded with a marked decline in counts over time ($F_{2, 1} = 15.4$, $p = 0.01$) a pattern which was mirrored in the broader area (pers. obs.). We also found that *Y. elata* counts varied between treatments at the onset of the experiment, with partial plots have higher counts than exclosures in June 2017, partials higher than either treatment in June 2018, and no difference in June 2019 or when lumping across dates (Table 3.5; Fig 3.27). For *F. jamesii*, clapdaisy (*P. arenaria*) and sacaton (*S. airoides*) we found no relationship between treatment and abundance or reproduction (Table 3.5; Figs 3.22 – 3.27).

We found no effect of treatment on sacaton cover (counts of point intercept hits) in repeated measure quadrats ($F_{2, 10} = 0.33$, $p = 0.73$), variation by date ($F_{4, 276} = 12.84$, $p < 0.001$) and a date by treatment interaction ($F_{8,276} = 2.35$, $p = 0.03$; Table 3.2; Fig 3.30). When subset by date we still found no effect of treatment on sacaton cover. We found a fence effect on counts of panicles in sacaton quadrats, with lower counts in control plots relative to exclosures or partial plots ($F_{2, 15} = 2.59$, $p = 0.08$; Tukey HSD E-C $p = 0.04$, P-C $p = 0.08$, P-E $p = 0.93$; Table 3.2,

Fig 3.31), a date effect ($F_{3, 207} = 30.76$, $p < 0.001$) and no data by treatment interaction ($F_{6, 207} = 0.59$, $p = 0.45$). When subset by date, we found multiple differences between treatments with most indicating likely fence effects (Table 3.2, Fig 3.31).

We found evidence that treatment effected focal clapdaisy herbivory, although the effect varied in directionality and widely with date. When lumping across dates we found no effect of treatment ($F_{2, 303} = 0.66$, $p = 0.52$), variation by date ($F_{4, 301} = 98.04$, $p < 0.001$) and a date by treatment interaction ($F = 2.76$, $p = 0.006$; Table 3.2; Fig 3.29). For individual dates, we found that herbivory was lower in exclosures than controls in November 2017 ($F_{2, 8} = 2.81$, $p = 0.12$; Tukey HSD E-C $p = 0.05$, P-C $p = 0.72$, P-E $p = 0.25$), herbivory was higher in exclosures than both other treatments in June 2019 ($F_{2, 57} = 3.43$, $p = 0.04$; Tukey HSD E-C $p = 0.06$, P-C $p = 0.99$, P-E $p = 0.05$). We no effect of treatment on reproduction (counts of reproductive structures) of focal clapdaisy ($F_{2, 10} = 0.84$, $p = 0.29$), variation by date ($F_{3, 184} = 148.09$, $p < 0.001$) and no date by treatment interaction ($F_{6,184} = 3.18$, $p = 0.39$; Table 3.2; Fig 3.28). When subset by date we found no effect of treatment on focal clapdaisy reproduction.

3.5 DISCUSSION

Our experimentally exclusion of lizards from patches of desert resulted in changes in densities of multiple arthropod taxa, spider microhabitat use, and herbivory (Table 3.2). To our knowledge this is the first experimental demonstration of trophic cascades from a desert reptile, and one of very few experimental confirmations of top down forcing from desert carnivores[26,36]. Although the majority of results suggest strong compensatory predation following lizard removal, we also found important complexities in the food web. All lizard effects detected varied substantially with date. Time and area constrained surveys revealed that web building spider densities increased dramatically following lizard removal (Fig 3.20). At one sampling date, spider webs were closer to the ground in lizard exclosures (Fig 3.21). At all and/or specific dates, pitfall trap captures of all arthropods, Coleoptera, Collembola and Formicidae were lower in lizard exclosures (Table 3.3). Sticky trap captures of were lower in exclosures for all arthropods and Hymenoptera (non-Formicidae) at one date each (Table 3.4). Finally, on our last sampling date we found higher herbivory on focal clapdaisy in exclosures (Fig 3.29). We found limited evidence that these shifts caused changes in plant biomass, abundance or reproductive effort (Table 3.2). Multiple instances of differences between only two treatments (e.g. exclosures and partial plots, but not controls) or statistical trends add to the complexity and are discussed below. Our results also underscore that it is essential to control for fence effects in these type of studies, as we found significant impacts of fencing on pitfall trap captures and sacaton reproduction (Table 3.2).

Ecologists increasingly appreciate that biotic interactions fundamentally shape desert ecosystems, including processes like herbivory and nitrogen mineralization[111,135,163]. Our work demonstrates that top-down forcing by carnivores needs to be seriously considered as well[25]. Indeed, top down forcing in White Sands is likely stronger than our results indicate as we only targeted lizards for exclusion and not avian or arthropod carnivores[36]. Insectivorous lizards generally exist in food webs rife with intraguild predation, being both predators and prey of arthropods[164-167]. This may be especially true in deserts, where large predatory macroinvertebrates are relatively abundant[127,136]. For example, at White Sands we have observed centipedes (*Scolopendra polymorpha*) and warrior beetles (*Pasimachus* sp.) predate adult lizards in relatively large (100x25cm) funnel traps. While this predation may be more age structured in

the wild, it still demonstrates that despite the dearth of vertebrate predators in White Sands lizards are not at the top of a simple 'food chain'[136]. While our focus here was on better understanding the ecological role of lizards in White Sands, future work should explore the role of additional carnivores for a broader understanding of top down forcing in this system.

Despite our demonstration of shifts across at least three links in a desert food web, our results are relatively equivocal regarding the ecological importance of trophic cascades in deserts and broader generalizations like the EEH. The only relatively straightforward effect of lizard exclusion we found on plants was shifts in herbivory of focal clapdaisy, and the directionality changed with date (Table 3.2, Fig 3.29). Our results are best understood as evidence for 'species-level' cascades, as opposed to 'community-level' cascades (sensu Polis 1999) since we did not see shifts in primary producer biomass[168]. Although we did not directly measure biomass, our detailed sacaton cover data is correlated with biomass[157] and was dynamic with date and season during the course of the experiment (Fig 3.30). Our results are therefore in agreement with other experimental investigations in arid ecosystems, which have not found evidence for strong community level cascades[26,34,35]. The majority of experimental evidence from drylands is therefore generally in agreement with the EEH's prediction that trophic cascades should be relatively weak in these systems[27,114,115]. While there is observational and quasi-experimental evidence from Australia that dingoes can shift plant biomass in arid ecosystems[129,138], proponents of the EEH point out correctly that these shifts are relatively small[169]. That said, distinguishing statistical from ecological significance, and what constitutes 'substantial' changes in biomass, is challenging and controversial[109]. More trophic cascade experiments that are rigorous, long term and grounded in natural history are clearly needed in arid ecosystems.

Variation of lizard effect by date

We found strong support for models of deserts as highly heterogeneous over time[119,123]. Captures of all arthropod taxa and several plant variables varied with date and many had date by treatment interactions (Table 3.2). The magnitude of differences between dates, with some important exceptions, was generally much higher than any treatment effects. We can also expect lizard foraging behavior, including composition of prey taxa and biomass consumed, to vary temporally with reproductive status and activity levels[170]. Pulse-reserve and pulse dynamic theories predict that in deserts ecological processes vary substantially over time, across scales from hours to decades, in response to precipitation[123]. While seasonally variable precipitation (winter and summer pulses of precipitation) and the resulting consequences (growth of C_3 and C_4 plants, respectively) are generally predictable in the northern Chihuahuan desert, heterogeneity is still the rule[104,117,120,123]. Precipitation legacies have multiyear impacts on plant communities, with transitions from wet to dry periods and vice versa having different effects depending on the relative dominance of C_3 and C_4 species[117]. At the other end of the scale individual precipitation events can lead to spikes in microbial and arthropod activity[123,171-173]. Although 2018 was slightly drier than 2017, annual precipitation was generally "normal" throughout the study period (see *Methods* and Fig 3.32).

November 2017 and March 2018 had significantly fewer arthropod captures than other dates, and no treatment effects (Table 3.2). While the lack of effects could partially be due to low statistical power with few captures, at very low water availability species interactions are reduced[28,111]. Winter 2017/2018 was dry, with Sept – Feb precipitation ~60% of average (Fig 3.32). While we sampled during this period because of possible legacy effects, most animals at

White Sands, including lizards, are also inactive which could equalize treatments (0 lizards seen in plots during these dates, 1 *H. maculata* seen in vicinity March 2018).

We did not find a clear and consistent difference between June and August sampling events in cumulative treatment effects, although there were many in August 2018 (Table 3.2). We initially speculated that there could be differences because in August primary productivity should be relatively strong following summer rains, which could strengthen top down forcing[27] (but see Letnic et al. 2018[129]). Conversely, lower ambient moisture levels in June could also increase interaction strengths[111]. White Sands lizards are likely similar to other desert insectivorous lizards in that they get almost all water from prey regardless of ambient moisture[174,175]. Arthropod carnivores and herbivores should interact more strongly with lower trophic levels when it is drier (to a point)[111]. While we didn't find support that top down forcing is generally stronger in August versus June, these contrasting dynamics (moisture limitation and primary productivity) could explain contrasting results between seasons. Our results also reinforce that trophic cascade experiments should be long and have as many sampling events as logistically feasible. This is especially important in deserts. As noted, these communities can vary dramatically in a matter of days, so we likely missed instances of top-down forcing on arthropods.

We could also expect shifts in treatment effects as arthropods and lizards shift their diets over the summer to take advantage of basal resources. Prior work has also demonstrated that in the spring desert food webs rely more on C_3 plants (e.g. clapdaisy), while in the late summer and in droughts C_4 plants (e.g. sacaton) are relatively important[104,123]. We did see higher herbivory in focal clapdaisies in June 2019 (following a relatively wet May), although herbivory also varied by treatment in November 2017 (Fig 3.29). While there was no effect of treatment on sacaton cover in either August sample, we did see the expected increase in this C_4 grass in 2018 following summer rains. The lack of a treatment effect on sacaton cover in 2018 is particularly interesting because prior work has indicated herbivore reliance on C_4 plants should be relatively strong following dry winters[104]. We conclude that any indirect link between lizards and sacaton in White Sands isn't strong enough to elicit a response even with winter droughts. As climate change progresses and the Chihuahuan deserts continue to get drier and precipitation more variable, the links between lizards and C_4 grasses like sacaton may strengthen[104,123].

Lizard effects on arthropods

We found that lizards limit densities of web building spiders, which were overwhelmingly *Metepeira* sp. (Fig 3.20). There are multiple possible mechanisms for this effect, with the two most likely direct predation or competition for arthropod prey[148]. We cannot determine which is more important at White Sands given our data, but hypothesize that while both contribute predation is more important. Lizards consume spiders at our field site (Table 3.1), although ground-dwelling spiders are also common in White Sands and we have only identified stomach contents to order. Cumulative experimentation in the Caribbean has determined that both competition and predation contribute to negative effects of lizards on *Metepeira*, but predation has a larger effect[38,148]. We found that mean web heights in exclosures were 15 cm lower than other treatments in August 2018, with no differences between treatments in June 2018 or June 2019 (Fig 3.21). Exclosures had multiple webs <10cm and none above 60, whereas partial and control plots were the opposite. This suggests that rather than being a purely consumptive effect (lizards eat spiders close to the ground, shifting mean web height upwards)

this is a trait-mediated indirect interaction (spiders select sites farther from the ground in the presence of lizards)[176]. The lack of a significant difference in spider densities between treatments in August 2018 also supports this interpretation. Manicom et al. (2008) also found that lizards effects on spider microhabitat and densities can be decoupled[155]. Scincid lizards shifted web height of 'exposed' spider species, but do not affect the height of species that build shelters and do not affect overall spider densities[155].

Seasonal shifts in food webs discussed above could explain the lack of lizard effect on spiders in August 2018. Other work has demonstrated stronger top-down effects on spiders is stronger during dry periods as predators shifted to other prey in ambient wet conditions[177]. While Spiller and Schoener (2008) found a hump shaped relationship between lizard effect on spiders and rainfall, precipitation extremes could disrupt this link through mechanical disturbance[149]. Summer storms in White Sands can be in intense, and while August 2018 was dry, July 2018 was wet. This interpretation probably doesn't fit our results, however, as overall spider densities in August 2018 were actually slightly higher than in June (Fig 3.20). Mechanical disturbance could explain why we only saw a lizard effect on web height in August. Spiders could prefer more sheltered microhabitats in stormy conditions, but could be precluded from selecting these sites due to lizard predation. The reduction in aerial arthropods in August 2018 in lizard exclosures (Fig 3.11, Table 3.4) may also be related to the web height result. Sticky traps were located 14-42 cm off the ground, meaning in August 2018 webs in exclosures overlapped with sticky trap heights more than those in other treatments. Spiders therefore may have had a higher impact on aerial arthropod captures in exclosures, even if abundance did not vary significantly with treatment[148]. It is also possible that reduced aerial arthropod captures in August 2018 were a legacy of higher spider densities in June 2018. All web heights were lower in June 2019, but overall sticky captures were not. We did see lower captures of Cicadellidae (Fig 3.13) and Hymenoptera (Fig 3.17) in our June 2019 sticky traps, and Thysanoptera in August 2017 (Fig 3.19), which could have been caused by the higher spider densities plus lower web heights. All aerial arthropod captures were also lower in exclosures in June 2018 and June 2019, but these differences were not statistically significant. Overall the aerial arthropod and spider surveys indicate that in exclosures there was compensatory predation from spiders released from lizards effects[38,144,148]. Future work detailing the relative strength of competition, predation, trait versus density mediated indirect interactions and legacy effects are needed to more fully understand these interactions[38].

Pitfall traps revealed a similarly positive, indirect effect of lizards on overall arthropod abundance in White Sands (Table 3.3). Exclosure captures of all arthropods were lower in June 2018, with a trend in August 2018 (Fig 3.2). Exclosure Coleoptera captures were lower in June 2018 and August 2018 (Fig 3.5). Collembola captures were lower in exclosures when analyzed across all dates (Fig 3.6). Formicidae captures were lower in exclosures in August 2018 (Fig 3.8) Hymenoptera captures were lower in exclosures when analyzed across all dates (and in August 2017, although exclosures were only significantly different from controls (Fig 3.10; P-E Tukey HSD $p = 0.11$ overall, $p = 0.13$ in August 2017)). We also found fence effects on pitfall captures of multiple taxa, discussed below (Tables 3.2 , 3.3). Changes to these taxa can be expected to have important consequences to desert ecosystems, although due to their within-taxa ecological diversity specific predictions are difficult. Formicidae, non-formicid Hymenoptera and Coleoptera play major roles in desert systems, as detritivores, carnivores and herbivores, mutualists, competitors and prey[119,135,136]. Much of the understood role of Collembola are as prey and detritivores, although their diversity is very high and even relative to other arthropods

understudied[178,179]. Any top down forcing by lizards therefore may have important broad implications for White Sands, and more taxonomically detailed studies will be needed to understand these.

We interpret declines in arthropods following lizard exclusion as resulting from compensatory predation as carnivorous arthropods are released from lizard top down control[38,144]. However there is an important gap in this interpretation – we did not record increases in any taxa with pitfall (or sticky) traps. There are four non-mutually exclusive reasons this could be the case. *First*, we have summed captures across very large taxonomic categories. There is considerable trophic diversity within arthropod orders (Table 3.1), and there could be increases in some predatory taxa that are concealed using our methods. *Second*, several of the taxa captured with pitfalls are partly or entirely aerial (e.g. Hymenoptera), so we could partially be seeing an effect of increased web building spiders. *Third* lizards could constrain carnivorous arthropods through trait-mediated indirect interactions, reducing predation but not abundance. This is part of what we saw with web-building spiders. These 'landscape of fear' type interactions could also play a role in arthropod-arthropod interactions, e.g. if carnivorous arthropods are constraining prey movement (and therefore trapping rates) but not abundances[176]. *Fourth*, our trapping methods may have been inadequate for large spiders and centipedes, which could be driving the compensatory predation. In the summers of 2015 and 2016 we surveyed arthropods at the same interdune as the current study, using different methods including very large pitfall traps (19 liter paint buckets) and funnel traps (100x25 cm). In 2015/2016 22% of spider captures were visually scored as too large to be potential lizard prey (mostly Lycosidae), whereas in the current study only ~3 were that large. Similarly, in 2015/2016 almost all centipedes were 5-7 cm in length (*Scolopendra polymorpha*), whereas in the current study all were <2 cm. It may be that the pitfall traps used in this study (530 ml plastic cups, depth = 117 mm, brim diameter = 92 mm) were too small to hold these some carnivorous arthropod, or these predators actively avoided the traps. While all four of these processes may have contributed to our results, we hypothesize that the first three were more important. Other work has found that pitfall traps (including some smaller than used in this study) can actually overrepresent large arthropods, including Lycosids[180,181]. We suggest that future food web experiments in desert systems use a mix of sampling techniques targeting ground dwelling spiders.

Lizards effects on plants

Herbivory of focal clapdaisy was higher in exclosures in June 2019 and there was a trend towards lower herbivory in exclosures in November 2017 (Fig. 3.29). We hypothesize that the majority of herbivory was from Lepidopteran larvae, as these were the most common herbivores seen on clapdaisy. Lepidopteran larvae were not quantified in this study, so this link is speculative. Other likely herbivores noted include Hemiptera, Coleoptera and Orthoptera. The results from June 2019 indicate that lizards indirectly help protect clapdaisy. They also suggest that a link between web building spiders and the herbivores is weaker than the lizard-herbivore link[38]. Although this may seem to contrast with our aerial arthropod and web building spider results, food webs are made up of multiple interlocking food chains[136]. This result also supports models of Chihuahuan desert food webs as more reliant on C3 plants like clapdaisy following wet winters/springs, as May 2019 was relatively wet (Fig 3.32)[104,123]. The lower herbivory in exclosures in November 2017 may reflect that herbivory accumulated over the course of the spring and summer is lower when lizards are absent. This implies that over the course of an

entire year lizards increase clapdaisy herbivory. The contrasting results in June 2019 and November 2017 could also reflect delayed effects of lizard exclusion or differences between years. Importantly, we did not see a treatment effect on clapdaisy reproduction (Fig 3.28). The fitness consequences of leaf herbivory are not straightforward, and more work is needed to understand any ramifications of shifts in herbivory caused indirectly by lizards[109,182].

We found little evidence for an effect of lizard exclusion on counts of plants (Table 3.5). The effects of top down forcing on plant communities can take multiple years to emerge, something that may be especially true with desert perennials with long generation times[33,117]. Our experiment was relatively short (2 years) so may not holistically reflect links between lizards and plants. Several responses that we found in arthropods, in particular major shifts in Coleoptera, Collembola and Formicidae, could have long term consequences for plant communities[119,135]. We did find lower counts of *E. torreyana* in exclosures than partial plots (Table 3.5), but this very likely reflects initial differences as opposed to any treatment effects as means did not shift over time (Fig. 3.24). This was also the case for *Y. elata* (higher counts in partials, including at start of experiment ; Fig 3.27) and *A. angustifolia* (lower counts in exclosures at start of experiment ; Fig 3.22). Despite the relative normal precipitation, we found that *A. angustifolia* counts declined over the two year study period (Fig 3.22), something that we also noted for the broader interdune. We also found higher reproduction in *E. torreyana* in both post June 2017 samples, with a significant difference between control and exclosure treatments in June 2019 (Fig 3.24). It is difficult to determine whether this is a fence effect or reflects an indirect effect of lizards. *E. torreyana* is wind pollinated but not self fertile[183], so proposing a mechanism for this result is difficult. *Ephedra* pollination ecology is relatively understudied, so it is possible that insects can play a role in *E. torreyana* pollination[183,184]. Detailed natural history observation in Israel did uncover that Diptera and Hymenoptera can pollinate *Ephedra*, although wind pollination is still more important[185]. More work is needed to understand any links between *E. torreyana* and lizards in White Sands. Any lizard effects on plant communities are particularly interesting in this system because plants play an important role in stabilizing the dunes[186].

Fence effects

Our inclusion of a partial fence treatment allowed us to parse out lizard from fence effects. We found that there were fence effects on arthropods and plants, and echo many others that controlling for these is essential for trophic cascade studies using enclosures or exclosures[36,147]. In particular, we found fences reduced captures when lumping across dates, or at specific dates, of all pitfall arthropods, Araneae, Coleoptera and there was a trend for Cicadellidae (Table 3.2). These results do make intuitive sense, as fragmentation should reduce movement. In particular, it was obvious in the field that large, mobile Tenebrionid beetle movement was impeded by fencing. We also found initial (June 2017) fence effects on Hymenoptera and Cicadellidae (Table 3.2). We suggest that rather than demonstrating initial differences or confounding factors between treatments, these mobile taxa may have been disturbed during fence construction. We also found a fence effect on panicle counts of sacaton (Table 3.2, Fig 3.31). This also makes sense, as we observed that panicles were susceptible to breaking in the wind and fences likely sheltered panicles to some degree[36].

Conclusions

We found that desert insectivorous lizards can have top down effects that extend to primary producers. But how generalizable are our findings? We are aware of only two studies that have experimentally investigated top down forcing by desert reptiles. Segoli et al. found that skink (possibly *Chalcides ocellatus*) along with arachnid and centipede predation reduces isopod (*Hemilepistus raemuri*) densities in the Negev desert, Israel[187]. Marrussich and Faeth (2009) excluded lizards (and ground dwelling arthropods) from urban shrubs in Phoenix, Arizona and had inconclusive results regarding the role of lizards specifically[188]. Existing observational evidence is also mixed. Polis et al. (1998) concluded that *Uta stansburiana* in desert islands in the Gulf of California do not influence spider densities[189]. In contrast, multiple observational studies in arid Australia focusing on invasive species induced cascades suggest that top down forcing from lizards occurs[39,150,151]. For example, *Varanus gouldii* activity is negatively correlated with toxic prey (*Rhinella marina*) abundance, which seems to increase abundances of *V. gouldii* prey (skinks, agamids, geckos, pygopods)[150].

The same attributes that make the White Sands system well suited to searching for trophic cascades (high lizard densities, natural enemy escape, relatively simple food webs, possibly high primary productivity) don't occur in most other desert ecosystems. Our results are perhaps most comparable to the suite of studies that have found effects of lizards (*Anolis*) extending to web building spider densities, aerial arthropods and herbivory in the Caribbean[38]. Schoener and Spiller (2010) review this body of work and conclude that trophic cascades are stronger on small islands. Several of the reasons this may be the can illuminate the generalizability of our results for other desert lizards. Lower diversity may strengthen cascades, as compensatory predation is limited[152]. Stroud (1950) has made the most intensive survey of arthropods at White Sands published, and concluded that insect diversity likely declines in the center opposed to edge of the dunefield[190]. We found that diversity of arthropod orders was lower in White Sands relative to the surrounding desert (Noss and Rosenblum, unpublished data). Nevertheless we found evidence for compensatory predation by arthropods following lizard removal (Table 2.2). We hypothesize that the relationship between lizards and carnivorous arthropods is generally similar in White Sands to other deserts. Lizard diversity is also lower in White Sands relative to many other desert ecosystems[7]. This could have several contrasting consequences for the strength of top down effects. Higher lizard diversity could have additive effects on lower trophic levels, especially if predators have distinct niches[191]. For example just outside of White Sands are ant several Formicidae specialists (*Phrynosoma*). Adding them to a lizard community would likely increase top down effects on Formicidae. Alternatively, if there is high overlap in diet between lizards then there may redundancy in any top down effects, with overall guild density mattering more than diversity[191]. This is likely the case for many desert lizards, which are relative generalists with a high degree of dietary flexibility[8]. Finally, if there is a high degree of intraguild predation the overall effect of lizards could be reduced[191,192]. For example, *Crotophytus collaris* is found just outside the dunefield and eats much of the same prey as White Sands lizards, but also preys on lizards. We hypothesize that the relationship between insectivorous lizard diversity and strength of top down effects of this guild is difficult to predict and likely ultimately depends on species identity[191]. Densities of lizards are also comparable or higher in White Sands relative to surrounding desert scrub[6](Noss and Rosenblum unpublished data), a feature is shares with small Caribbean islands[38]. It is likely that at least some of the top down forcing we found is consumptive and density mediated (e.g. 'density-mediated indirect

interaction')[38,193]. This may limit the generality of our findings, at least to many other desert ecosystems where lizard densities are lower than White Sands. However it is possible that the mechanism behind the effect of lizards in White Sands is behavioral, or trait-mediated indirect interactions[176,193]. Indeed, we have evidence that at least part of the effect of lizards on spiders is behavioral (e.g. web locations shift downwards with lizard removal, Fig 3.21). White Sands lizards have also undergone trophic niche shifts during ecological release, including higher individual specialization [15] (Noss and Rosenblum unpublished data). Increasing predator individual specialization has been hypothesized to increase the strength of top-down effects as prey are more efficiently targeted, but the few empirical tests of this hypothesis have not supported it[194,195]. We conclude that further experimental tests of the role of insectivorous lizards are urgently needed. Tests in higher diversity systems and factorial approaches that manipulate factors like lizard density, identity and primary productivity would be especially useful.

We found that desert lizards exert top down forcing on arthropods that cascades to herbivory. In many ways this was an exploratory study, as connecting patterns to process often remained challenging and speculative even under a rigorous experimental approach. In other systems decades of research are still leading to better understanding of these complex interactions[38]. The fact that we only manipulated one guild in a diverse carnivore community, embedded within a landscape of where lizard effects remain, and still found an effect is showing. We conclude that ecologists need to consider top down forcing by carnivores in our understandings of desert ecosystems.

Acknowledgements

We thank the Rosenblum Lab for help constructing and tearing down the exclosures. We thank Madeline Moore, Sam Wasserman, Katherine Kinkopf, Yibing Yu, Aaron Luu, Kea Rutherford, Shannon Buttimer, Maggie Grundler, Collin Bos and Linnea Norton for help with fieldwork. We thank Jimmy Wehsener, Poojan Karnik, Nicole Kim, Aidan Maese-Czeropski, Analise Hober, Abrielle Leeder and Niko Frost for help with lab work. Thanks to the Rosenblum lab for valuable feedback on the manuscript. Funding was provided by the National Science Foundation, the Herpetologist's League, the Philomathia Foundation and the Museum of Vertebrate Zoology. All animals were handled in accordance with New Mexico Department of Game and Fish Scientific Collecting Permit (authorization number 3184) and under the University of California, Berkeley, Institutional Animal Care and Use protocol #AUP-2014-11-6857.

Table 3.1. Lizard diet by arthropod taxa at study site (specific interdune) in summer 2015 (two years before onset of current study). Based off of dry mass of stomach contents from n = 40 lizards ; 16 *A. inornata*, 7 *H. maculata*, 17 *S. cowlesi*. Trophic position (TP) estimated with $\partial^{15}N$ isotope of taxa ($(\partial^{15}N_{consumer})$ relative to mean $\partial^{15}N$ plant isotope at study site ($\partial^{15}N_{basal}$) ; $TP = \lambda + (\partial^{15}N_{consumer} - \partial^{15}N_{basal}) / \Delta_n$; with Δ_n (fractionization) = 3.4%. Based off of Post 2002[16]. Stomach contents recovered through stomach flushing, see Chapter 2 for field and lab method details. Proportions do not include 'unknown' taxa (~23% of total stomach contents), which were mostly highly digested and/or soft bodied arthropods (e.g larvae, excluding Coleoptera larvae which were easier to identify). Not listed is vegetation, which is likely incidentally consumed and was 1.3% of stomach contents.

Taxa	Percent of diet	Mean TP	TP Range	TP Stdev
Araneae	2.5	2.54	2.26-3.22	0.59
Coleoptera	54.8	2.32	1.19 – 3.56	0.61
Diptera	1.2	2.01	1.38-2.58	0.60
Ephemeroptera	1.0	0.92	-	-
Formicidae	11.3	2.36	1.84 – 2.96	0.30
Hemiptera	20.2	2.54	2.01 – 3.50	0.41
Hymenoptera	2.1	2.99	2.9 – 3.1	0.17
Orthoptera	4.7	1.96	1.56 – 2.7	0.47

Table 3.2. Table on next page. Summary of the effect of treatment (C – control, P – partial fence, E – exclosure) on plants and arthropods. Results of Tukey HSD tests for treatment effects are shown if any comparison had a $p < 0.1$ (see other tables and main text for more specific p values). Blank cells indicate that data were not collected on a given date, and dashes indicate no comparisons had $p < 0.1$. Cell color corresponds with the directionality of effects – red indicates values in exclosures were lower, green indicates values in exclosures were higher, and yellow indicates results in C differed from P or E (possible fence effects). Value (lightness) indicates whether a given treatment differed from just one (lighter) or both other treatments (darker). Three cases where the partial treatment differed from the other treatments (pitfall Araneae across all dates, *E. trifurca* N, *Y. elata* N) are not colored. June 2017 data collected as baselines and are also not colored. See the main text and other figure captions for more details and interpretations.

Table 3.2. Caption on previous page.

		June 2017	All dates (post June 2017)	August 2017	November 2017	March 2018	June 2018	August 2018	June 2019
Pitfall traps	All	-------	C > E , P	C > E	-------	-------	P, C > E	P > E	-------
	Arachnida	-------	-------	-------	-------	-------	-------	-------	-------
	Araneae	-------	C > P > E	-------	-------	-------	C > E	-------	C > E, P
	Coleoptera	-------	C > E , P	C > E , P	-------	-------	P , C > E	P , C > E	-------
	Collembola	-------	C , P > E	-------	-------	-------	-------	-------	C > E
	Diptera	-------	-------	-------	-------	-------	-------	C > P	-------
	Formicidae	-------	C > E	-------	-------	-------	-------	P , C > E	-------
	Hemiptera	-------	-------	-------	-------	-------	-------	-------	-------
	Hymenoptera	-------	C > E	C > E	-------	-------	-------	-------	-------
Sticky traps	All	-------	-------	-------	-------	-------	-------	P , C > E	-------
	Araneae	-------	-------	-------	-------	-------	-------	-------	-------
	Cicadellidae	C , P > E	C > P	-------	-------	-------	-------	-------	C > E
	Coleoptera	-------	-------	-------	-------	-------	-------	-------	-------
	Diptera	-------	-------	-------	-------	-------	-------	P > E	-------
	Hemiptera	-------	-------	-------	-------	-------	-------	-------	-------
	Hymenoptera	C > E , P	-------	-------	-------	-------	-------	-------	P , C > E
	Neuroptera	-------	-------	-------	-------	-------	-------	-------	-------
	Thysanoptera	-------	-------	C > E	-------	-------	-------	-------	-------
Spider surveys	Counts						E > P, C	-------	E > P, C
	Web heights						-------	P , C > E	-------
Plant sampling	*A.angustifolia* N	P , C > E	-------				P > C		-------
	A.angustifolia R	-------	-------				-------		-------
	E. torreyana N	-------	P > E				P > E, C		P > E
	E. torreyana R	-------	E > P				-------		E > C
	F. jamesii N	-------	-------				-------		-------
	F. jamesii R	-------	-------				-------		-------
	P. arenaria N	-------	-------				-------		-------
	P. arenaria R	-------	-------				-------		-------
	S. airoides N	-------	-------				-------		-------
	S. airoides R	-------	-------				-------		-------
	Y. elata N	P > E	-------				P > E , C		-------
	Y. elata R	-------	-------				-------		-------
***S, airoides* Quadrats**	Point intercept	-------	-------	-------			-------	-------	-------
	Panicle counts	-------	P , E > C	P , E > C			P , E > C	E > C	E > C
***P. arenaria* focal**	Reproduction	-------	-------	-------			-------	-------	-------
	Herbivory	-------	-------	-------	C > E		-------	-------	E > P, C

Table 3.3. Results of GLMMs (family = Poisson) exploring the effect of treatment (C – control, P – partial fence, E – exclosure) on arthropod pitfall captures. The F / p column includes F values with asterisks indicating p values (with * indicating p <0.1, ** indicating p < 0.05, *** indicating p < 0.01 and **** indicating p < 0.001). The HSD column denotes the results of Tukey HSD post-hoc tests, with relationships between treatments shown if p < 0.1, and asterisks indicating level. 'All dates' models include all post June 2017 data and include Treatment, Date and Date*Treatment as fixed effects, and Array, Plot and Trap as random effects. Models were run for each taxa / data combination, with Treatment as fixed effect and Array and Plot as random effects. June 2017 data were collected at the very beginning of the experiment to serve as baselines. The 'All' model for June 2018 was analyzed under a gaussian distribution and array was dropped as a random effect, which did not shift conclusions but resulted in better model validation.

	All dates		Jun 2017		Aug 2017		Nov 2017		Mar 2018		Jun 2018		Aug 2018		Jun 2019	
	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD
All			-	-	4.3	C > E**	4.3	-	1.3	-	5.4**	C > E**	5.0*	P > E***	0.2	-
Treatment	9.8***	C > E****										P > E**				
Date	827.8****	C > P***														
*Date*Treatment*	10.1**															
Arachnida			2.3	-	2.0	-	2.7	-	0.2	-	0.6	-	0.03	-	1.9	-
Treatment	0.9	-														
Date	146.8****															
*Date*Treatment*	2.9															
Araneae			1.6	-	1.9	-	0.4	-	1.1	-	3.7*	C > E**	0.3	-	8.5***	C > E****
Treatment	7.8**	C > P*														C > P**
Date	20.4****	P > E*														
*Date*Treatment*	2.2**															
Coleoptera			0.1	-	10.5****	C > E****	1.5	-	0.3	-	6.4****	C > E****	5.2**	C > E***	0.9	-
Treatment	13.6****	C > E****				C > P**						P > E***		P > E*		
Date	28.6****	C > P**														
*Date*Treatment*	3.8**															
Collembola			0.1	-	0.8	-	0.2	-	0.5	-	0.1	-	2.4	-	2.9	C > E**
Treatment	0.3	C > E**														
Date	2264.4****	P > E***														
*Date*Treatment*	26.4															
Diptera			0.2	-	1.1	-	2.2	-	1.1	-	1.6	-	2.9	C > P*	1.6	-
Treatment	2.5	-														
Date	91.6****															
*Date*Treatment*	1.3															
Formicidae			0.4	-	2.1	-	0.9	-	0.8	-	1.4	-	12.5***	C > E***	0.6	-
Treatment	3.1*	C > E*												P >E****		
Date	499.8****															
*Date*Treatment*	20.9**															
Hemiptera			0.2	-	1.2	-	0.6	-	0.7	-	0.8	-	0.1	-	0.5	-
Treatment	1.9	-														
Date	7.8****															
*Date*Treatment*	0.8															
Hymenoptera			1.8	-	3.4*	C > E**	0.4	-	1.9	-	0.7	-	0.8	-	0.1	-
Treatment	1.9	C>E**														
Date	14.9****															
*Date*Treatment*	1.1															

Table 3.4. Results of GLMMs (family = poisson) exploring the effect of treatment (C – control, P – partial fence, E – exclosure) on arthropod sticky trap captures. The F / p column includes F values with asterisks indicating p values (with * indicating p <0.1, ** indicating p < 0.05, *** indicating p < 0.01 and **** indicating p < 0.001). The HSD column denotes the results of Tukey HSD post-hoc tests, with relationships between treatments shown if p < 0.1, and asterisks indicating level. 'All dates' models include all post June 2017 data and include Treatment, Date and Date*Treatment as fixed effects, and Array, Plot and Trap as random effects. Models were run for each taxa / data combination, with Treatment as fixed effect and Array and Plot as random effects. June 2017 data were collected at the very beginning of the experiment to serve as baselines. Captures were very low for Araneae (~0.24/trap) and Neureoptera (0.26/trap), and while they did pass model validation these results may not be ecologically relevant.

	All dates		Jun 2017		Aug 2017		Nov 2017		Mar 2018		Jun 2018		Aug 2018		Jun 2019	
	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD	F / p	HSD
All			1.3	-	0.5	-	0.4	-	0.6	-	2.1	-	3.7	C > E** P > E**	0.7	-
Treatment	1.8	-														
Date	449.9****															
*Date*Treatment*	3.7															
Araneae			0.01	-	0.03	-	0.1	-	0	-	0.001	-	0.2	-	0.6	-
Treatment	0.04	-														
Date	19.9****															
*Date*Treatment*	0.3															
Cicadellidae			3.5	C > E* P > E*	1.9	-	0.6	-	0.5	-	0.5	-	0.4	-	2.4*	C > E*
Treatment	2.8*	C > P*														
Date	50.8****															
*Date*Treatment*	0.6															
Coleoptera			0.5	-	0.9	-	0.3	-	0.1	-	0.8	-	0.5	-	0.6	-
Treatment	3.8	-														
Date	13.6****															
*Date*Treatment*	0.4															
Diptera			1.9	-	0.5	-	1.2	-	0.4	-	1.9	-	2.7	P > E*	0.02	-
Treatment	1.4	-														
Date	256.5****															
*Date*Treatment*	2.4															
Hemiptera			1.3	-	0.2	-	0	-	1.3	-	0.9	-	0.4	-	0.6	-
Treatment	0.9															
Date	12.3****															
*Date*Treatment*	1.2															
Hymenoptera			5.6**	C > E*** C > P**	0.3	-	0.5	-	2.2	-	1.4	-	0.5	-	3.3	C > E**** P > E****
Treatment	2.1	-														
Date	51.1****															
*Date*Treatment*	4.7**															
Neuroptera			0.6	-	1.8	-	-	-	0	-	0	-	0.2	-	0.1	-
Treatment	0.3	-														
Date	2.8****															
*Date*Treatment*	0.4															
Thysanoptera			0.2	-	2.6	C > E*	2.5	-	0.6	-	0.4	-	0.2	-	1.1	-
Treatment	1.3	-														
Date	125.4****															
*Date*Treatment*	3.6															

Table 3.5. Results of GLMMs exploring the effect of treatment (C – control, P – partial fence, E – exclosure) on plant species counts (N ; family = poisson) and proportion reproductive (R ; family = binomial or gaussian). The F / p column includes F values with asterisks indicating p values (with * indicating p <0.1, ** indicating p < 0.05, *** indicating p < 0.01 and **** indicating p < 0.001). The HSD column denotes the results of Tukey HSD post-hoc tests, with relationships between treatments shown if p < 0.1, and asterisks indicating level. 'All dates' models include all post June 2017 data and include Treatment, Date and Date*Treatment as fixed effects, and Array and Plot as random effects. Models were run for each taxa / data combination, with Treatment as fixed effect and Array and Plot as random effects. June 2017 data were collected at the very beginning of the experiment to serve as baselines. Counts were relatively low for *Y. elata* so while these models were validated, they may not be ecologically relevant. Dashes indicate cases where data were not collected (June 2017 *S. airoides* reproduction, see repeated measures quadrats for baselines) or where there was no reproduction (June 2019 *A. angustifolia* and June 2018+2019 *Y. elata*).

	All dates (post June 2017)							June 2017			June 2018			June 2019		
	Treatment			Date		Date*Treatment										
	F	p	HSD	F	p	F	p	F	p	HSD	F	p	HSD	F	p	HSD
A. angustifolia										P > E**						
N	0.95	0.49	-	15.42	0.01	0.98	0.26	9.49	0.11	C > E****	4.98	0.28	C > P***	0.11	0.97	-
R	0.19	0.84	-	2.66	0.33	0.19	0.84	0.11	0.89	-	0.28	0.76	-	-	-	-
E. torreyana													P >E****			
N	3.2	0.25	P > E**	0.09	0.50	0.83	0.02	1.69	0.41	-	8.72	0.11	P > C**	3.58	0.47	P > E**
R	2.91	0.09	E > P*	0.02	0.88	1.85	0.19	0.11	0.90	-	1.95	0.18	-	3.85	0.05	E > C**
F. jamesii																
N	0.14	0.86	-	0.93	0.17	1.09	0.17	11.81	0.48	-	2.58	0.66	-	0.37	0.95	-
R	0.28	0.76	-	0.18	0.68	0.03	0.97	0.79	0.24	-	0.12	0.89	-	0.49	0.63	-
P. arenaria																
N	0.98	0.39	-	5.54	0.06	0.43	0.87	2.05	0.71	-	5.58	0.32	-	2.94	0.49	-
R	0.18	0.84	-	0.04	0.84	0.37	0.69	0.49	0.63	-	0.24	0.79	-	0.19	0.83	-
S. airoides																
N	0.27	0.92	-	18.9	<0.001	0.37	0.77	1.95	0.73	-	0.13	0.98	-	1.46	0.84	-
R	0.09	0.92	-	38.88	<0.001	0.24	0.79	-	-	-	0.14	0.87	-	0.23	0.80	-
Y. elata													P > C*			
N	1.76	0.25	-	1.27	0.18	0.14	0.51	4.53	0.23	P > E**	4.62	0.20	P > E**	2.24	0.38	-
R	0.12	0.89	-	3.28	0.09	0.12	0.88	0.72	0.53	-	-	-	-	0.11	0.89	-

Fig 3.1. Representative experimental array, including lizard exclosure (foreground), partial fence treatment (to right) and then control plot (far right)

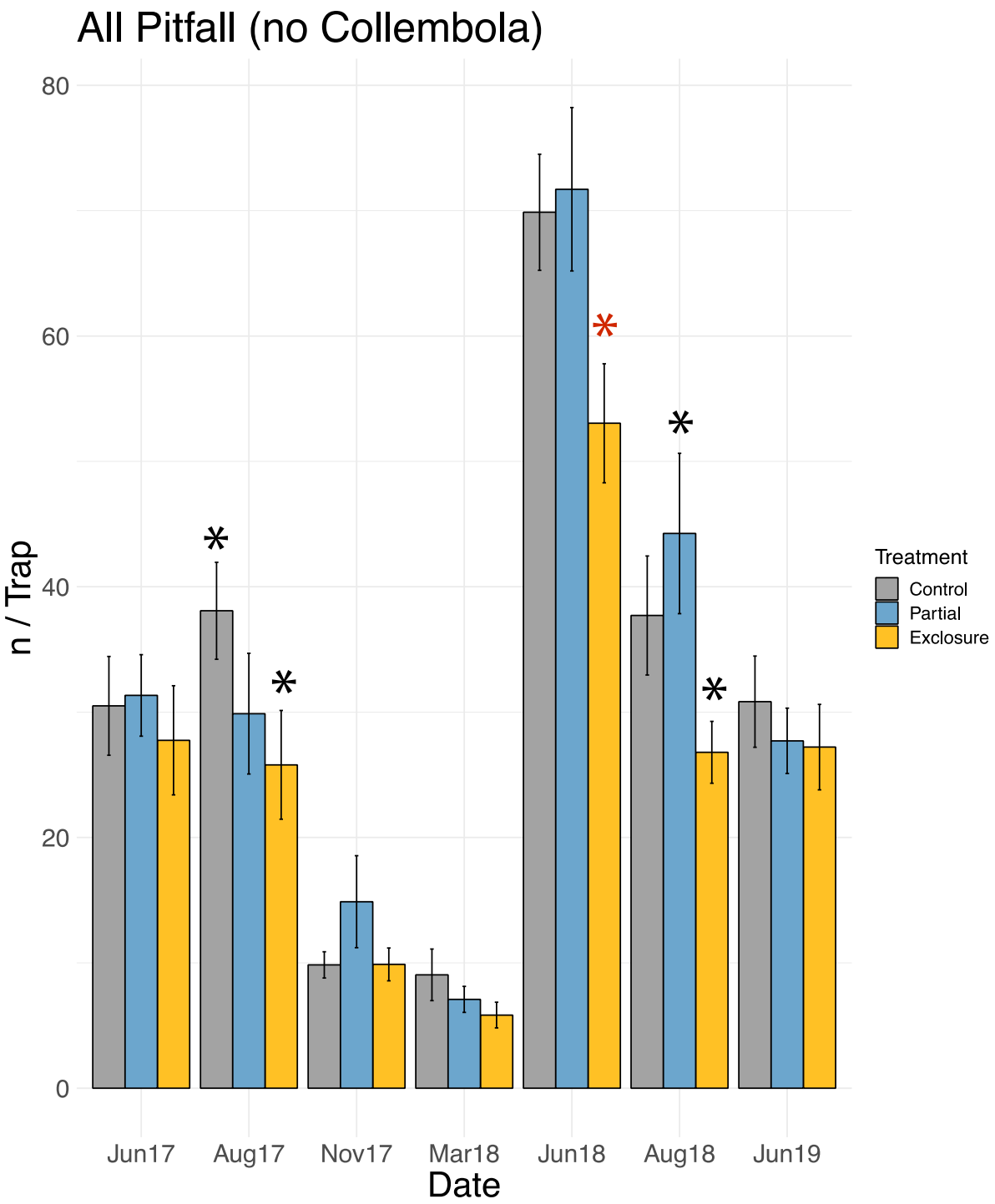

Fig 3.2. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

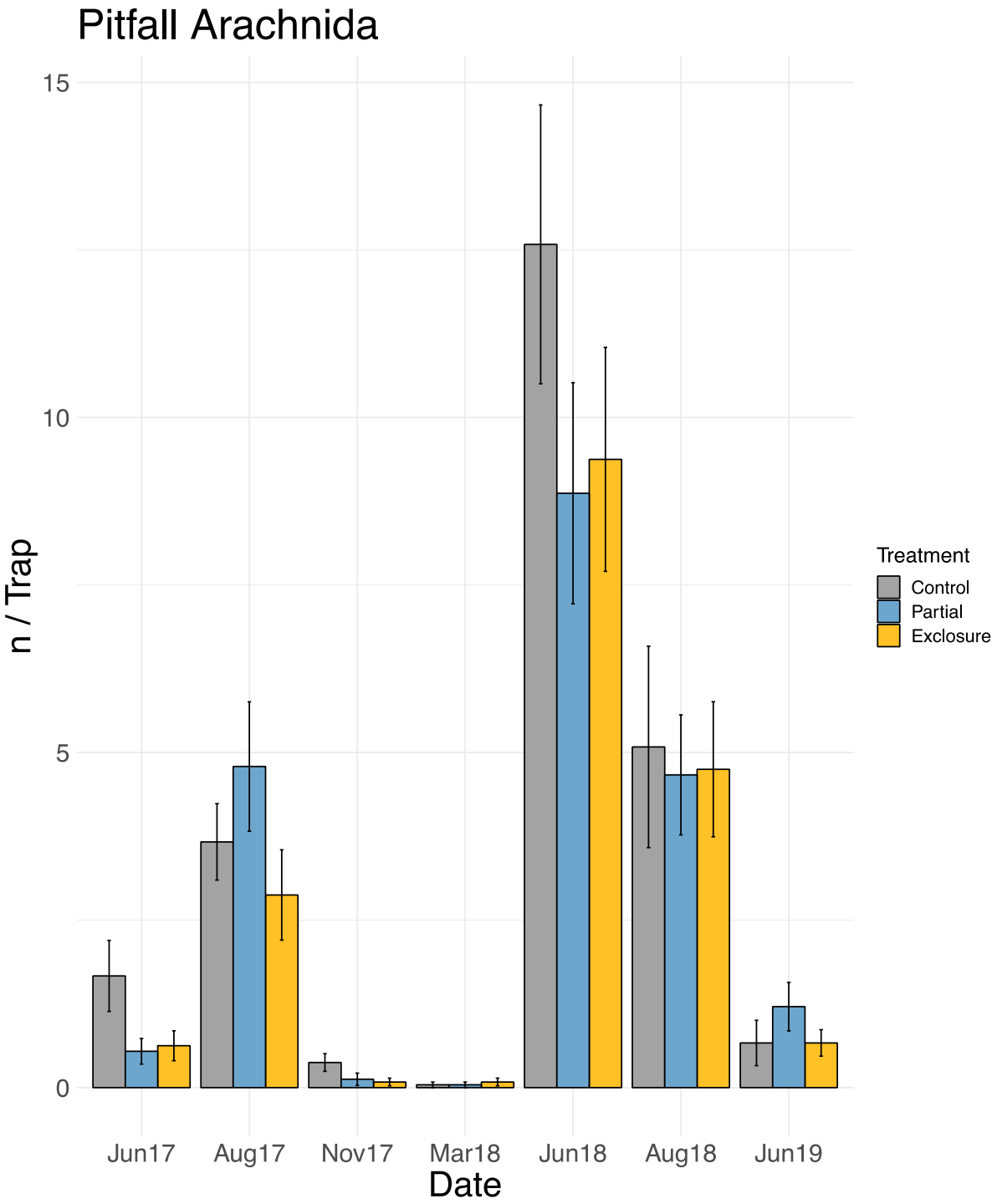

Fig 3.3. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

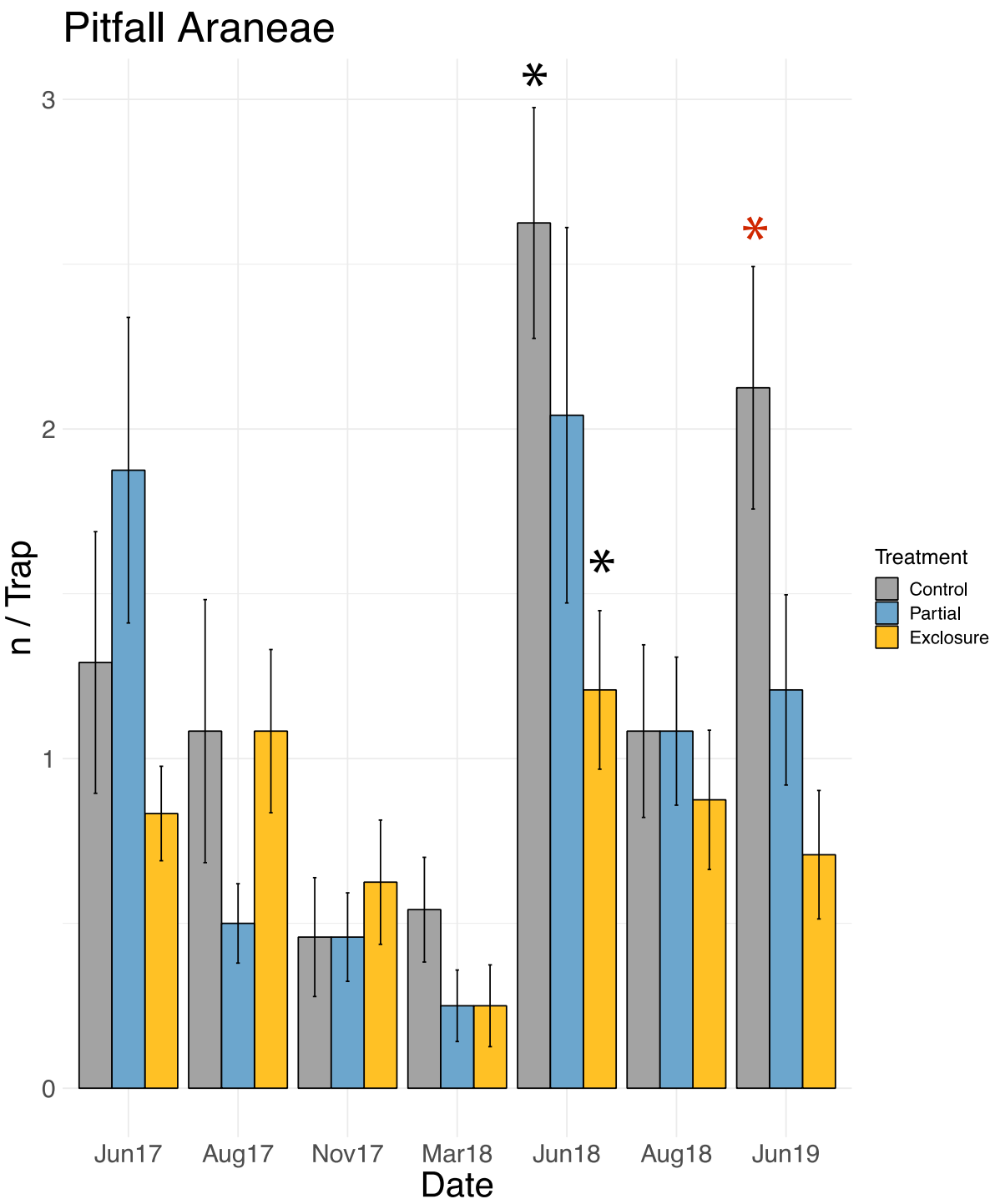

Fig 3.4. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

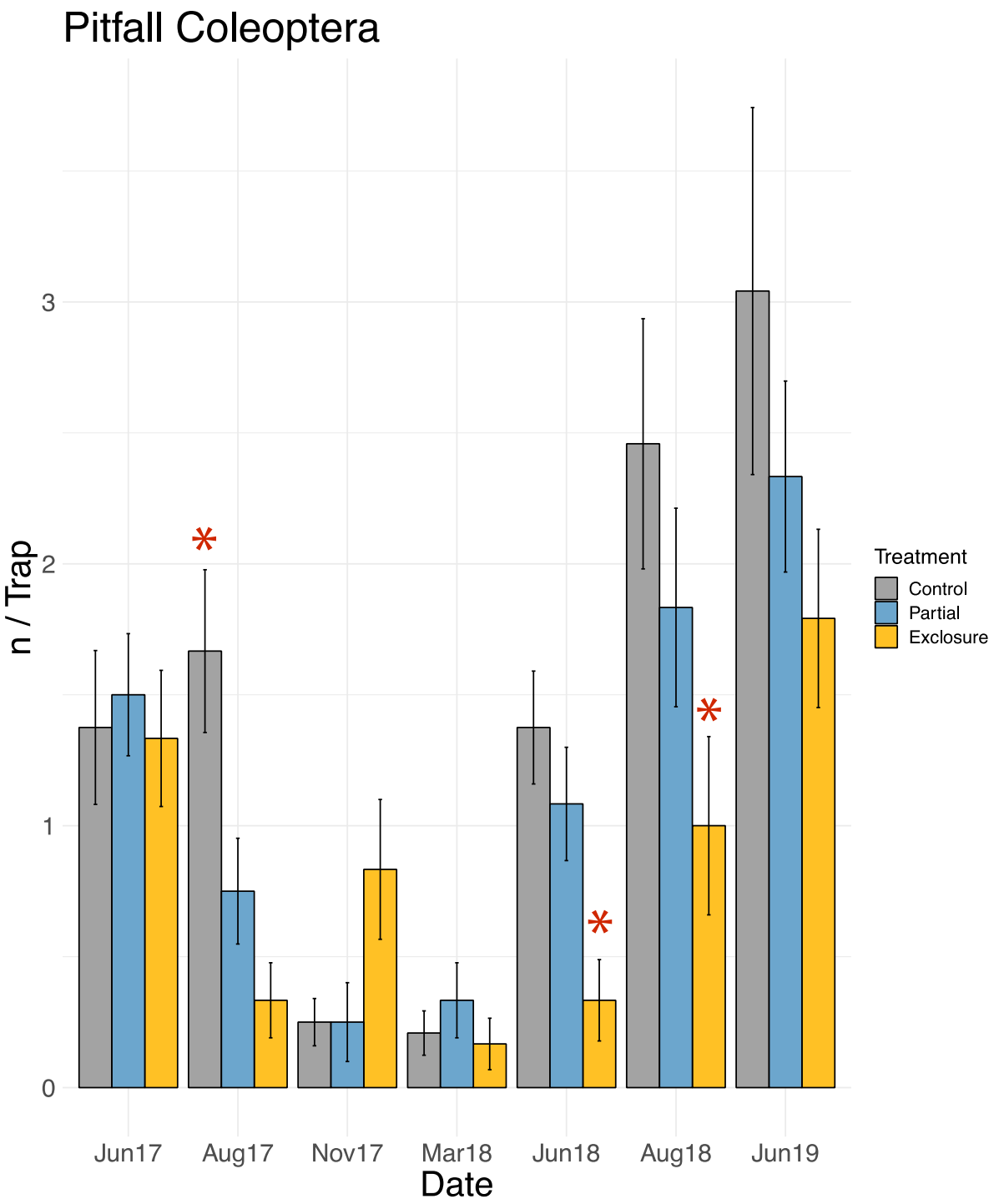

Fig 3.5. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

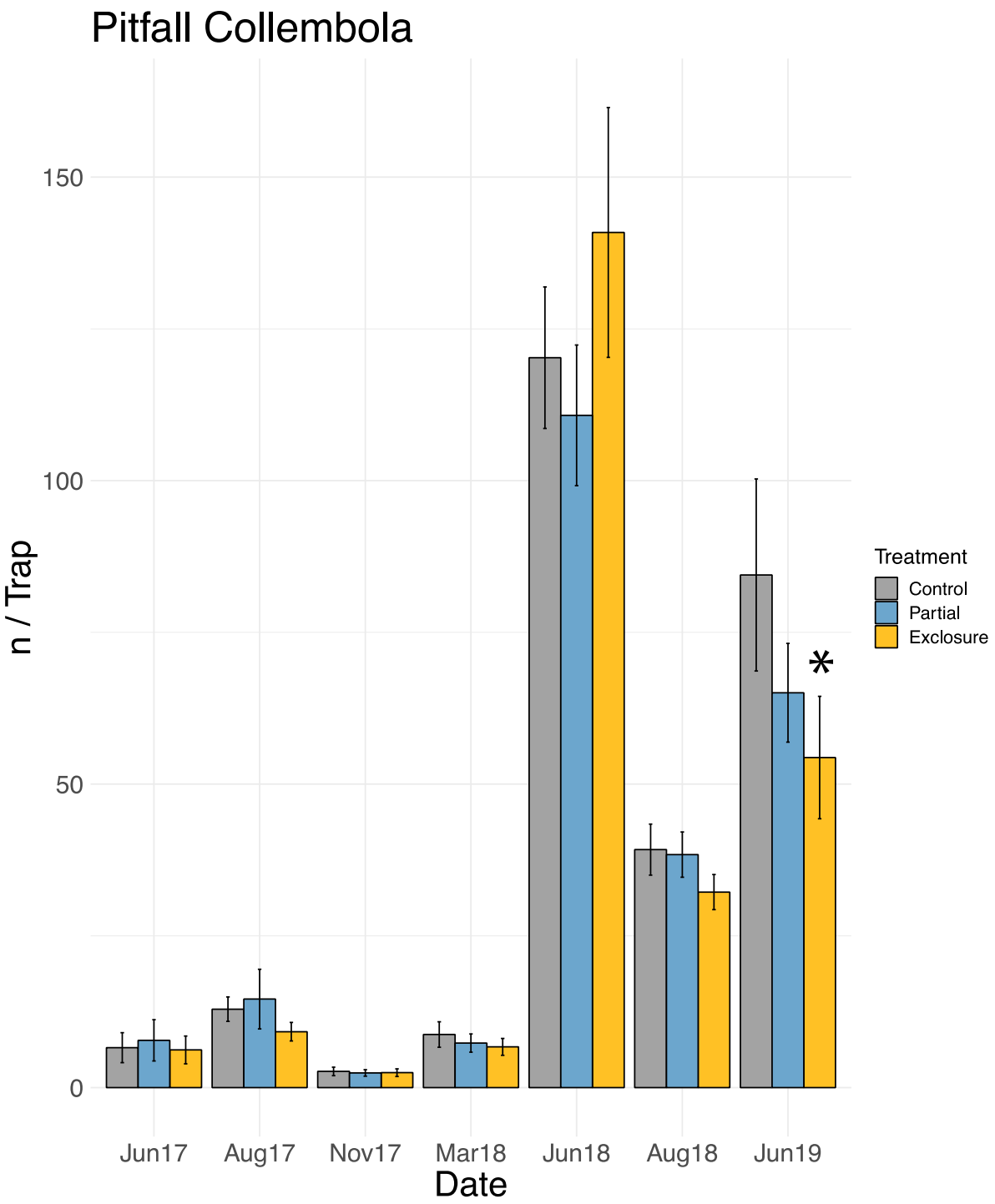

Fig 3.6. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

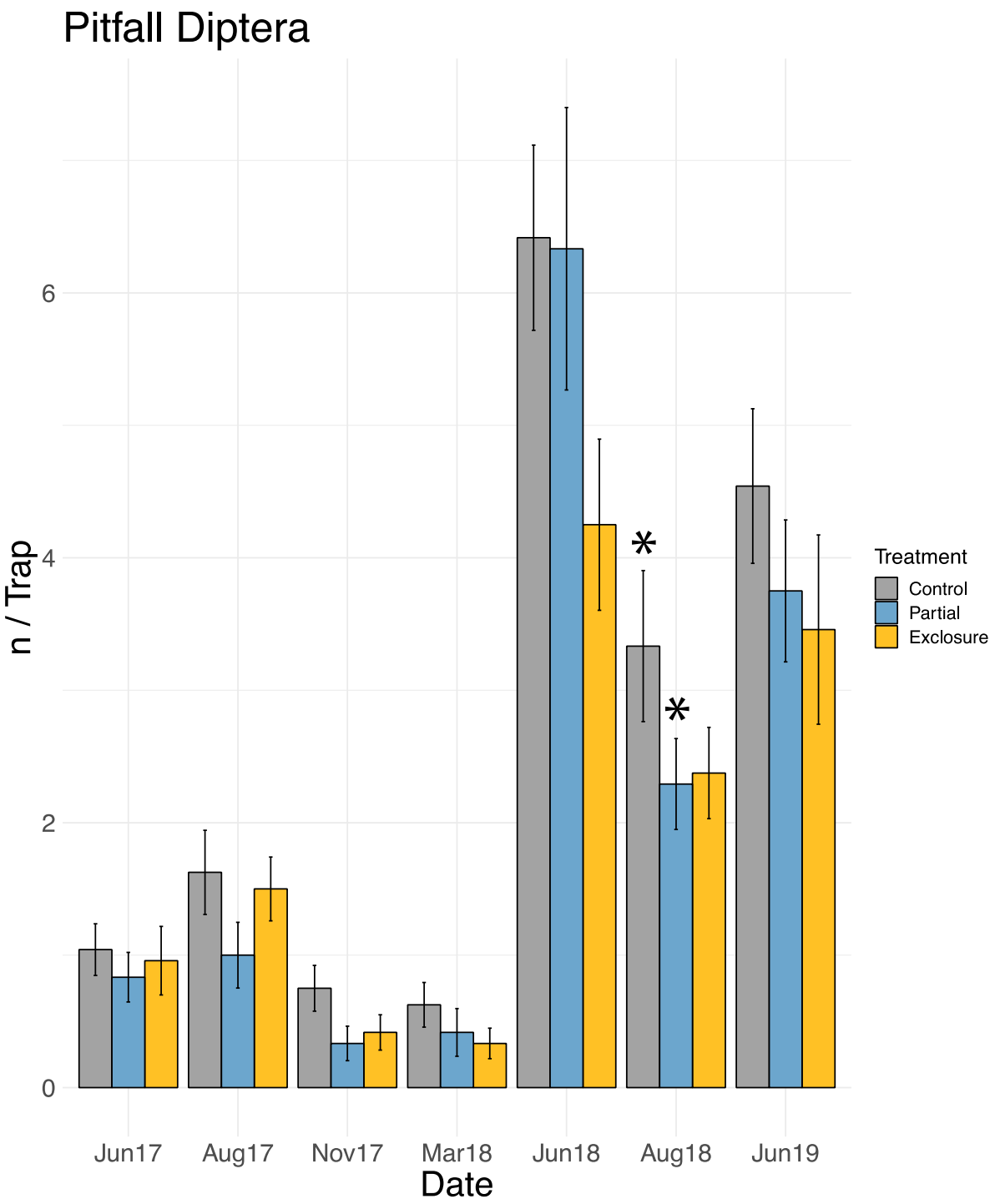

Fig 3.7. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

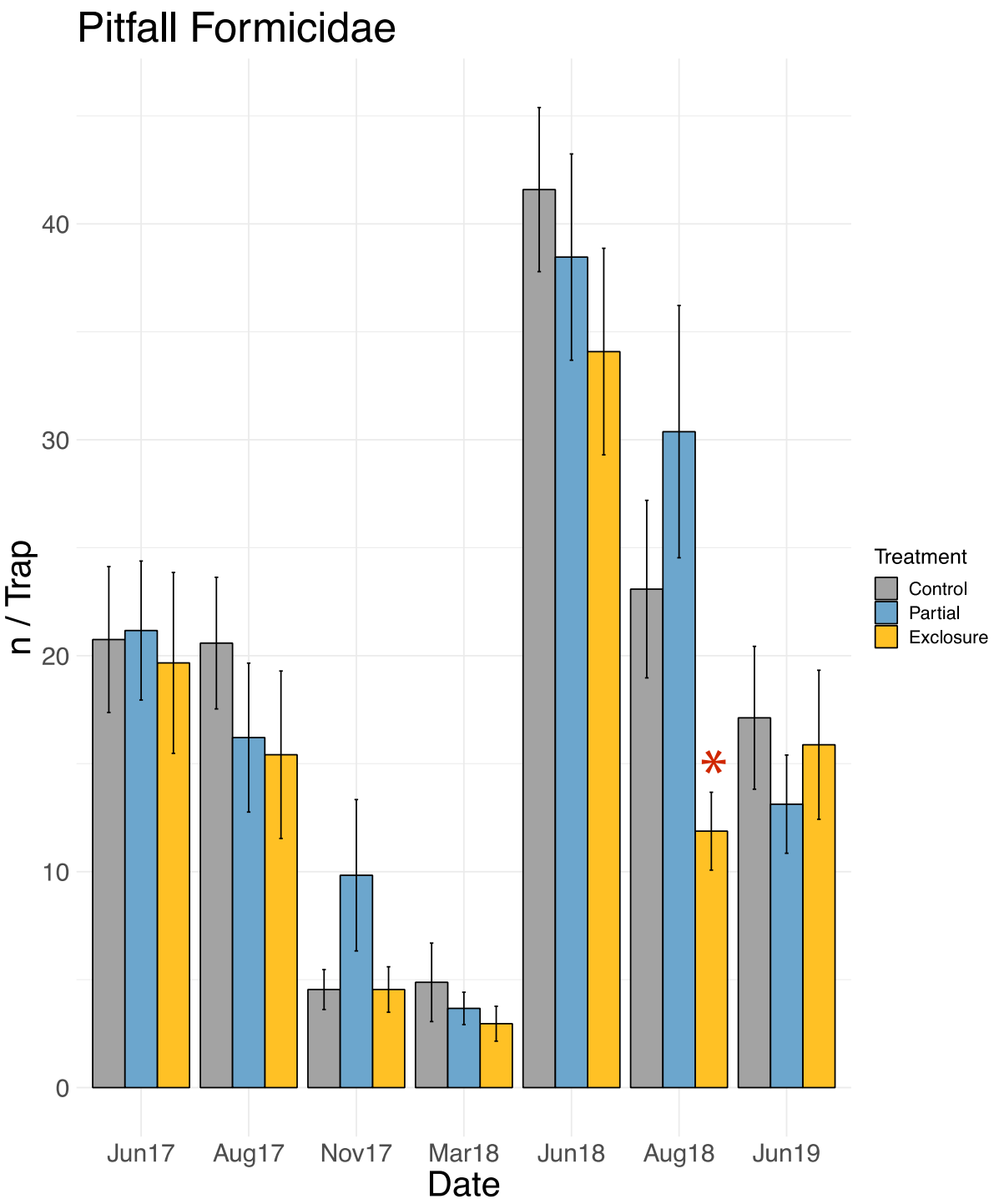

Fig 3.8. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

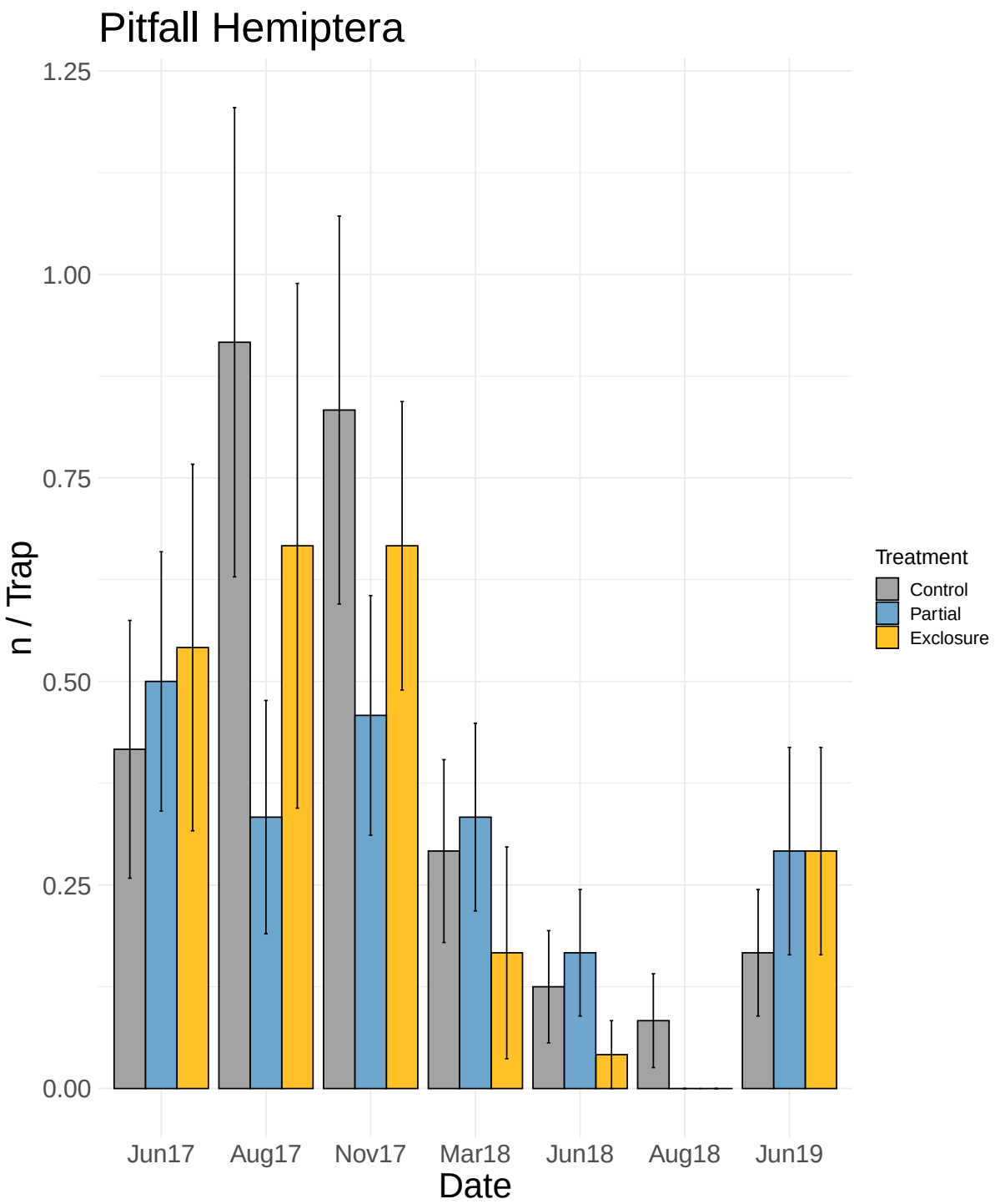

Fig 3.9. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

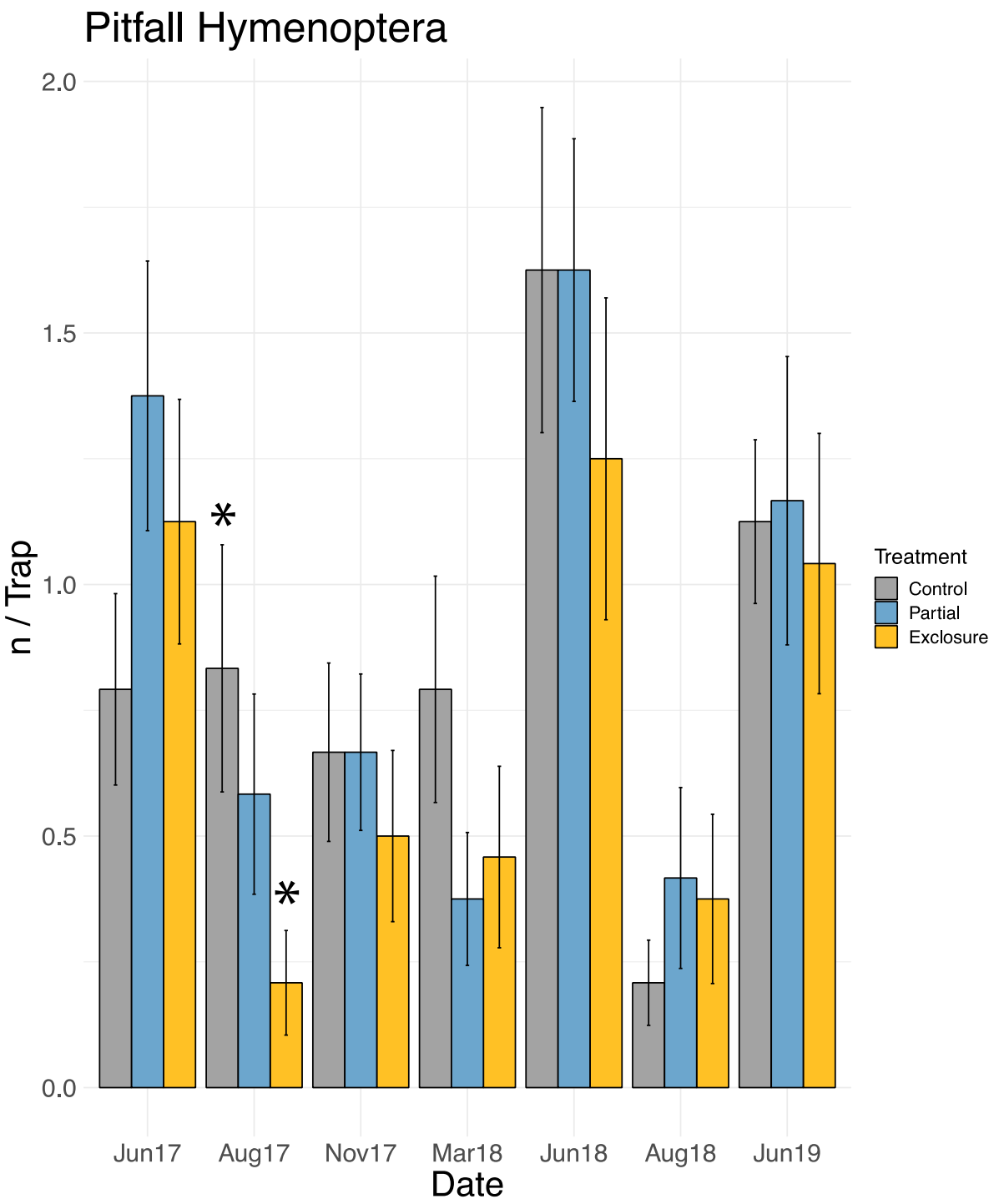

Fig 3.10. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.3 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

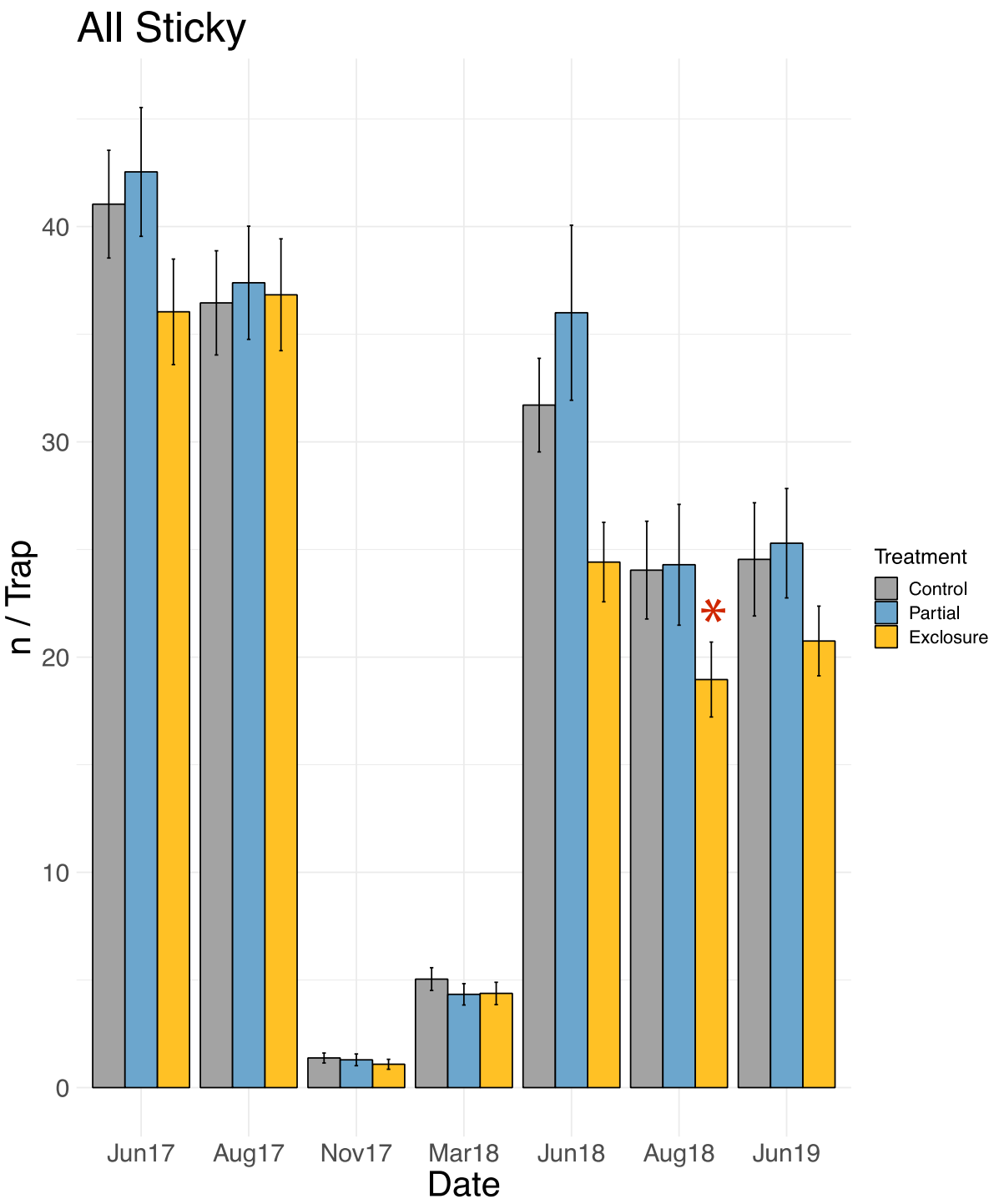

Fig 3.11. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

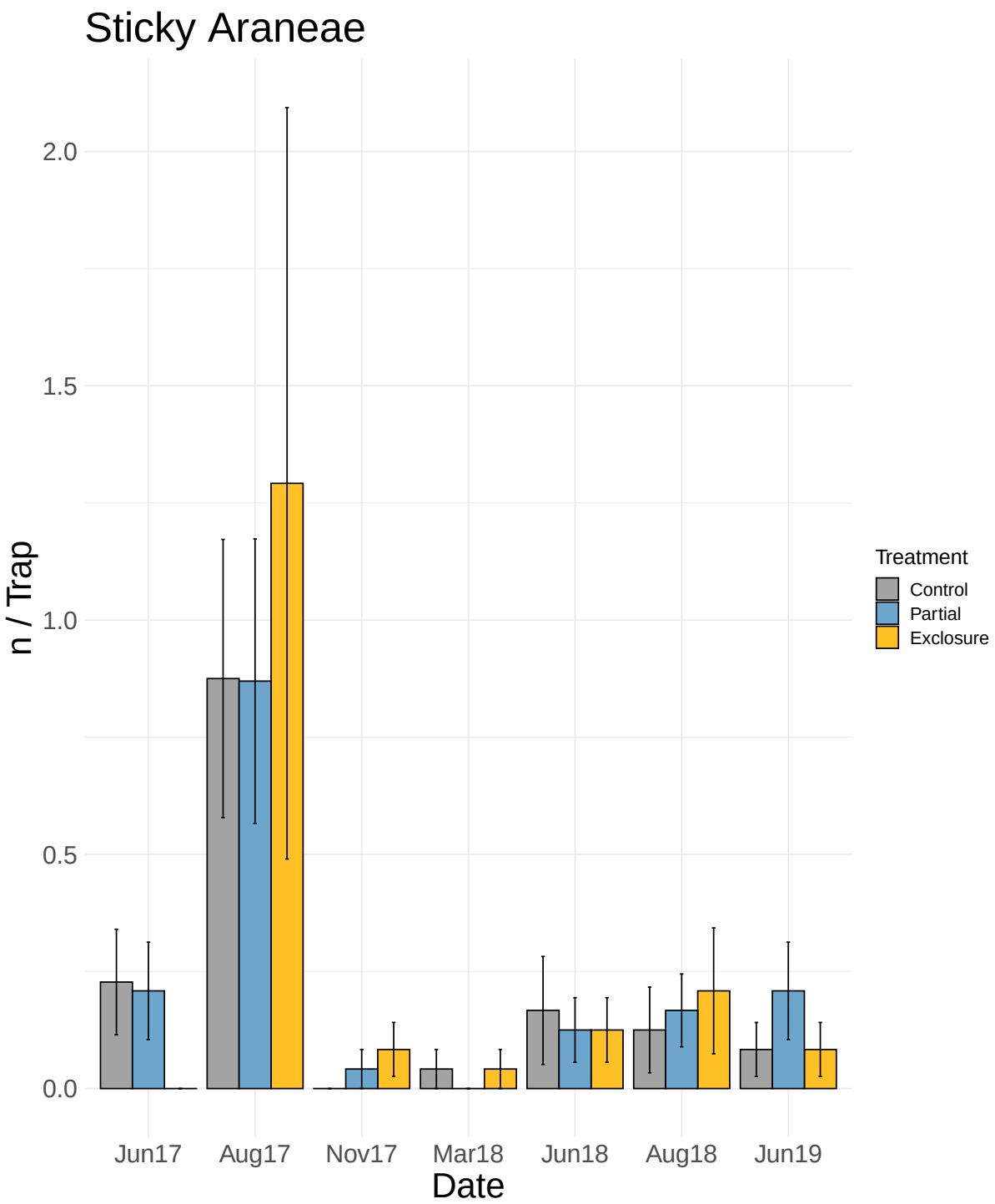

Fig 3.12. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

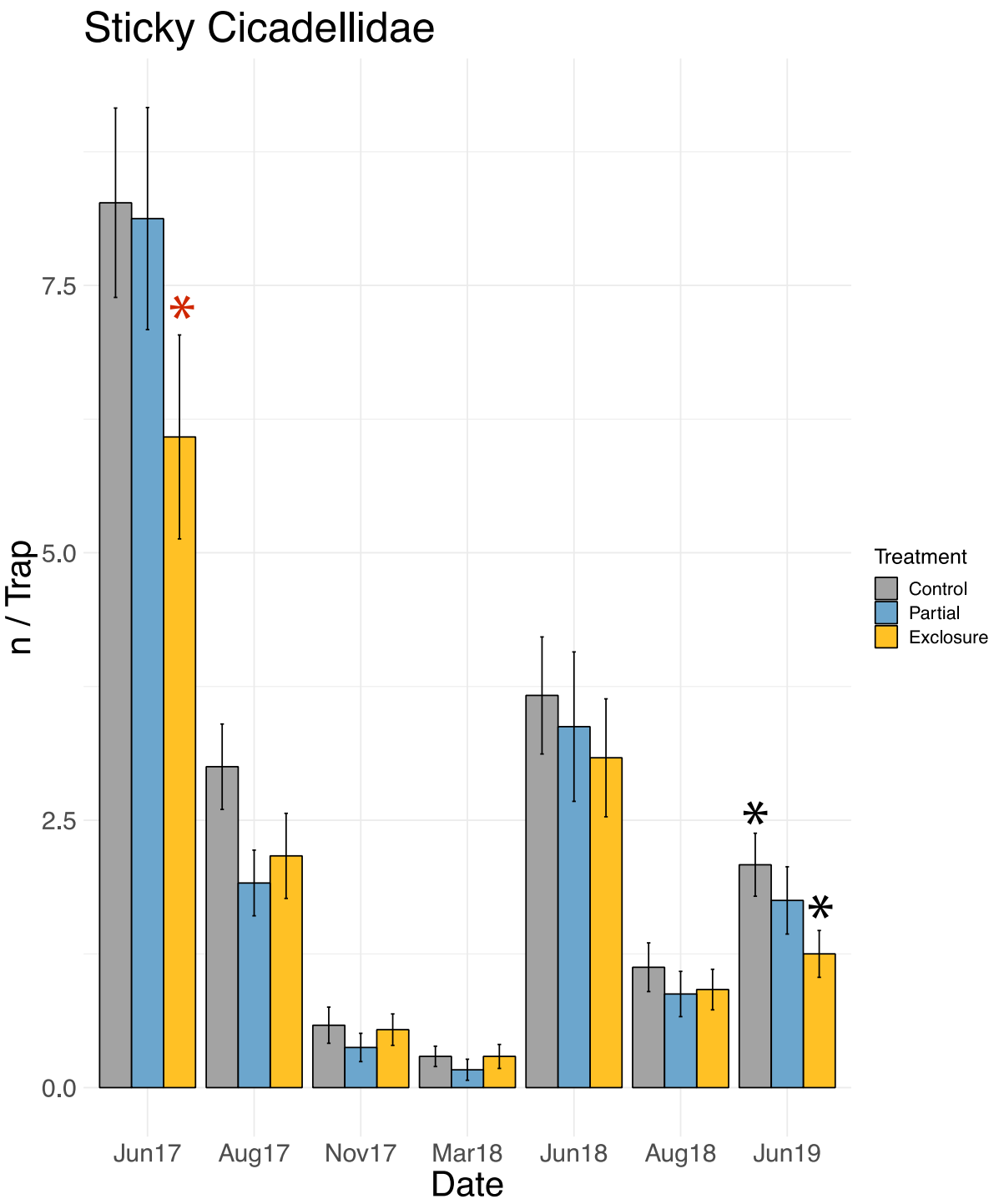

Fig 3.13. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

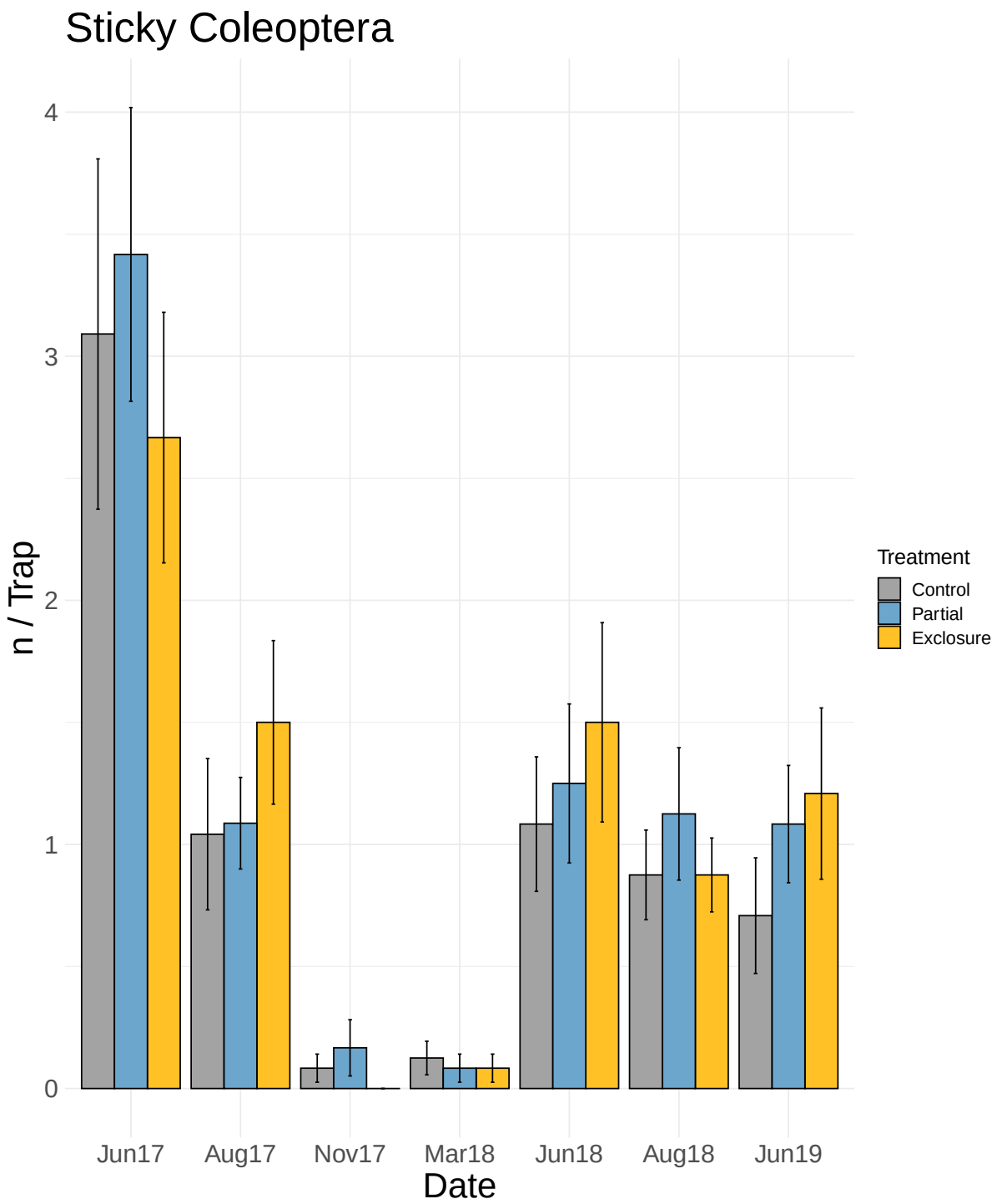

Fig 3.14. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

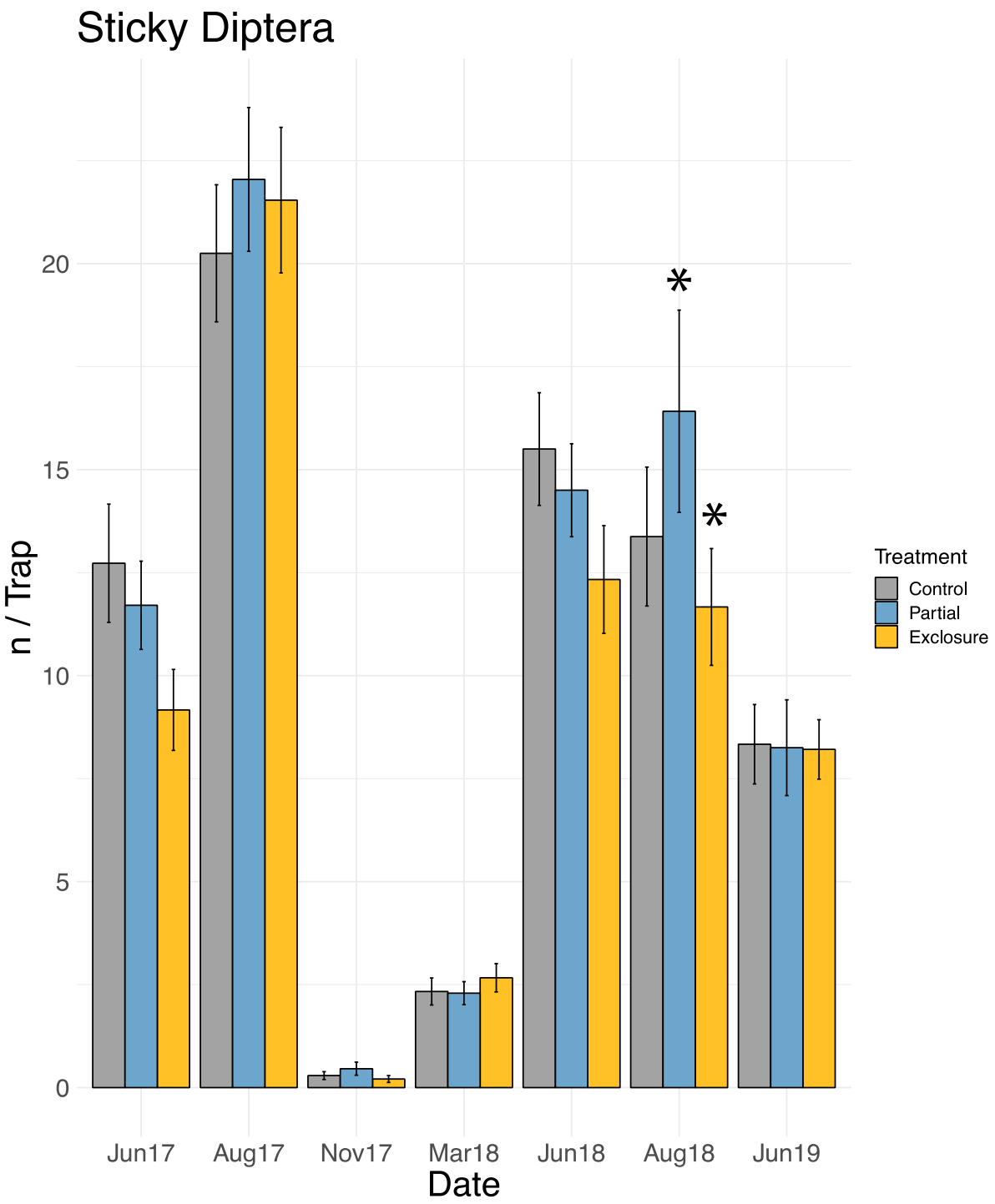

Fig 3.15. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

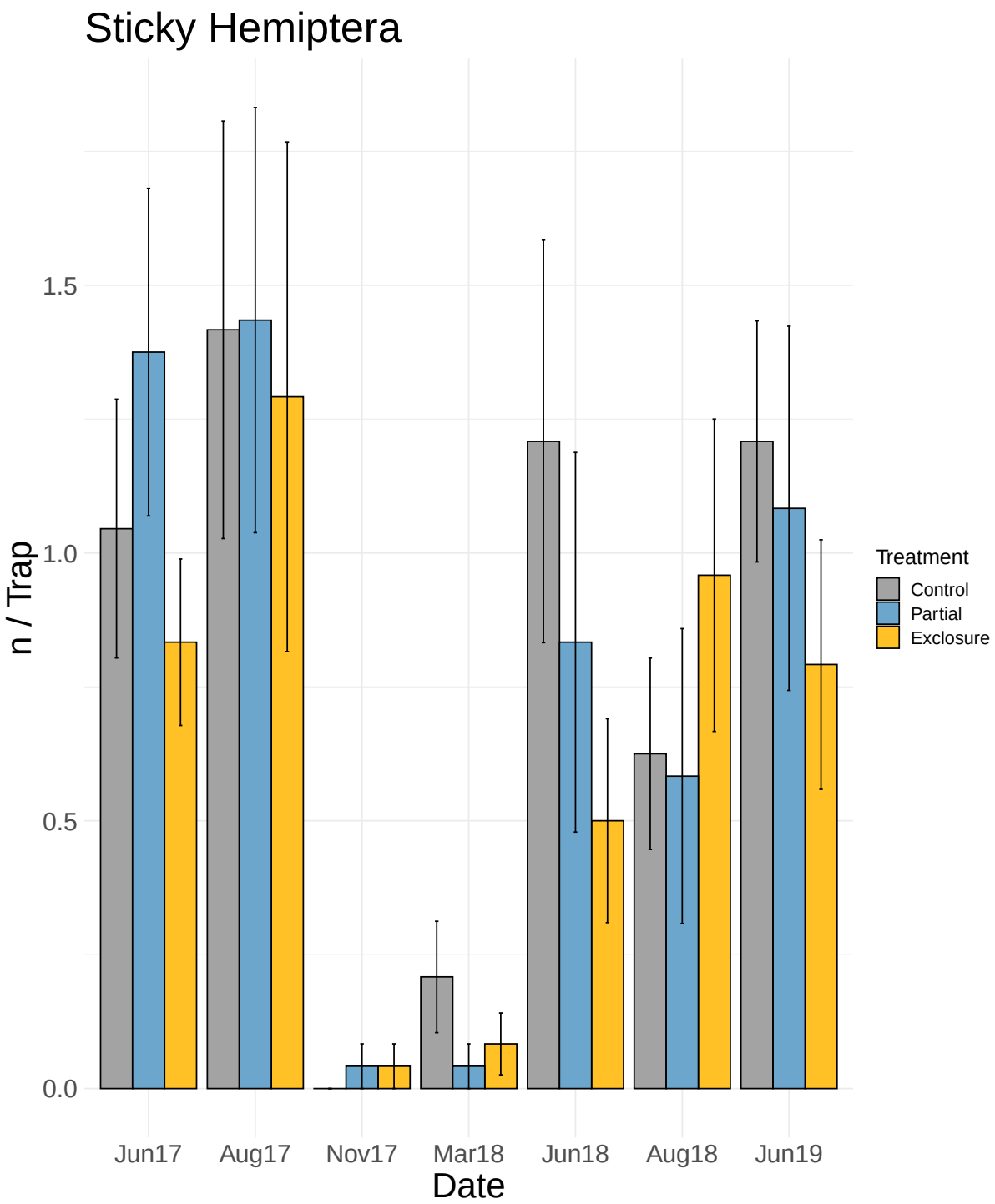

Fig 3.16. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

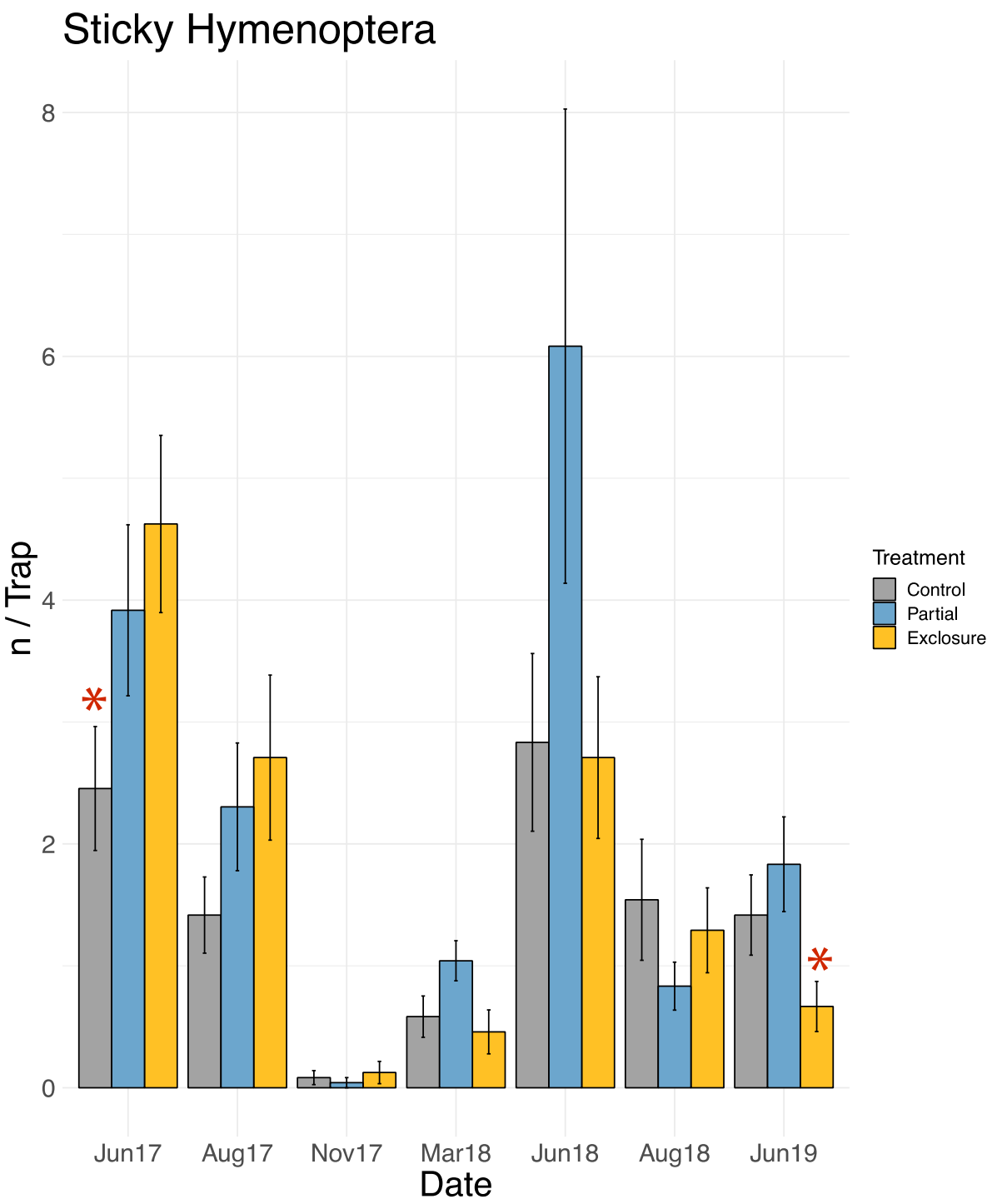

Fig 3.17. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

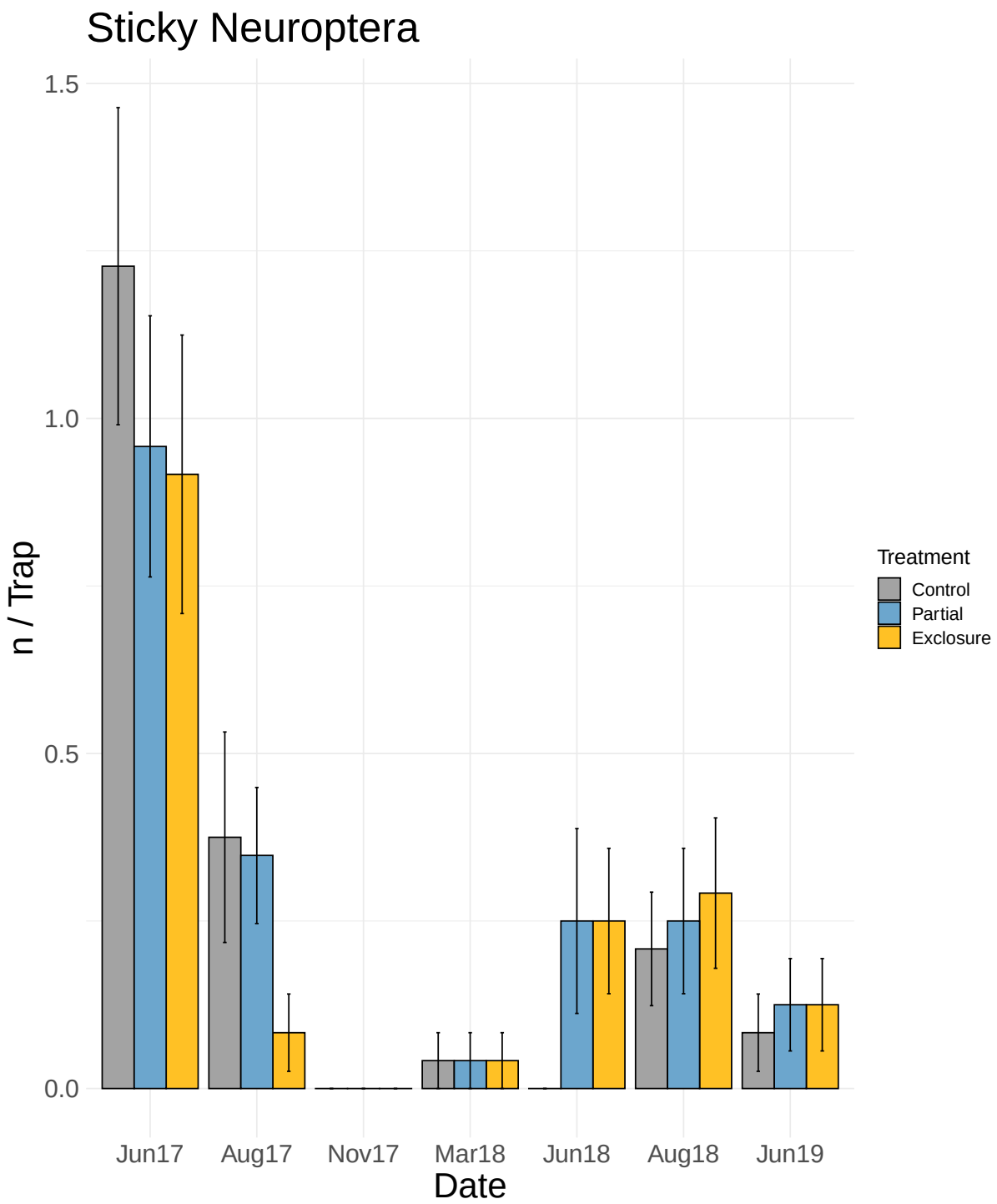

Fig 3.18. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

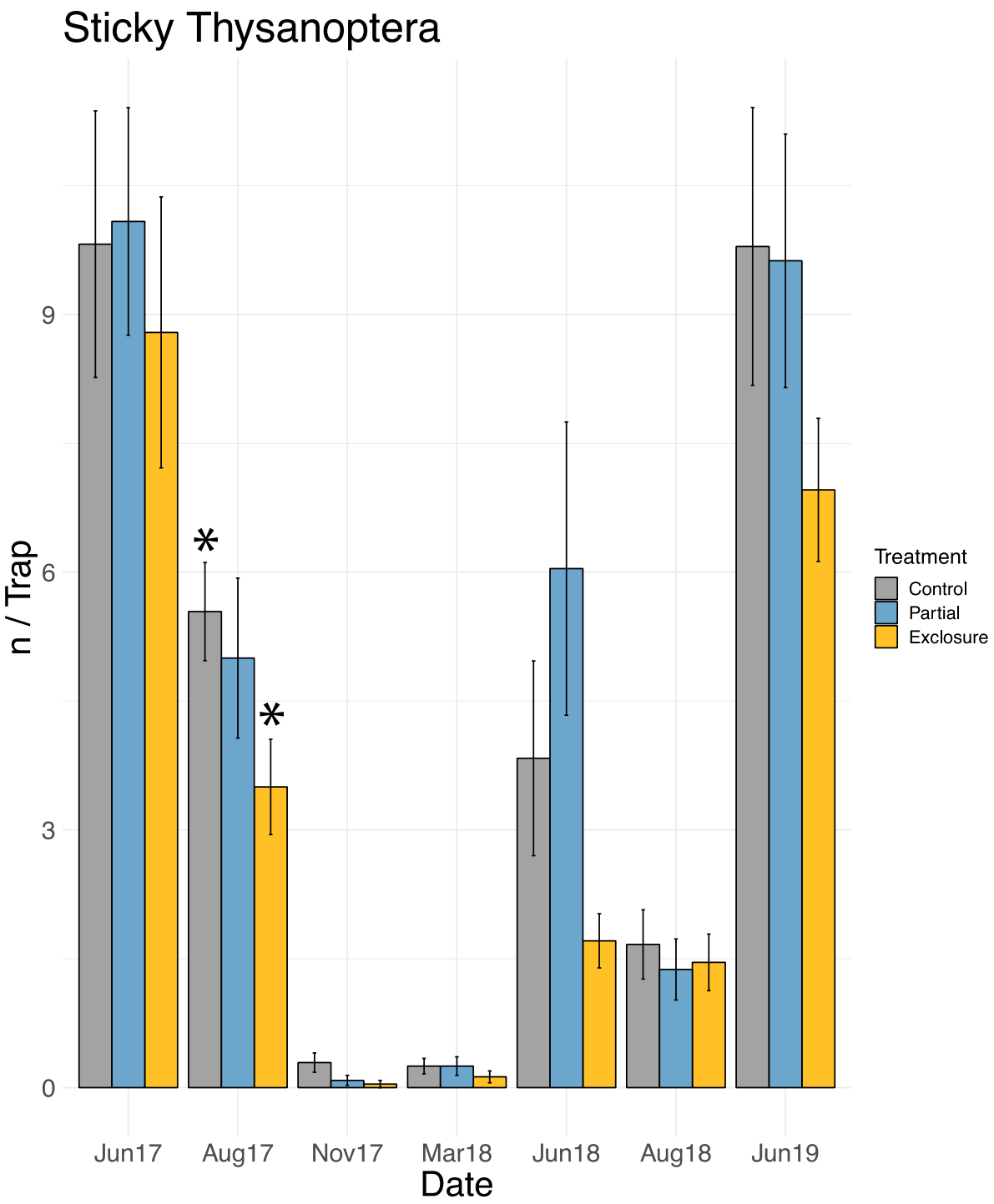

Fig 3.19. Mean captures per trap by date and treatment. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.4 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected 1 week after fence construction as baseline data.

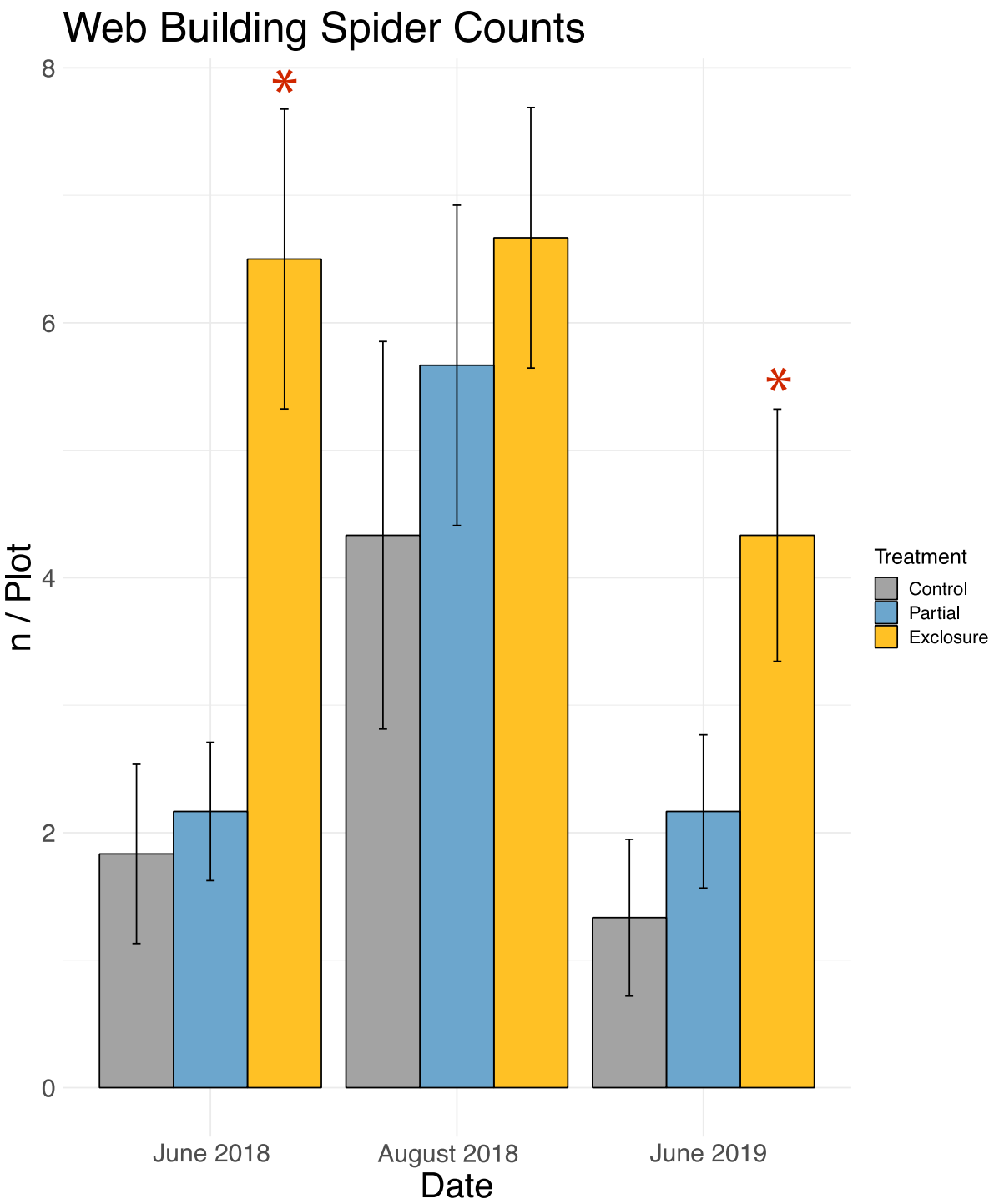

Fig 3.20. Mean web building spiders per plot by treatment and date. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. Surveys were initiated in June 2018. Spiders were counted in time and area constrained surveys, see main text for details.

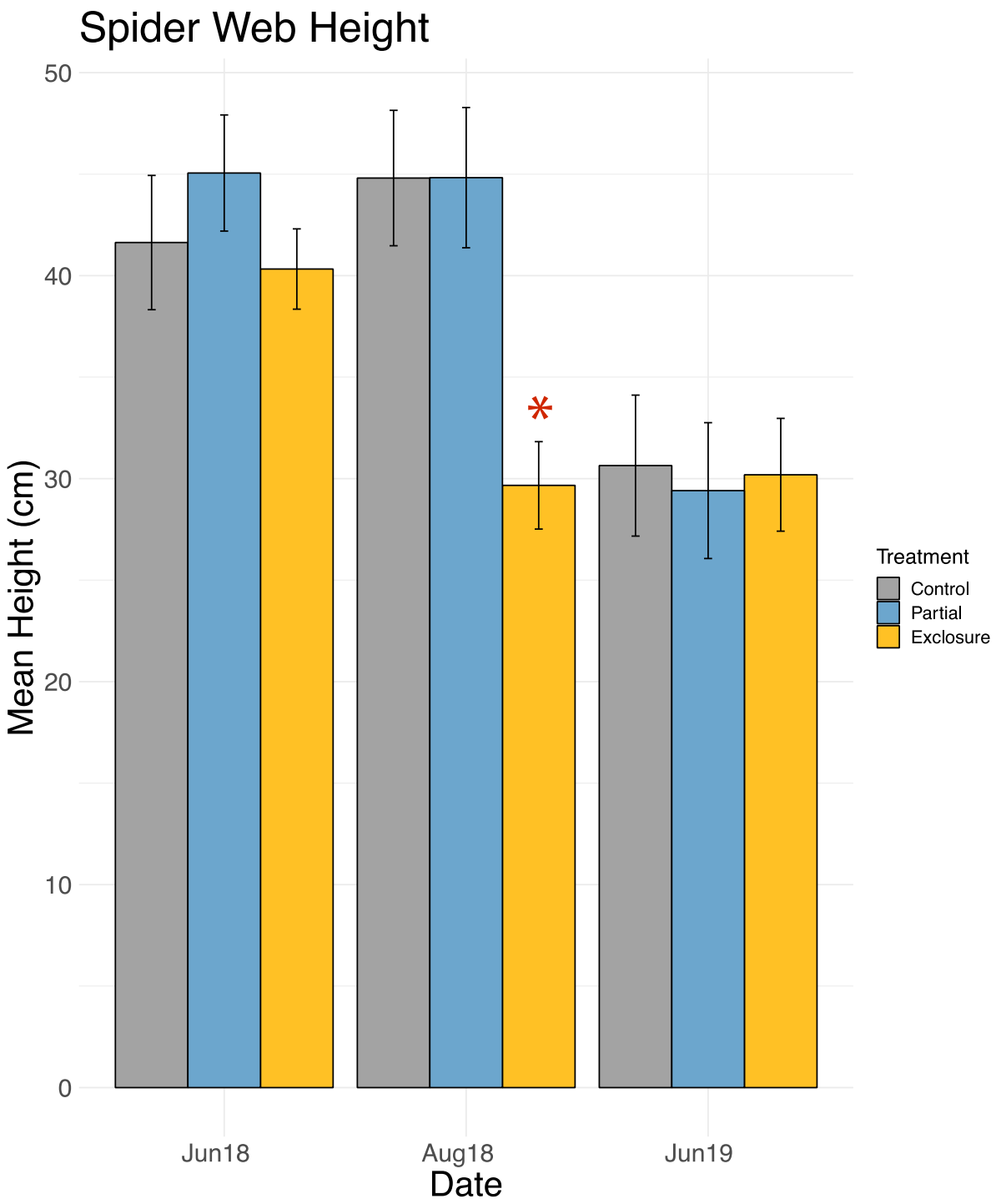

Fig 3.21. Mean spider web height (lowest point of frame thread) by treatment and date. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. Surveys were initiated in June 2018. Webs were counted in time and area constrained surveys, see main text for details.

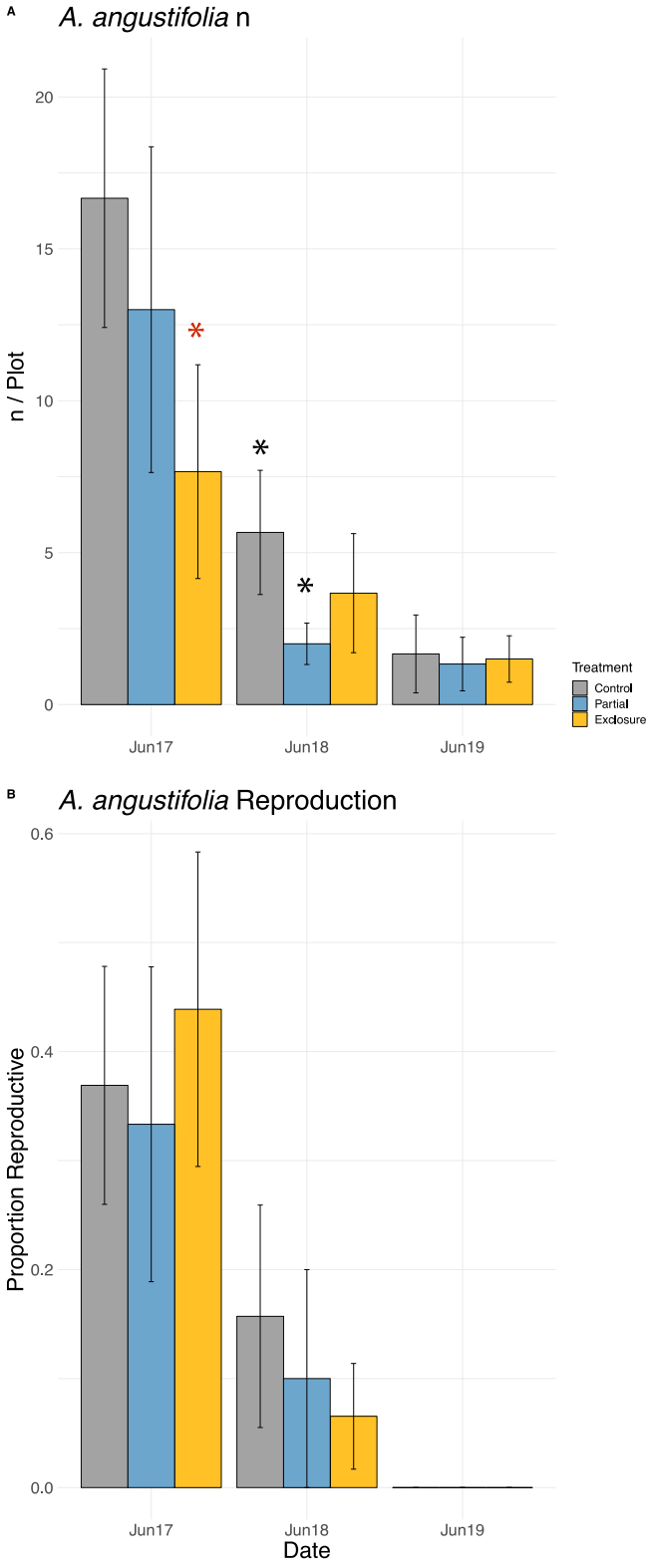

Fig 3.22. (A) Mean counts of *A. angustifolia* by Treatment (B) Mean proportion of individuals that had visible reproductive structures. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

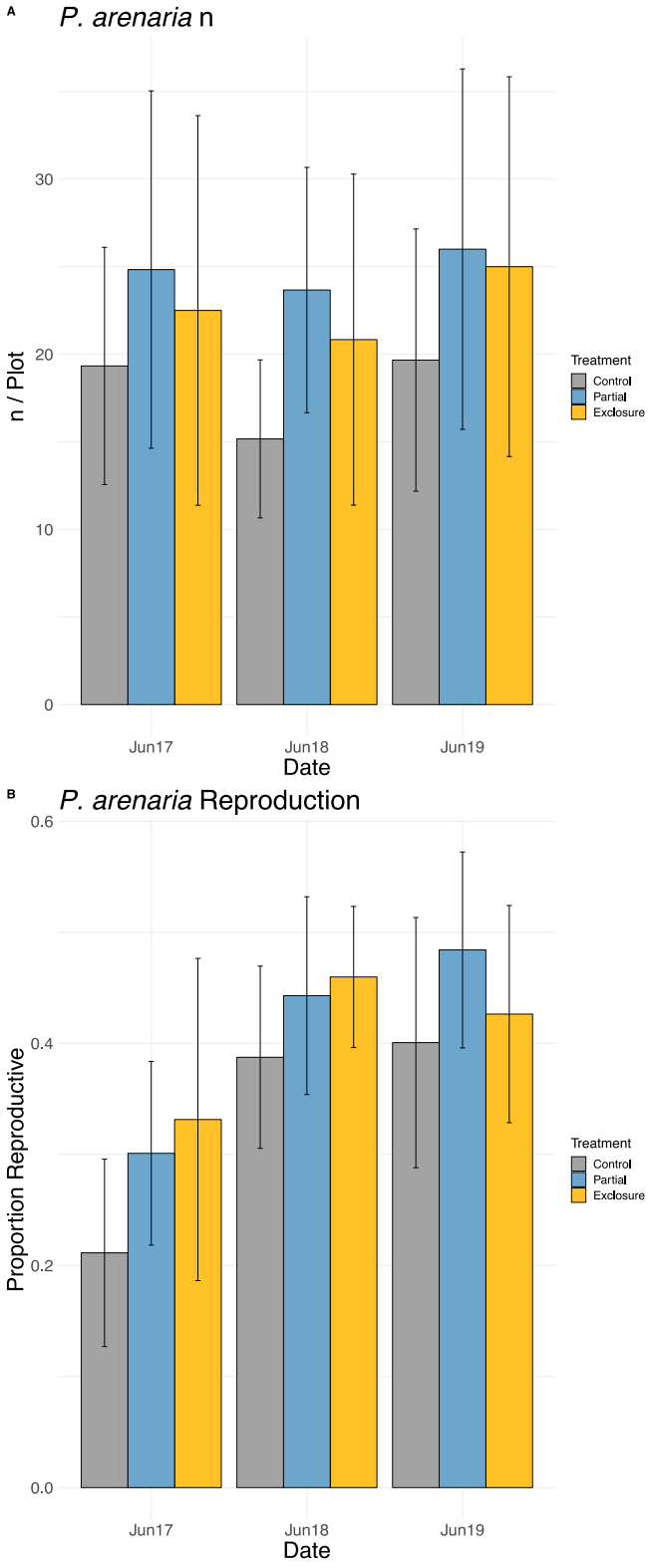

Fig 3.23. (A) Mean counts of *P. arenaria* by Treatment (B) Mean proportion of individuals that had visible reproductive structures. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

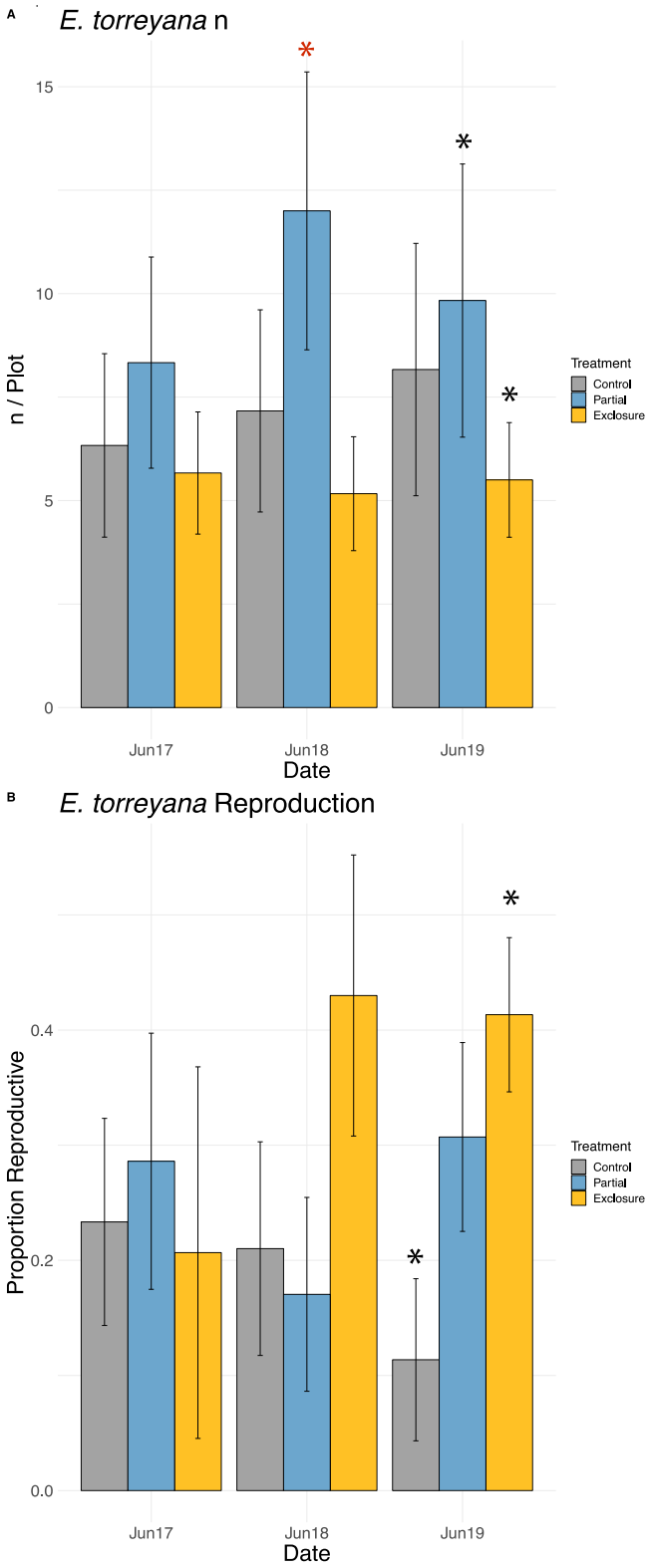

Fig 3.24. (A) Mean counts of *E. torreyana* by Treatment (B) Mean proportion of individuals that had visible reproductive structures. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

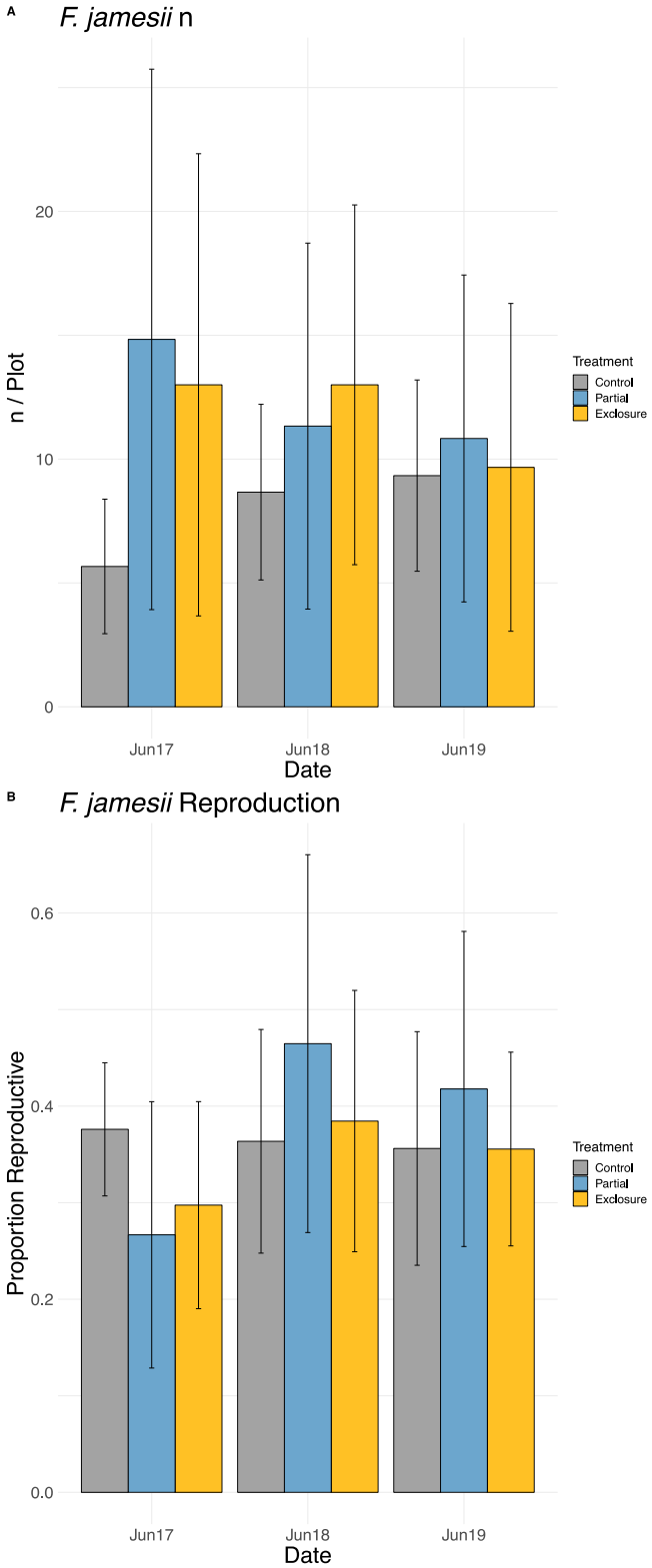

Fig 3.25. (A) Mean counts of *F. jamesii* by Treatment (B) Mean proportion of individuals that had visible reproductive structures. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

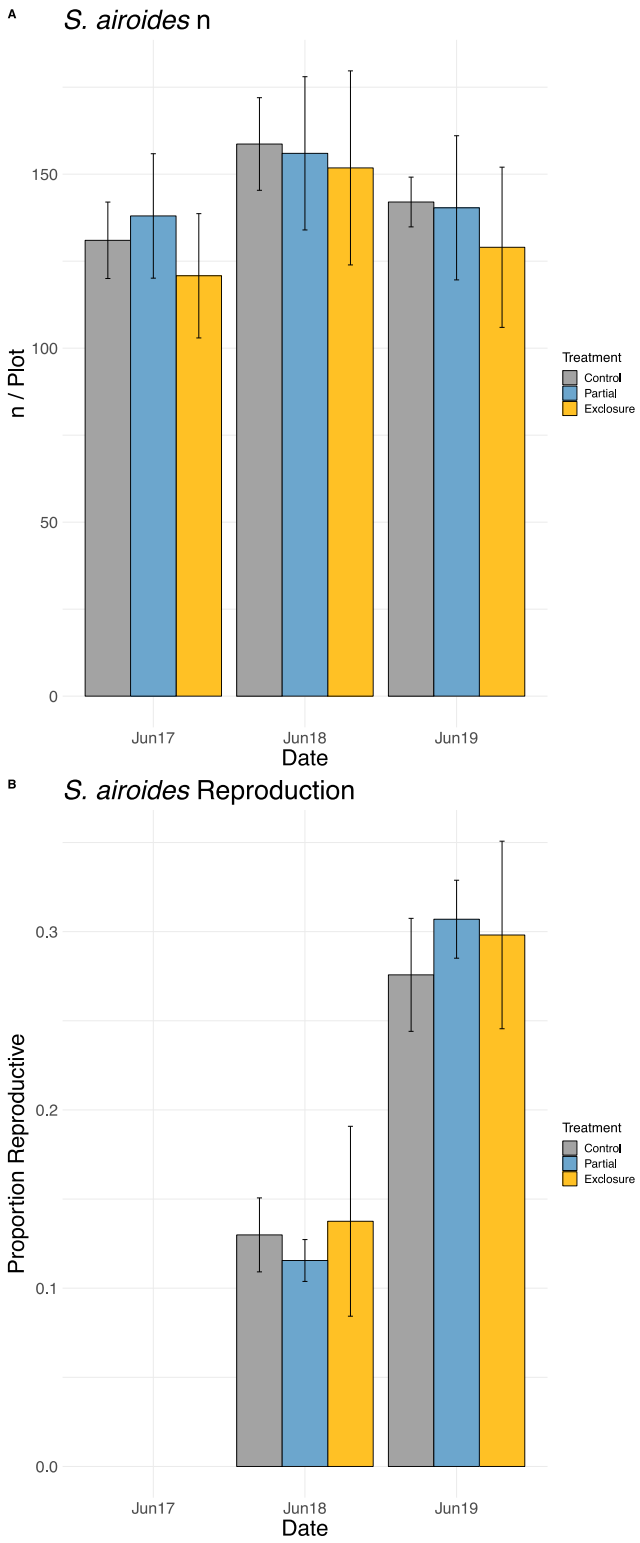

Fig 3.26. (A) Mean counts of *S. airoides* by Treatment (B) Mean proportion of individuals that had visible reproductive structures (data not collected in 2017, see Sacaton Quadrat results for baselines). Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

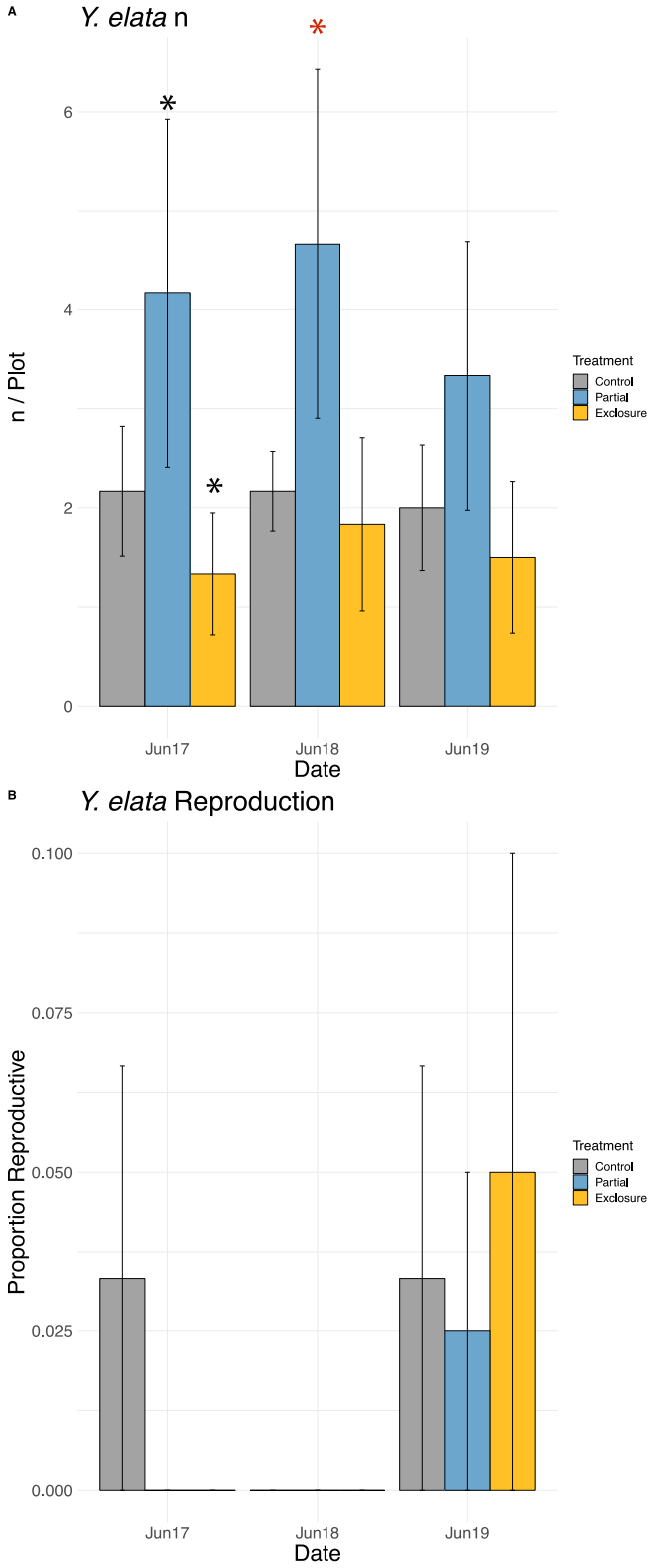

Fig 3.27. (A) Mean counts of *Y. elata* by Treatment (B) Mean proportion of individuals that had visible reproductive structures. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see Table 3.5 and main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction as baseline data.

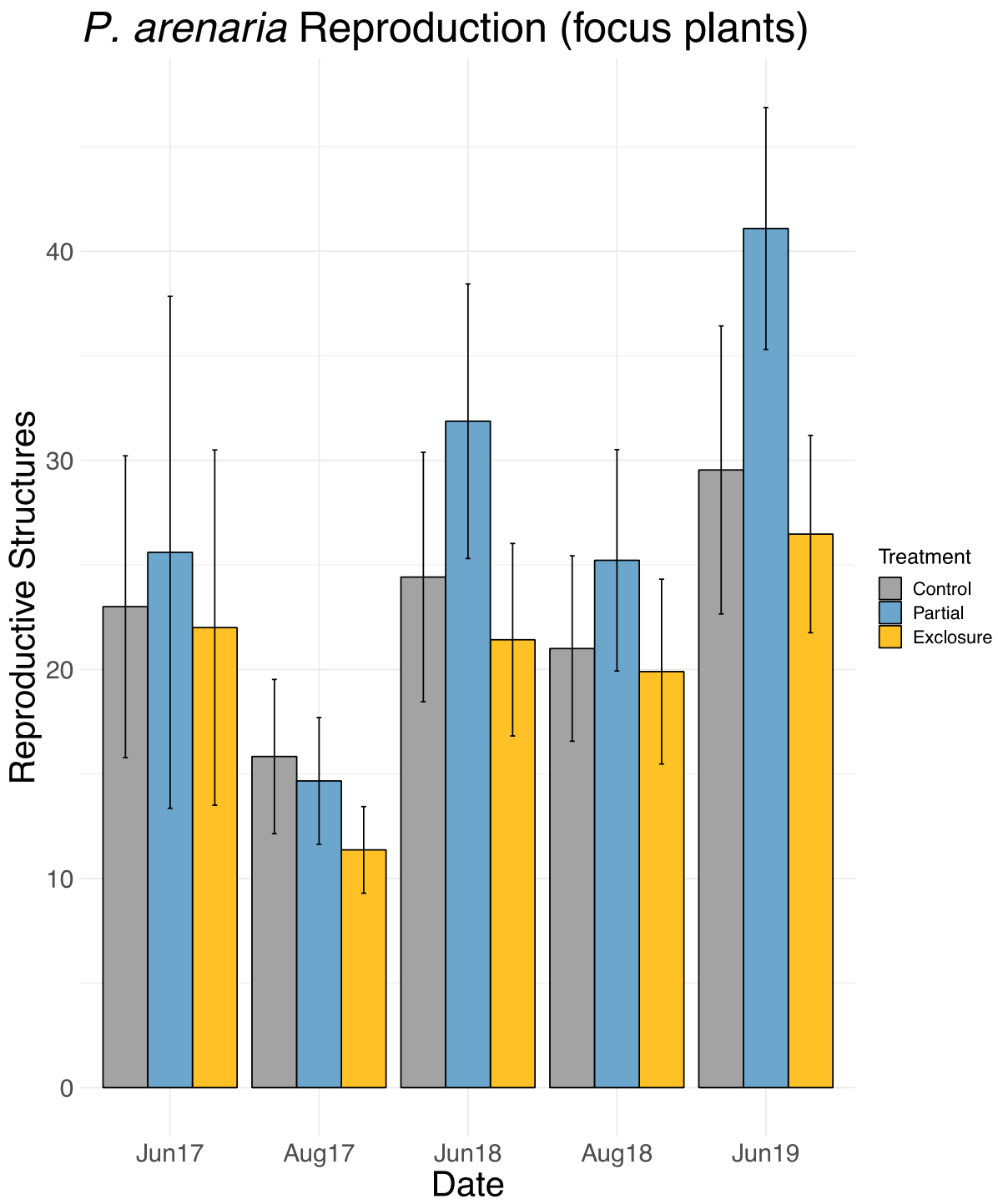

Fig 3.28. Mean counts of *P. arenaria* reproductive structures by treatment and date, from individuals followed throughout the study. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data represent a subset of individuals (n=1 per plot ; 6 per treatment) that were selected to establish a baseline.

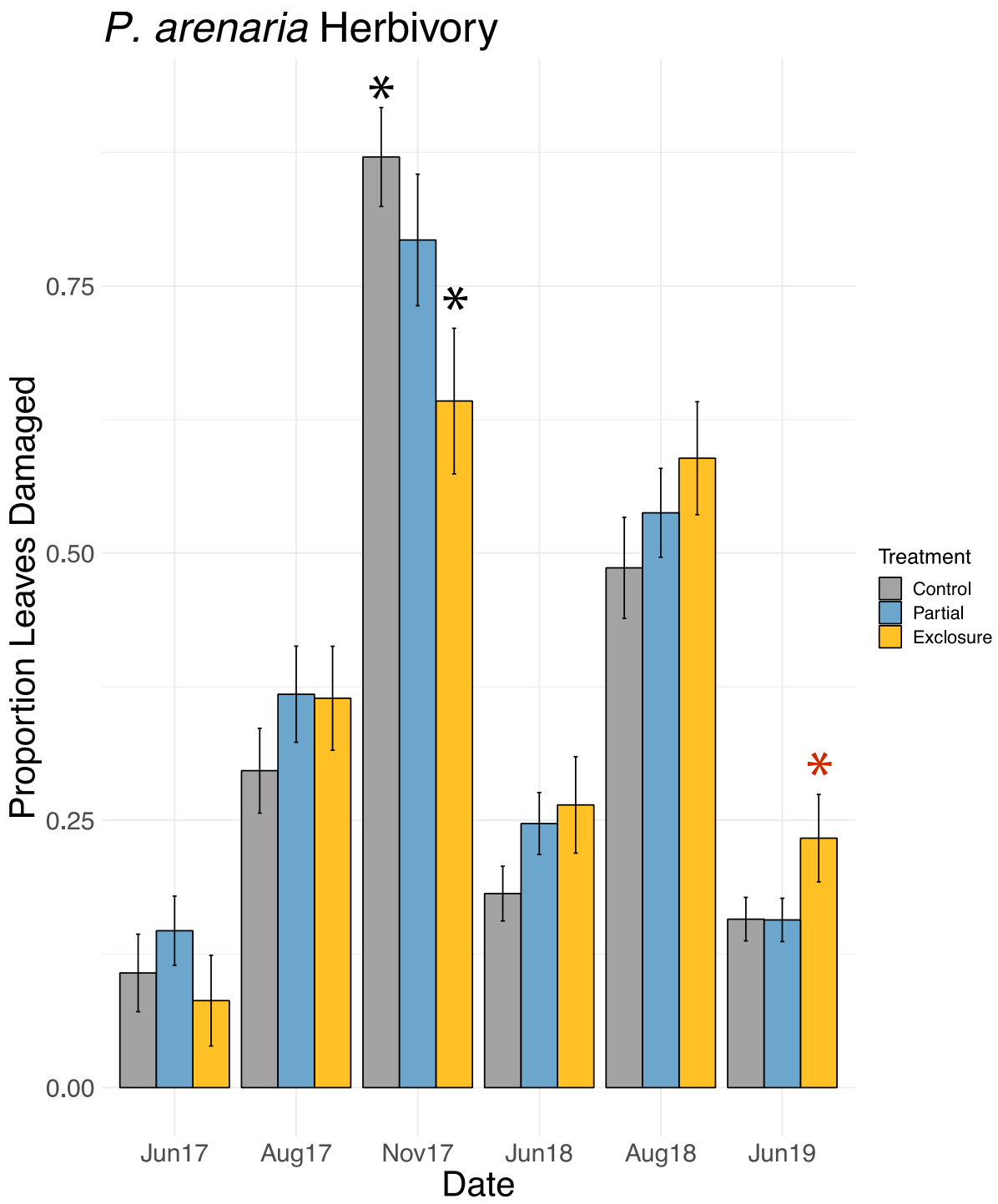

Fig 3.29. Mean proportion of *P. arenaria* leaves damaged by herbivores, by treatment and date. From individuals followed throughout the study. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data represent a subset of individuals (n=1 per plot ; 6 per treatment) that were selected to establish a baseline.

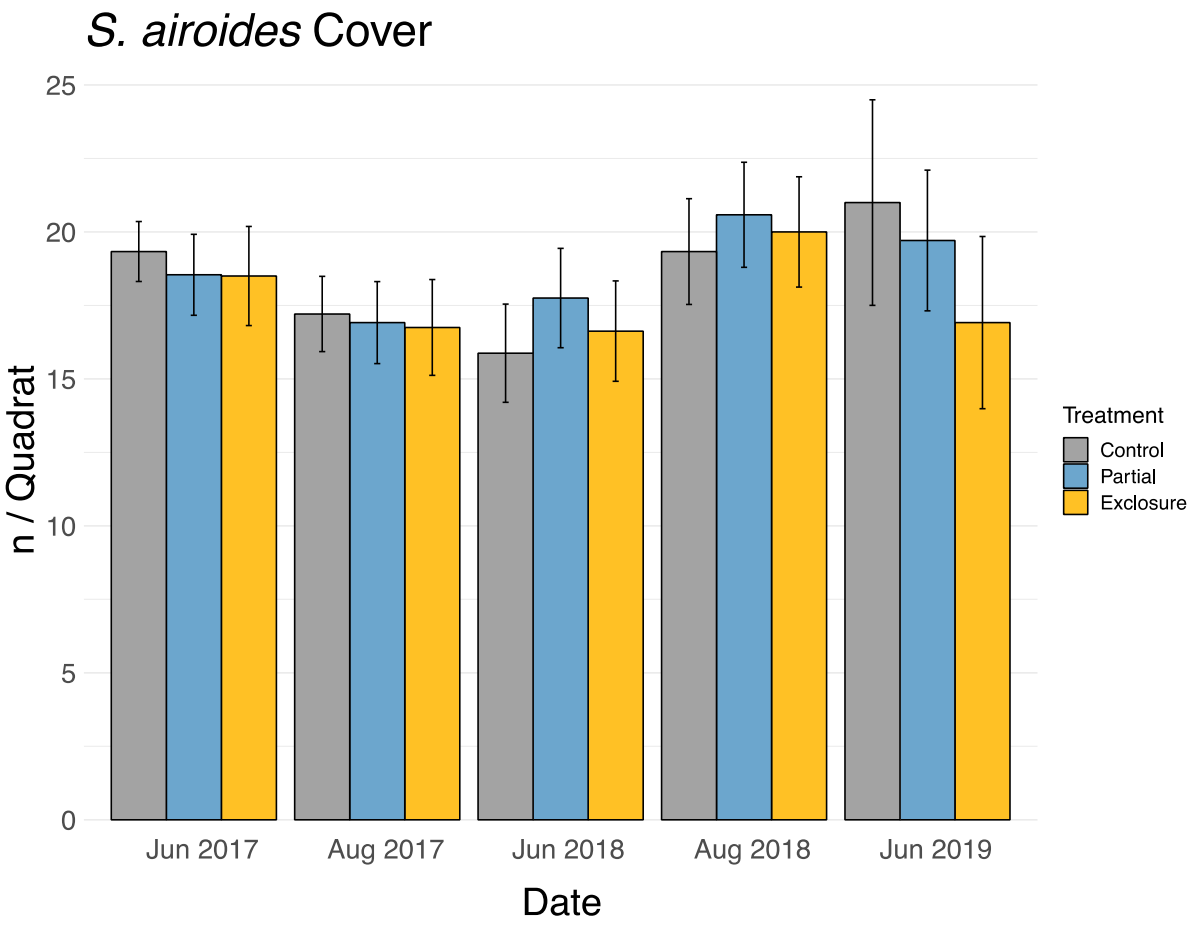

Fig 3.30. Mean number of point intercept hits of live *S. airoides* per repeatedly sampled quadrat. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction to establish a baseline.

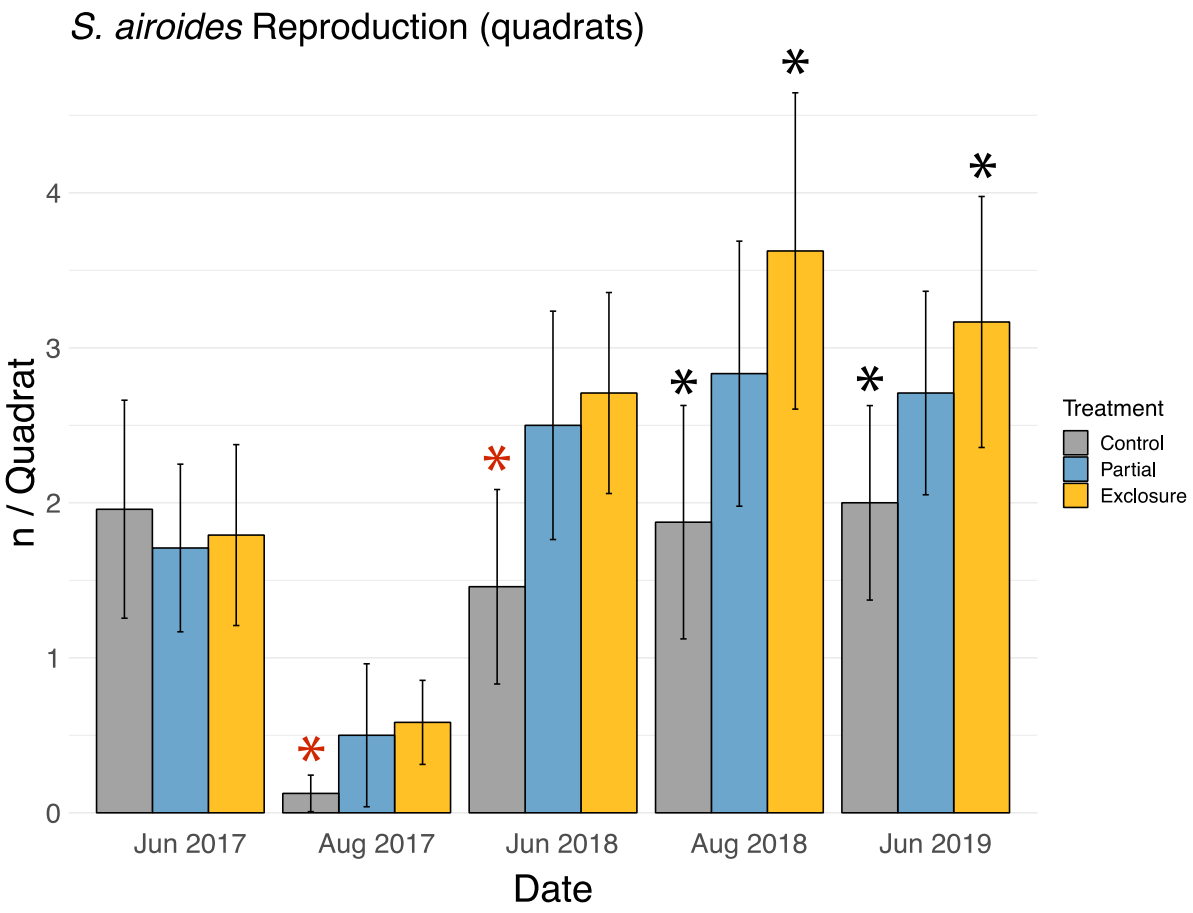

Fig 3.31. Mean number of *S. airoides* panicles per repeatedly sampled quadrat. Error bars indicate the standard error of the mean. Asterisks indicate cases where Tukey HSD tests revealed differences between treatments means with $p < 0.1$ (see main text for details). Black asterisks denote differences between the given treatment and one other treatment and red denotes differences with both other treatments. June 2017 data were collected soon after fence construction to establish a baseline.

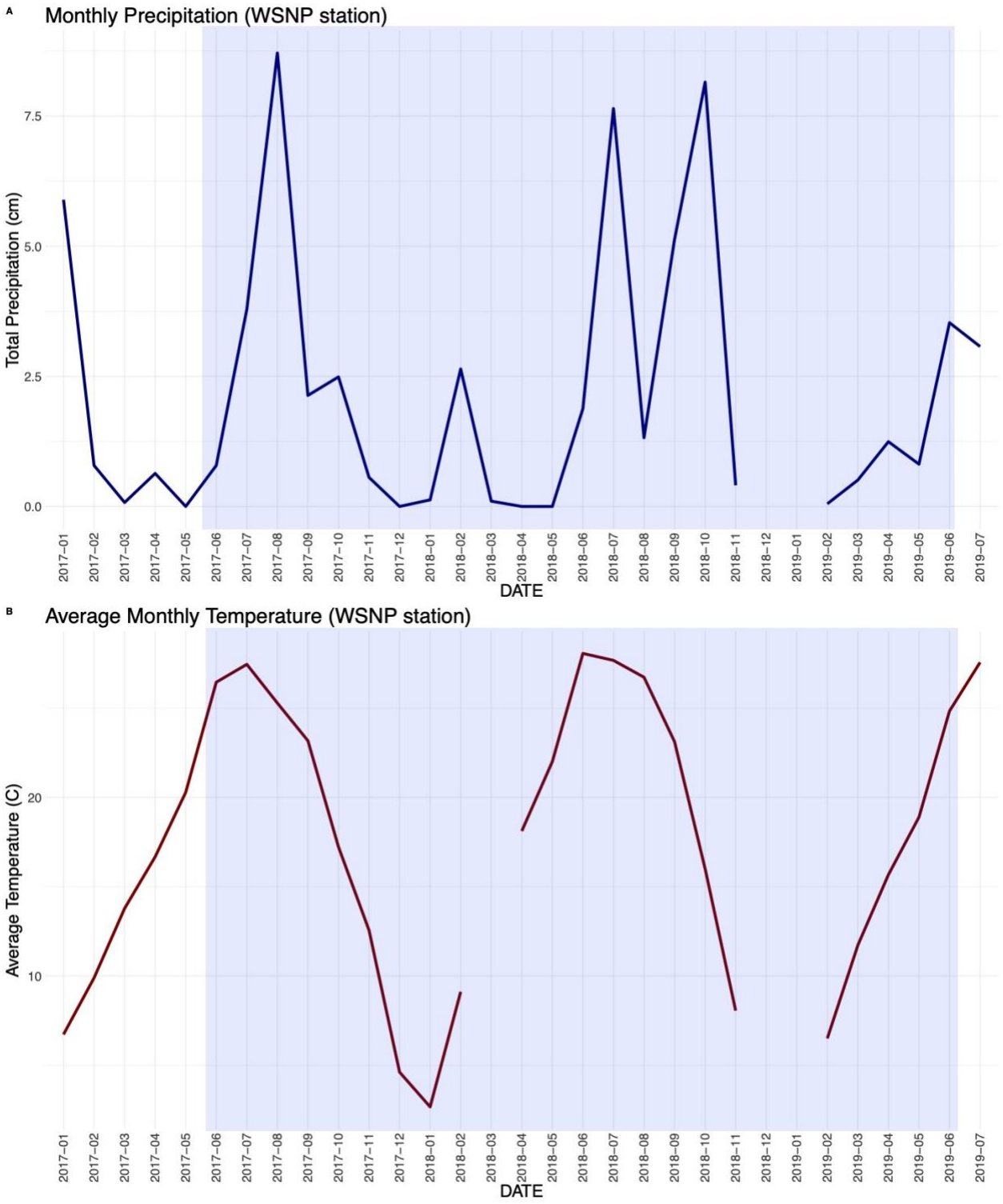

Fig 3.32. Weather records from White Sands National Park headquarters (~9 km from study site) from January 2016 to July 2019 (study period highlighted in blue). **(A)** total monthly precipitation (cm) and **(B)** average temperature (C). Note that no data were recorded in December 2018 and January 2019.

CHAPTER 4
HIGH ECTOPARASITISM IS NOT A CONSEQUENCE OF ECOLOGICAL RELEASE IN WHITE SANDS LIZARDS

4.1 ABSTRACT

Mite ectoparasitism is an important process for lizards, with broad ecological consequences. Previous work has documented large variation in ectoparasitism between species, populations, individuals, and over time. We hypothesized that lizards in White Sands had high rates of ectoparasitism due to multiple attributes of this system including high densities and relatively low species diversity. We tested this hypothesis by quantifying ectoparasitism in four lizard species across habitats and years. We also leveraged this dataset to test multiple other hypotheses for what can cause variation in parasitism between populations and individuals. We found two types of ectoparasites on lizards, including trombiculid mites and ixodid ticks. Contrary to our primary hypothesis, mite loading was lower in White Sands than in the surrounding desert scrub across species. We also found strong variation with species and year, with year effects dwarfing any other drivers of ectoparasitism. Consistent with other work, we found higher ectoparasitism on males than females and a positive relationship between body condition and ectoparasitism. Date, conspecific abundance, lizard abundance and squamate richness also had correlations with mite loading, with the directionality varying with species. Connecting pattern to process remains difficult, but our results are consistent with encounter dilution effects, diverse hosts acting as parasite reservoirs, and abiotic processes structuring ectoparasitism in this system.

4.2 INTRODUCTION

Host – parasite dynamics can have profound effects on ecological and evolutionary processes[196-199]. In reptiles, a relatively well studied interaction is between ectoparasitic Acari (mites including ticks[200]) and lizards[197]. Ectoparasitic mites typically embed in the host integument and can localized tissue damage and broader health consequences[41,201]. High infestations can lead to direct moratlity[202,203]. More commonly there are a variety of sublethal effects, which can be more severe with coinfection by multiple parasites[197,204]. Mite parasitism can reduce hematocrits in lizards[204,205] and transmit lethal diseases[206]. Multiple behavioral shifts have been linked with mite ectoparasitism, including reduced sprint speeds and movement[207], increased basking[207,208] and reduced territoriality[205]. Behavioral effects can even be intergenerational, with maternal mite load shifting dispersal behavior and sprint speeds in offspring[42]. Taken together these changes may also increase the probability that parasitized lizards are predated[197,199]. Importantly, multiple studies have found limited effects on lizards, suggesting that they are well adapted to mite ectoparasitism[44,52,209,210]. Infection dynamics can vary strongly with species, populations and individuals, likely affecting community structure and broader ecological processes[197,198].

Like with other parasites, studies that quantify mite ectoparasitism across multiple species of lizards find variation between species[43,197,211-214]. Within the same community, host species traits like microhabitat use, morphology and movement ecology are likely important for shaping parasite identity and prevalence[52,197,213]. Within a species, rates of infection can vary at the continental scale[44], between nearby habitats[49,215,216], and likely by microhabitat[45,217,218].

Variation in abiotic conditions within all of these scales, especially temperature and moisture, can have strong and species specific consequences for parasitic mite distributions and abundance[45,217,219,220]. Changes in temperature and precipitation also partially drives the strong seasonal and annual changes often found in mite parasitism[46,51,212,214,221]. Mite hatching and development are highly correlated with climatic factors (although temperature independent diapause is also important[222]), and lizard parasitic loads are often a result of ambient mite populations[46,51]. In addition to abiotic conditions, shifts in lizard activity (e.g. due to reproduction) can influence parasite loading over time[50].

Population and community structure may also have important implications for mite ectoparasitism in lizards. Host population density can have varied effects on parasitism rates[223,224]. Mean parasite burden may have an asymptotic relationship with host density, increasing to a saturation point[225,226]. In these scenarios, host density increases parasite transmission rate[224,227]. Increased host densities could also increase the probability that individual parasites will find hosts, and that they will eventually successfully reproduce[224,226]. For example, Swei et al. (2011) found that following experimental removal of fence lizards (*Sceloporus occidentalis*), tick (Ixodidae) densities declined significantly[228]. High densities may also increase host susceptibility to parasites as immunity is compromised with high intraspecific competition and stress[229]. However, the relationship between host density and parasitism is likely highly mediated by parasite strategy[47]. The 'encounter dilution effect' is a scenario where parasitism risk declines with density, because parasites have more alternative hosts[223]. This could be especially prevalent when parasites, like ectoparasitic mites, wait to ambush hosts and likely have limiting factors besides host density due to free living life stages[47,230]. Similar to host density, host species diversity can have contrasting effects on parasite loading, depending on species identity[48,231,232]. Multiple host species can act as reservoirs for parasites, allowing parasites to maintain densities even as individual host populations fluctuate[48]. Host diversity could include species that can harbor high loads which then spill-over to other species, a form of apparent competition[233,234]. There can also be a dilution effect where parasite abundance declines with increased host richness, especially if some species are less effective spreaders[48].

Within a population, multiple processes contribute to variation in ectoparasite loading between individuals. Parasite aggregation, where most parasites occur in a few individuals and most hosts have few or none, has been described as a universal phenomenon[224,232,235]. Several factors have been found to contribute to variance in mite loading in lizards. Many studies find a strong sex effect on mite loading, with the majority find that males host more mites ectoparasites than females[49,221,236]. Multiple mechanisms likely explain this pattern, including that males generally move more and thus likely encounter more mites[49]. For example, sex biased tick loading in *Scelporus occidentalis* is higher in the spring when males are territorial and moving more than females[49]. Additionally, testosterone has been found to reduce immunocompetence, contributing to higher mite loads in males[237-239]. Reproductive status can effect status in females as well as males, as increased energy needs can increase susceptibility of gravid individuals to mites[50]. Age effects are also commonly found, with host-parasite dynamics in hatchling and juvenile lizards often distinct from adults[47,51]. Body condition (a measure of overall health) can have contrasting effects on ectoparasite loading, with some studies finding a positive correlation as mites target individuals that are healthier and/or move more and others finding that mites are associated with unhealthy individuals, especially at high loads[52,204].

Lizard population and community structure varies strongly along habitat gradient from desert scrub to the interior of the gypsum sand dunes of White Sands, New Mexico[7,10]. Lizards in

White Sands (*Aspidoscelis inornata, Sceloporus cowlesi* and *Holbrookia maculata*) have escaped many predators and competitors and show signs of ecological release[2,10]. While prior work has demonstrated increased White Sands lizard densities with ecological release, we hypothesize here that there is a cost. Specifically, we predict that increased densities, along with other components of White Sands lizard ecology, have led to higher rates of ectoparasitism in these populations relative to lizards in the surrounding desert. Besides increased densities there are multiple reasons to suspect ectoparasitism may be high in White Sands lizards. Previous work has demonstrated that mite ectoparasites are found on lizards in Chihuahuan desert dunes[240]. The gypsum dunes are generally cooler and moister than the surrounding desert, which could allow higher densities of parasitic mites[153,220,241]. There may be a dilution effect across this habitat gradient, with lizards in White Sands more targeted by ectoparasites as host diversity decreases[48]. Furthermore, White Sands lizards have convergently reduced melanin production[9,53]. Melanin production is genetically linked with stronger immune response and parasite resistance in multiple taxa[54], although it isn't well understood in lizards[242]. Variation in pigmentation is associated with differences in mite ectoparasitism in lizards[243,244]. We test our hypothesis that ectoparasitism is relatively high in White Sands lizards, and also leveraged our dataset to test multiple other hypotheses for what can drive variation parasitism between individuals. Specifically, we tested for a relationship between habitat, site, year, date, sex, age class, gravidity, body condition, size, trophic position, conspecific abundance, lizard abundance and squamate richness on mite ectoparasitism.

4.3 METHODS

We sampled lizards and snakes across sites in White Sands, the surrounding desert scrub, and the ecotone between the two habitats and measured their ectoparasite loads. Study animals for this project overlapped with those for Chapter 1, see those methods for details. Briefly, we used a combination of trapping (drift fences with bucket and funnel traps) and time and area constrained surveys to capture reptiles. We sampled in summer 2015 (6/17 to 8/12) and 2016 (6/10 to 7/30). Between 2015 and 2016 we shifted some sites for sampling efficiency, maintaining a minimum of two sites per habitat per year and multiyear sampling for at least one site in every habitat. Calculation of population and community metrics that may contribute to ectoparasite loads (conspecific and lizard abundances, and squamate richness) are described in more detail in Chapter 1. We departed from that work by lumping snakes with other lizards into squamate richness, as we more interested in snakes as potential hosts as opposed to teasing apart predation and competition. Conspecific and lizard abundance were estimated using standardized effort (just trapping).

The same observer (C. Noss) conducted all ectoparasite counts and measured lizard morphology. Lizards were examined thoroughly for ectoparasites with a hand lens. We noted the total number of ectoparasites, and their spatial distribution on the lizard[245]. We found two distinct ectoparasites on lizards, both of which were mites (subclass Acari). The most common is very likely a species of Trombiculid, being relatively distinctively bright red. A likely candidate is *Eutrombicula alfreddugesi*, which is known to commonly infect lizards, including in the Chihuahuan desert[212,240,246-249]. Other parasitic, red mites are known to infect lizards in the region, including multiple species of *Eutrombicula*[212,237,250-252], so more work is needed to identify these mites. The other ectoparasite was a species of hard tick (Ixodidae) that was larger and only found on *S. cowlesi*. Multiple species of ixodid ticks that parasitize lizards are found in

the United States[49,249,253-256]. Trombiculids are lizard parasites in their larval stage, ticks in multiple life stages, and both damage the hosts epidermis and cause other possible health consequences[201,211,214,218,250,256].

We measured morphological attributes that may contribute to ectoparasitic loads in every lizard. We measured snout-vent length (SVL) using a clear plastic ruler. Mass was measured to 0.1 g using a spring scale (Pesola 10 g scale). We calculated a body condition index (BCI) for every individual by dividing mass by SVL[257]. There are non-invasive indices for body condition, all of which have strengths and weaknesses, but the most common method is calculation of residuals from ordinary least squares regression[258]. Sion et al. (2021) found that the simple mass/SVL measure was the most accurate when compared against more technical lethal (chemical extraction of fat) and non-lethal (dual-energy X-ray absorptiometry) approaches, and that mass/SVL is highly correlated with the regression approach[257].

Trophic position at the individual level was estimated using the standard methodology of

$$TP = \lambda + (\partial^{15}N_{consumer} - \partial^{15}N_{basal}) / \Delta_n$$

where λ is the trophic position of the basal resource (1), $\partial^{15}N_{consumer}$ is directly measured for each lizard, $\partial^{15}N_{basal}$ is averaged across plant samples for each site and Δ_n is the trophic fractionization of $\partial^{15}N$[16]. See Chapter 1 for more details regarding calculation of trophic position and sampling for plant and lizard isotopes. While we did not have specific predictions for the relationship between trophic position (or even diet) and ectoparasitic load per se, diet is highly correlated with microhabitat use and movement in lizards[106,259]. Both of these factors can influence ectoparasitic loads and diet, which can then shift trophic position[10]. We therefore chose to leverage our existing individual level dietary data to inform other interpretations and generate hypotheses.

Statistical methods

We tested for effects of ecological and morphological attributes on ectoparasite counts using generalized linear models (GLMs; using R 4.0.3, 'glm.nb' function in package MASS version 7.3-57[260]). Our data had a high proportion of zeroes and over dispersion, so a the negative binomial distribution with a log link function was used for all analyses[93]. Parasite data often follow a negative binomial distribution[224]. Post-hoc analyses (Tukey tests) were performed using the package 'emmeans'[261]. Three primary approaches were used. *First*, we tested for an effect of each explanatory variable individually on ectoparasite counts for each species individually. Data were subset as appropriate for each explanatory variable, for example only females were analyzed when testing for an effect of gravidity while gravid females were excluded from BCI models. *Second*, we performed automated model selection ('dredge' function in package 'MuMIn'[96]) to test for an effect of multiple explanatory variables in conjunction, again for each species separately. The dredge function compares models with every combination of fixed effects using AICc[96]. We included habitat, year, a habitat by year interaction, date, sex and body condition in these models. Juveniles and gravid females were excluded from these analyses. *Third*, we performed automated model selection, again using dredge, for data including all species with species, habitat, a species by habitat interaction, year, habitat by year, date and sex as fixed effects. We used the package 'DHARMa' for model validation, inspecting residuals and performing diagnostic tests (K-S tests, dispersion tests, outlier tests)[162]. Four species had

high enough samples for statistical analyses, including *A. inornata, H. maculata, S. cowlesi,* and *Uta stansburiana*.

4.4 RESULTS

We captured and inspected 430 lizards across two summers (144 *A. inornata*, 76 *H. maculata*, 120 *S. cowlesi* and 90 *U. stansburiana*). We also screened 21 individuals of 9 other squamate species (including lizards *Aspidoscelis marmorata, Crotaphytus collaris, Phrynosoma modestum, Phrynosoma cornutum,* and snakes *Heterodon nasicus, Hypsiglena jani, Masticophic flagellum, Rhinocheilus lecontei,* and *Sonora semiannulata*) but these sample sizes were not high enough for statistical analyses. Few of these other species had ectoparasites, but these captures were so low that this is likely a statistical artifact. One coachwhip (*M. flagellum*) found in the desert scrub in 2015 had 24 trombiculids. One juvenile Texas horned lizard (*P. cornutum*) found in desert scrub in 2015 had 5 trombiculids. All of the four study species had trombiculid parasites, although captures varied widely with site, habitat and year (Fig 4.1). Ticks (Ixodidae) were found almost entirely on *S. cowlesi,* with only two individual ticks found on other species. These included one *H. maculata* (male caught in White Sands in 2016) and one *U. stansburiana* (female caught in desert scrub in 2015). In contrast *S. cowlesi* had an average of 0.56 Ixodida per individual (Fig 4.4).

We found differences between species in mean loads of trombiculids ($z_{3,430}$ =7.67, p <0.001), with post hoc tests revealing that most species were different from each other (Fig 4.1; *A. inornata* > *H. maculata* p < 0.001, *A. inornata* > *S. cowlesi* p < 0.001, *A. inornata* – *U. stansburiana* p = 0.99, *H. maculata* < *S. cowlesi* p = 0.01 , *H. maculata* < *U. stansburiana* p <0.001, *S. cowlesi* < *U. stansburiana* p <0.001). Similar results were found when ixodids and trombiculids were combined ($z_{3,430}$ = 2.05, p <0.001). Model selection with dredge (all species combined) resulted in 3 models with $\Delta_i < 2$, including various combinations of species, habitat, species*habitat, year, habitat*year, date and sex as fixed effects (Table 4.8).

Analyses subset by species revealed multiple relationships between ectoparasite load and ecological factors. For *A. inornata*, we found variation with site, habitat, year, conspecific abundance and lizard abundance, with a trend for squamate richness and age class (Table 4.1). Model selection with dredge resulted in 3 models with $\Delta_i < 2$, all including habitat, year, habitat*year and one each including date and body condition (Table 4.7).

For *H. maculata* we found variation with conspecific abundance and trends for effects of sex, body condition and SVL (Table 4.2). Model selection with dredge resulted in 10 models with $\Delta_i < 2$, with no factors included in all models and combinations of habitat, date, sex and body condition (Table 4.7).

For *U. stansburiana* we found variation with site, year, date, conspecific abundance, lizard abundance, and squamate richness (Table 4.3). Model selection with dredge resulted in 6 models with $\Delta_i < 2$, all including habitat and year then various combinations of habitat*year, sex and body condition (Table 4.7).

For *S. cowlesi* we found that relationships between ecological factors and ectoparasites varied depending on if trombiculids, ixodids, or both were analyzed (Fig 4.4). When lumped we found variation with site, habitat, year, conspecific abundance, lizard abundance and squamate richness (Table 4.4). Model selection with dredge resulted in 4 models with $\Delta_i < 2$, including combinations of habitat, year, habitat*year and sex (Table 4.7). When just considering

trombiculids we only found variation with site and habitat (Table 4.5). Model selection for trombiculids resulted in 6 models with $\Delta_i < 2$, including various combinations of habitat, year, date, sex, and body condition (Table 4.7). When just considering ticks we found variation with site, habitat, year, sex conspecific abundance, lizard abundance and squamate richness, and trend with SVL (Table 4.6). Model selection for ticks resulted in 4 models with $\Delta_i < 2$, all of which included habitat and sex and then various combinations of year, date and body condition (Table 4.7).

Body condition was not significant when included as the only predictor for ectoparasite loads for any species, but there was a positive relationship for some models in all species in larger models (Fig 4.3 ; Table 4.7). Similarly, sex was only significant when the sole predictor for *S. cowlesi* ticks (Table 4.6) and *H. maculata* (trend, Table 4.2). However following model selection sex was included in at least some top models for all species except *A. inornata* (Fig 4.2 ; Table 4.7).

4.5 DISCUSSION

Contrary to our hypothesis that high rates of parasitism would be a cost of ecological release in White Sands lizards, we found that mite loading was higher in desert scrub for *A. inornata* and *S. cowlesi* (Fig 4.1). Following model selection habitat was included in most models in all species (Table 4.7). Most species differed from each other in ectoparasitic load, with *A. inornata* and *U. stansburiana* the only pair not distinguished (Fig 4.1, Table 4.8). We also found that differences between years dwarfed differences between habitats, with much more parasitism in 2015 than 2016 in the desert scrub (Fig 4.1, Table 4.7). Consistent with other studies, we found higher ectoparasite loads on males in all species except for *A. inornata* (Fig 4.2 ; Tables 4.7. 4.8). When sex was the only predictor it was only statistically significant for ticks on *S. cowlesi* with a trend ($p = 0.06$) in *H. maculata*. Larger models with multiple predictors revealed contrasting seasonal shifts in ectoparasite load between species (Table 4.7). When date was the sole predictor it was only statistically significant for *U. stansburiana* which showed a slight increase in trombiculid loading later in the summer (Table 4.3). Body condition was never related to ectoparasite counts when the sole predictor, but a positive association with ectoparasite load was revealed in a subset of larger models for all species (Table 4.7, Fig 4.3). *A. inornata* and *S. cowlesi* showed negative relationships between both conspecific and lizard abundance with ectoparasites, while *U. stansburiana* was the opposite. *A. inornata* and *U. stansburiana* showed negative relationships between squamate richness and ectoparasites, while *S. cowlesi* had a positive one.

We initially hypothesized that ectoparasites would be more prevalent in White Sands than in the surrounding desert scrub, but found the opposite pattern (Fig 4.1). Connecting pattern to process is difficult in many observational studies, and this is particularly true in this system where multiple biotic and abiotic factors vary strongly across the gradient from desert scrub into the gypsum dunes. What we can do is consider various alternative hypotheses and whether our results are consistent with them or not. High density in the White Sands lizards is largely what originally motivated us to quantify ectoparasitism in this system, as multiple lines of evidence predict a positive correlation between host and parasite density[224,225,228]. We are aware of only of only a handful of studies that have compared lizard density and ectoparasitic mite abundance. Sorci et al. (1997) found that ectoparasitic loading was reduced at higher densities of common lizards (*Lacerta vivpara*)[262]. Hawlena et al. (2010) experimentally reduced lizard densities by

introducing predators and found that while ectoparasitism of juveniles declined, it increased for adults[263]. Experimental manipulation of common lizard densities resulted in lower tick infestation, although high densities were associated with reduced immune function[47]. In contrast, Swei et al. (2011) removed *Sceloporus occidentalis* and found that tick populations declined precipitously[228]. Taken together, these results as well as ours support an encounter-dilution model, where at higher densities lizards have a lower probability of being parasitized[223]. In this context, the Swei et al. result may indicate that in systems with limited host switching, complete elimination of hosts causes parasites to pass a threshold where they cannot sustain populations[228]. Work on ectoparasites in other systems also supports the generality of the encounter-dilution effect[223], and it is conceptually similar to when prey aggregation reduces individual probability of predation[264].

We suspect that encounter-dilution processes explain some but not all of the variation between habitats in ectoparasite loading. In encounter-dilution models, the number of parasites per individual varies because there are other limiting factors for the parasite besides host abundance[223]. Standardized trapping of hosts should therefore reveal that the total number of ectoparasitic mites is similar between sites or higher with higher densities (with parasites per lizard still lower in high density scenarios). To explore this, we subset our data to just included standardized sampling of lizards that was comparable across all sites within in each year (trapping) and summed trombiculid counts across these individuals by year and site. In 2015 despite the much higher standardized captures of lizards in White Sands (95 in White Sands, versus 6 in ecotone and 41 in desert scrub) summed trombiculids on these lizards were much higher in the desert scrub than other habitats (47 in White Sands, 88 in the ecotone, 1486 in desert scrub). Encounter-dilution effects cannot be solely responsible for our results in 2015, because the relative abundance of trombiculids was much higher in desert scrub irrespective of lizard density. In 2016, lizard counts were somewhat similar to 2015 (78 in White Sands, 24 in the ecotone, 35 in desert scrub) but mite counts were much lower in desert scrub (39 in White Sands, 0 in the ecotone, 8 in desert scrub). Encounter-dilution processes could therefore explain our 2016 results, as there were more trombiculids in White Sands but they were spread amongst more hosts. Two other lines of evidence suggest that encounter-dilution processes cannot explain all of our results. First, densities were always lowest in ecotonal sites, but these lizards generally had zero trombiculid parasites (Fig 4.1). The relatively high 2015 ecotone count was caused entirely by one individual *A. inornata* that had 88 trombiculids. Second, *U. stansburiana* actually showed a positive relationship between conspecific and total lizard abundance. This was again driven by the ecotone, where both lizard captures and ectoparasite loading were very low. We conclude that the encounter-dilution effect likely explains some of our results, especially from 2016, but other processes are likely responsible as well.

Variation in squamate richness between habitats may explain some of our results. Both *A. inornata* (Table 4.1) and U. *stansburiana* (Table 4.3) showed a negative relationship between richness and trombiculid loads. It may be that in the desert scrub the higher diversity of potential hosts act as reservoirs for trombiculids[48]. Cox et al. (2020) demonstrated that higher richness of lizard hosts (two versus ones species) maintains trombiculid parasites over lizard generations[234]. Importantly, trombiculids (including *E. alfreddugesi*) can infect a broad range of hosts including vertebrates and invertebrates[249,265,266]. While prior work has generally found a reduction in diversity across taxa in White Sands[6,190], we lack natural history data on trombiculid infection and broader richness data to test for the role of species richness here. Infections of ixodid ticks in *S. cowlesi* showed a contrasting pattern in this system, being positively correlated with squamate

richness (Fig 4.4, Table 4.6). Other work has found that trombiculids and ixodid infections can have different dynamics in the same system[221]. We lacked community composition data from the only desert scrub site with *S. cowlesi*, but we suspect it would have maintained or strengthened this relationship. This correlation is likely spurious, as we have not observed ixodid ticks on any other squamates in this system. The higher ixodid infections in the ecotone relative to White Sands could be related to the relatively high number of rodents (e.g. *Perognathus*) we observed in this habitat (Noss unpublished data). While Swei et al. found that ixodid ticks were highly reliant on *Sceloporus*[228], other work has demonstrated they can readily infect mammals[48,249]. Although speculative, our results are consistent with diverse hosts as reservoirs in this system[48,234].

We confirmed prior work demonstrating that the decline in richness from desert scrub to White Sands includes a loss of lizard avian and reptilian predators as well[6,7]. Our results do not support ideas that predators reduce parasitism by limiting densities and consuming individuals with high parasitism ('healthy herds hypothesis')[199]. Instead, we add to a growing body of evidence that low predation can be associated with lower parasitism as well[199]. For example Hawlena et al. (2010) hypothesize that the positive correlation between ectoparasitism and predation intensity they found in lizards could be due to changes in lizard microhabitat use or decrease in immunocompetence[263]. As with other possible reasons that we saw differences between habitats, predation cannot completely explain the differences between habitats that we observed. Parasitism was lower in the ecotone than White Sands, yet the ecotone has higher densities of predators (Noss unpublished data). Predator identity and modes of predation are likely important for any relationship between predation and parasitism[199], and further work should more explicitly test for a link in this system.

Abiotic conditions vary between White Sands and the surrounding desert scrub. White Sands is generally cooler and moister, due to the reflective properties of the gypsum sand and a higher water table[153,241]. Ectoparasitic mites are responsive to these changes, which can cause large shifts over space and time[46,219]. Indeed, the drastic difference between years in ectoparasitism (Fig 4.1), which was much stronger than any other factor, was probably caused by precipitation changes (Fig 4.5). Summer 2015 was wetter than 2016, and this likely increased trombiculid populations, although ixodid parasitism was relatively stable between years. Although we did see find an increase in ixodids from 2015 to 2016 (Table 4.6), it was nowhere near the magnitude of changes in trombiculids (Fig 4.1). Other work in the Chihuahuan desert has found shifts in trombiculid ectoparasitism between years[212]. In general, we would expect mites to prefer the cooler and moister conditions in White Sands[45], although little is known about the natural history of mites in our system. Multiple factors vary strongly between White Sands and the surrounding desert. There may be a habitat requirement for trombiculid free living adults that is relatively limited in in the dunes such as leaf litter, which mites can be associated with[220]. In contrast to desert scrub White Sands and ecotonal trombiculid parasitism was stable between years (Fig 4.1). This may reflect that these habitats experience less intense fluctuations with regional climate patterns, or it may be an artifact of our relatively limited sample size.

Our findings that species has a large effect on ectoparasitism is similar to other studies of trombiculid ectoparasitism in lizards (Fig 4.1)[212-214]. We found that ixodid ticks were almost entirely on *S. cowlesi*. This was somewhat surprising because other studies have documented ixodid parasitism in *U. stansburiana*[214] and *Aspidoscelis*[43]. While differences in microhabitat or life history may explain some of this, we hypothesize that *S. cowlesi*'s relatively large and keeled scales provide secure attachment points for the ticks[52]. The other study species have relatively

granular scales[8]. While we did observe ticks using mite pockets (skin invaginations between the neck and shoulder that often host ectoparasitic mites) they were found on many other parts of the body as well. Other known differences in species natural history are consistent with our results. For example, at a given site *A. inornata* generally had more trombiculids than other species (Fig 4.1). These lizards are active foragers and move large distances in a given day relative to the other species, which should increase mite loads because they encounter more parasites[49,246].

Like other studies that examine parasitism within populations, we found heavy aggregation, with some individuals hosting many parasites and most having zero (Fig 4.4). Our results echo a large body of work that has found much of this variation is a result of heavier loading on males[49,221,236] (Fig 4.2), date[46,214] (Table 4.3), and likely age class[51,263] (Table 4.1). Body condition was never a statistically significant predictor of mite load when the sole predictor (Fig 4.3, Tables 4.1-4.6). A subset of larger models for all species included a positive relationship between body condition and ectoparasite load (Table 4.7). Multiple studies have found a positive association between host health or survival and ectoparasitic load in lizards[52,204,210]. Although there is evidence that ectoparasites actively target healthy, higher quality hosts in other taxa[267], there is limited evidence for this in lizards. It may be that healthier lizards also move more, encountering more mites, and that ectoparasitic load has limited health consequences[52,210]. More work, including long term tracking and experimentation, is needed to assess the ultimate fitness consequences of mite ectoparasitism in this system. Prudence is also warranted when interpreting these results, because although our measure of body condition (mass/SVL) is highly correlated with fat reserves[257] it likely misses important components of host health[268].

Here, we have demonstrated that White Sands has a relative dearth of mite ectoparasites, in addition to the known rarity of predators and reduced competitor richness. Unlike predators and competitors, the relative ecological release in White Sands is highly mediated by year. Our results are consistent with hypotheses that density (encounter-dilution effects), species diversity (diverse host as reservoirs) and abiotic differences could mediate mite ectoparasitism in lizards. Currently we only have evidence of higher intraspecific competition as a potential 'cost' of ecological release in this system. Future work should explore what factors are limiting lizard densities in White Sands and explore the ecological and evolutionary consequences of this broad ecological release.

Acknowledgements

We thank Katharine Boyce, Tyler Cino, Allison Litmer and Seth LaRosa for help with fieldwork. Funding was provided by the National Science Foundation, the American Society of Ichthyologists and Herpetologists, the Philomathia Foundation and UC Berkeley's Department of Environmental Science, Policy, and Management, and the Museum of Vertebrate Zoology. All animals were handled in accordance with New Mexico Department of Game and Fish Scientific Collecting Permit (authorization number 3184) and under the University of California, Berkeley, Institutional Animal Care and Use protocol #AUP-2014-11-6857.

Table 4.1. Results for *A. inornata* of generalized linear models (family = negative binomial) exploring the relationship between Trombiculid (likely *Eutrombicula* sp.) ectoparasite counts of individual lizards and various explanatory variables.

	Coefficient	Standard Error	z	df	p	Pairwise comparisons
Site	-	-	-	9, 135	<0.001	Many differences
Habitat	-	-	-	2, 142	<0.001	DS > WS (p <0.001)
Year	-2.65	0.59	-4.49	1, 143	<0.001	2015 > 2016
Date	0.004	0.02	0.19	1, 143	0.82	
Sex	0.64	0.65	0.99	1, 132	0.33	
Age class	-4.31	1.84	-2.20	1, 143	0.09	A > J
Gravidity	0.45	0.95	0.47	1, 61	0.64	
Body condition	-20.24	17.08	-1.19	1, 99	0.46	
SVL	0.08	0.06	1.38	1, 143	0.36	
Trophic position	1.71	1.03	1.66	1, 131	0.49	
Conspecific abundance	-0.19	0.03	-6.78	1, 139	<0.001	
Lizard abundance	-0.09	0.02	-4.91	1, 139	<0.001	
Squamate richness	-0.61	0.22	-2.91	1, 139	0.09	

Table 4.2. Results for *H. maculata* of generalized linear models (family = negative binomial) exploring the relationship between Trombiculid (likely *Eutrombicula* sp.) ectoparasite counts of individual lizards and various explanatory variables. Note that no juvenile *H. maculata* were captured

	Coefficient	Standard Error	z	df	p	Tukey HSD
Site	-	-	-	6, 70	0.14	
Habitat	-	-	-	2, 75	0.99	
Year	0.49	0.96	0.51	1, 75	0.61	
Date	-0.04	0.03	-1.09	1, 76	0.27	
Sex	2.19	1.17	1.87	1, 74	0.06	M > F
Age class	-	-	-	-	-	
Gravidity	19.41	11717.26	0.002	1, 28	0.29	
Body condition	68.42	36.79	1.86	1, 56	0.09	
SVL	0.26	0.13	2.00	1, 75	0.06	
Trophic position	2.86	1.99	1.44	1, 67	0.28	
Conspecific abundance	0.23	0.09	2.34	1, 74	0.003	
Lizard abundance	-0.02	0.03	-0.85	1, 74	0.54	
Squamate richness	-18.97	6442.18	-0.003	1, 74	0.99	

Table 4.3. Results for *U. stansburiana* of generalized linear models (family = negative binomial) exploring the relationship between Trombiculid (likely *Eutrombicula* sp.) ectoparasite counts of individual lizards and various explanatory variables.

	Coefficient	Standard Error	z	df	p	Tukey HSD
Site	-	-	-	6, 84	<0.001	Multiple differences
Habitat	-	-	-	1, 89	0.99	
Year	-3.44	0.26	-13.45	1, 89	<0.001	2015 > 2016
Date	0.03	0.01	2.76	1, 89	0.001	
Sex	0.61	0.55	1.41	1, 72	0.27	
Age class	0.10	0.57	0.17	1, 89	0.86	
Gravidity	0.62	0.83	0.74	1, 32	0.46	
Body condition	34.93	19.46	1.79	1, 56	0.16	
SVL	0.01	0.03	0.51	1, 89	0.61	
Trophic position	-0.98	0.45	-2.16	1, 80	0.21	
Conspecific abundance	0.11	0.02	7.49	1, 77	<0.001	
Lizard abundance	0.09	0.02	4.77	1, 77	<0.001	
Squamate richness	-0.49	0.08	-6.2	1, 77	<0.001	

Table 4.4. Results for *S. cowlesi* – all ectoparasites (Trombiculidae and Ixodidae). Results of generalized linear models (family = negative binomial) exploring the relationship between ectoparasite counts of individual lizards and various explanatory variables.

	Coefficient	Standard Error	z	df	p	Tukey HSD
Site	-	-	-	6, 114	<0.001	None below p < 0.1
Habitat	-	-	-	2, 118	0.002	DS > WS p = 0.006 ECO > WS p = 0.08
Year	1.07	0.48	2.25	1, 119	0.03	
Date	-0.008	0.01	-0.74	1, 119	0.51	
Sex	0.49	0.35	1.40	1, 115	0.16	
Age class	-18.74	2858.77	-0.007	1, 119	0.99	
Gravidity	0.93	0.67	1.39	1, 54	0.17	
Body condition	-5.25	12.95	-0.41	1, 84	0.73	
SVL	-0.04	0.06	-0.68	1, 119	0.59	
Trophic position	-0.62	0.49	-1.26	1, 119	0.51	
Conspecific abundance	-0.06	0.03	-2.12	1, 108	0.05	
Lizard abundance	-0.03	0.01	-2.52	1, 108	0.02	
Squamate richness	0.65	0.28	2.31	1, 108	0.02	

Table 4.5. Results for *S. cowlesi* – just Trombiculidae. Results of generalized linear models (family = negative binomial) exploring the relationship between ectoparasite counts of individual lizards and various explanatory variables.

	Coefficient	Standard Error	z	df	p	Tukey HSD
Site	-	-	-	6, 114	0.001	Several significant
Habitat	-	-	-	2, 118	0.003	DS > WS p = 0.05 DS > ECO p = 0.04
Year	0.79	0.64	1.24	1, 119	0.23	
Date	-0.01	0.01	-0.99	1, 119	0.32	
Sex	0.15	0.47	0.32	1, 115	0.75	
Age class	-18.14	2858.77	-0.006	1, 119	0.15	
Gravidity	0.61	0.71	0.86	1, 54	0.39	
Body condition	2.72	12.98	0.21	1, 84	0.83	
SVL	-0.004	0.04	-0.10	1, 119	0.92	
Trophic position	-0.99	0.66	-1.51	1, 119	0.22	
Conspecific abundance	-0.009	0.04	-0.25	1, 108	0.80	
Lizard abundance	-0.02	0.01	-1.13	1, 108	0.26	
Squamate richness	0.15	0.41	0.36	1, 108	0.69	

Table 4.6. Results for *S. cowlesi* – just Ixodidae (hard ticks). Results of generalized linear models (family = negative binomial) exploring the relationship between ectoparasite counts of individual lizards and various explanatory variables.

	Coefficient	Standard Error	z	df	p	Tukey HSD
Site	-	-	-	6, 114	0.003	Several significant
Habitat	-	-	-	2, 118	<0.001	DS > WS p = 0.07 ECO > WS p < 0.001
Year	1.28	0.54	2.36	1, 119	0.03	
Date	<0.001	0.01	0.005	1, 119	0.99	
Sex	1.56	0.66	2.38	1, 115	0.02	M > F
Age class	-17.96	2858.77	-0.006	1, 119	0.99	
Gravidity	-0.55	0.99	-0.56	1, 54	0.58	
Body condition	14.19	14.36	0.99	1, 84	0.32	
SVL	0.12	0.06	1.93	1, 119	0.09	
Trophic position	-0.41	0.75	-0.55	1, 119	0.48	
Conspecific abundance	-0.24	0.06	-3.72	1, 108	<0.001	
Lizard abundance	-0.09	0.03	-3.83	1, 108	<0.001	
Squamate richness	1.53	0.38	3.99	1, 108	<0.001	

Table 4.7. Best performing models ($\Delta_i < 2$) after automated model selection using function dredge in package MuMom, which explored every combination of explanatory variables after screening for multicollinearity. Data were subset to exclude juveniles and gravid females so that body condition could be included. Trophic position varied with habitat for most species, so was not included. Values are coefficients, + indicates a term was included in the model, and – indicates a term was not included.

Species	ΔAICc	Habitat	Year	Habitat*Year	Date	Sex	Body condition
A. inornata	0	+	+	+	-	-	-
	1.63	+	+	+	-0.03	-	-
	1.74	+	+	+	-	-	25.45
H maculata	0	-	-	-	-0.12	+	94.13
	0.21	+	-	-	-0.12	-	109.53
	0.38	-	-	-	-0.11	-	105.31
	0.41	-	-	-	-0.09	+	-
	0.89	+	-	-	-0.08	+	-
	1.31	+	-	-	-	+	-
	1.49	+	-	-	-0.11	+	82.34
	1.82	+	-	-	-0.08	-	-
	1.86	+	-	-	-	-	-
	1.95	-	-	-	-0.08	-	-
U. stansburiana	0	+	+	-	-	-	27.39
	0	+	+	+	-	-	27.39
	0.47	+	+	-	-	+	44.16
	0.47	+	+	+	-	+	44.16
	0.81	+	+	-	-	-	-
	0.81	+	+	+	-	-	-
S. cowlesi (all ectoparasites)	0	+	+	+	-	+	-
	0.30	-	+	-	-	+	-
	1.09	+	-	-	-	+	-
	1.10	+	+	+	-	-	-
S. cowlesi (Trombiculidae)	0	+	-	-	-	-	30.51
	0.47	-	-	-	-	-	-
	1.40	+	-	-	0.02	-	26.87
	1.55	+	-	-	-	-	-
	1.72	-	-	-	-	+	-
	1.72	-	+	-	-	-	-
S. cowlesi (Ixodida)	0	+	-	-	-	+	-
	0.76	+	-	-	-0.04	+	-
	1.04	+	+	-	-	+	-
	1.87	+	-	-	-	+	13.43

Table 4.8. Best performing models lumping across all species ($\Delta_i < 2$) after autos mated model selection using function dredge in package MuMom, which explored every combination of explanatory variables after screening for multicollinearity. Data were subset to exclude juveniles and gravid females so that body condition could be included. Trophic position varied with habitat for most species, so was not included. Values are coefficients, + indicates a term was included in the model, and – indicates a term was not included.

ΔAICc	Species	Habitat	Species*Habitat	Year	Habitat*Year	Date	Sex
0	+	+	-	+	+	-0.02	+
0.71	+	+	-	+	+	-	+
0.93	+	+	+	+	+	-	+

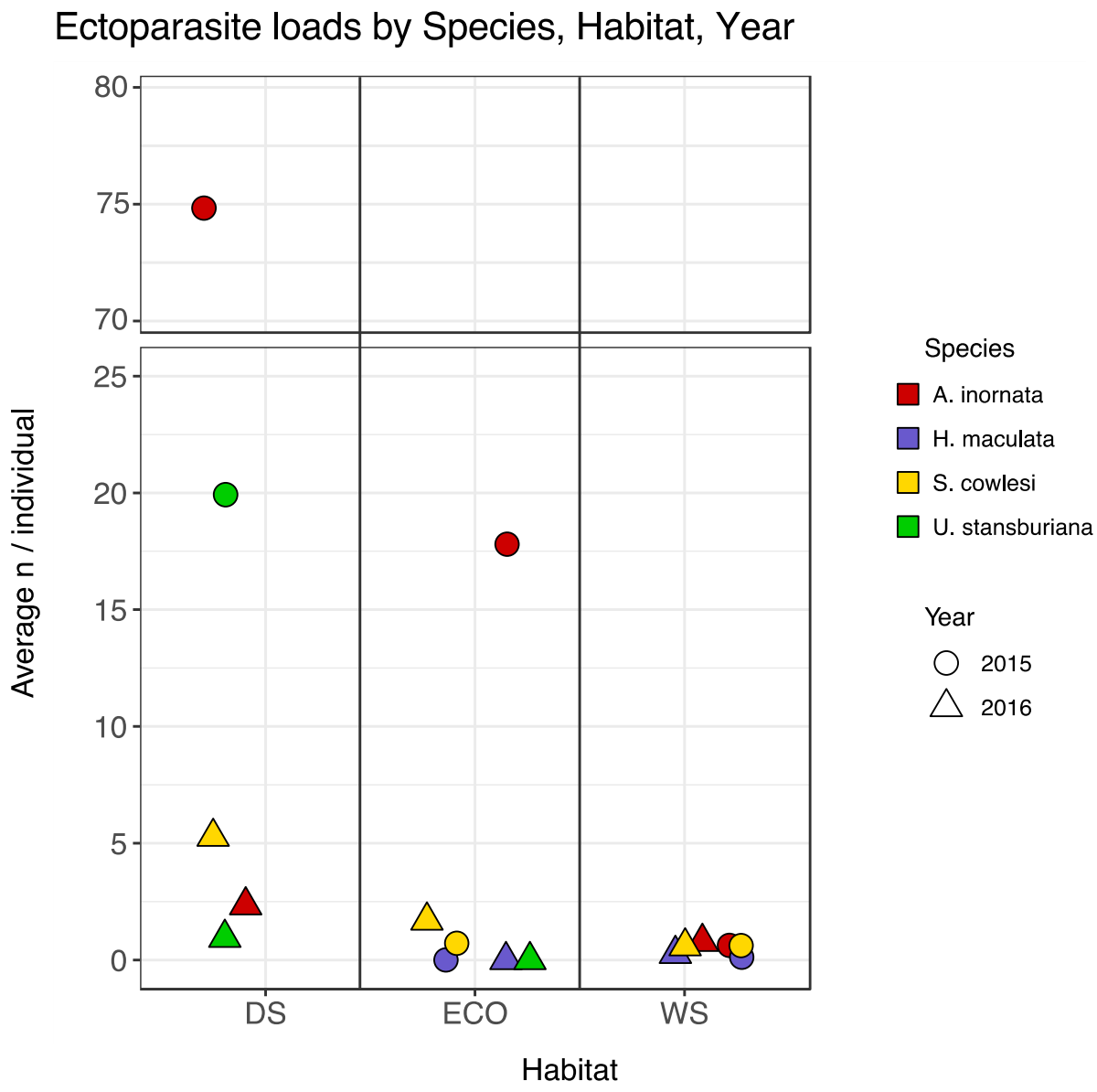

Fig 4.1. Mean number of ectoparasites per individual per date and habitat (DS – desert scrub, ECO – ecotone, WS – White Sands). Horizontal jittering was used to reduce point overlap. Error bars were omitted in order to increase the clarity of the figure. Note that ecotonal *U. stansburiana* and *A. inornata* in 2016 are not visible due to point clustering, their means were 0. The high *A. inornata* 2015 ecotonal mean was driven by an outlier with n = 88.

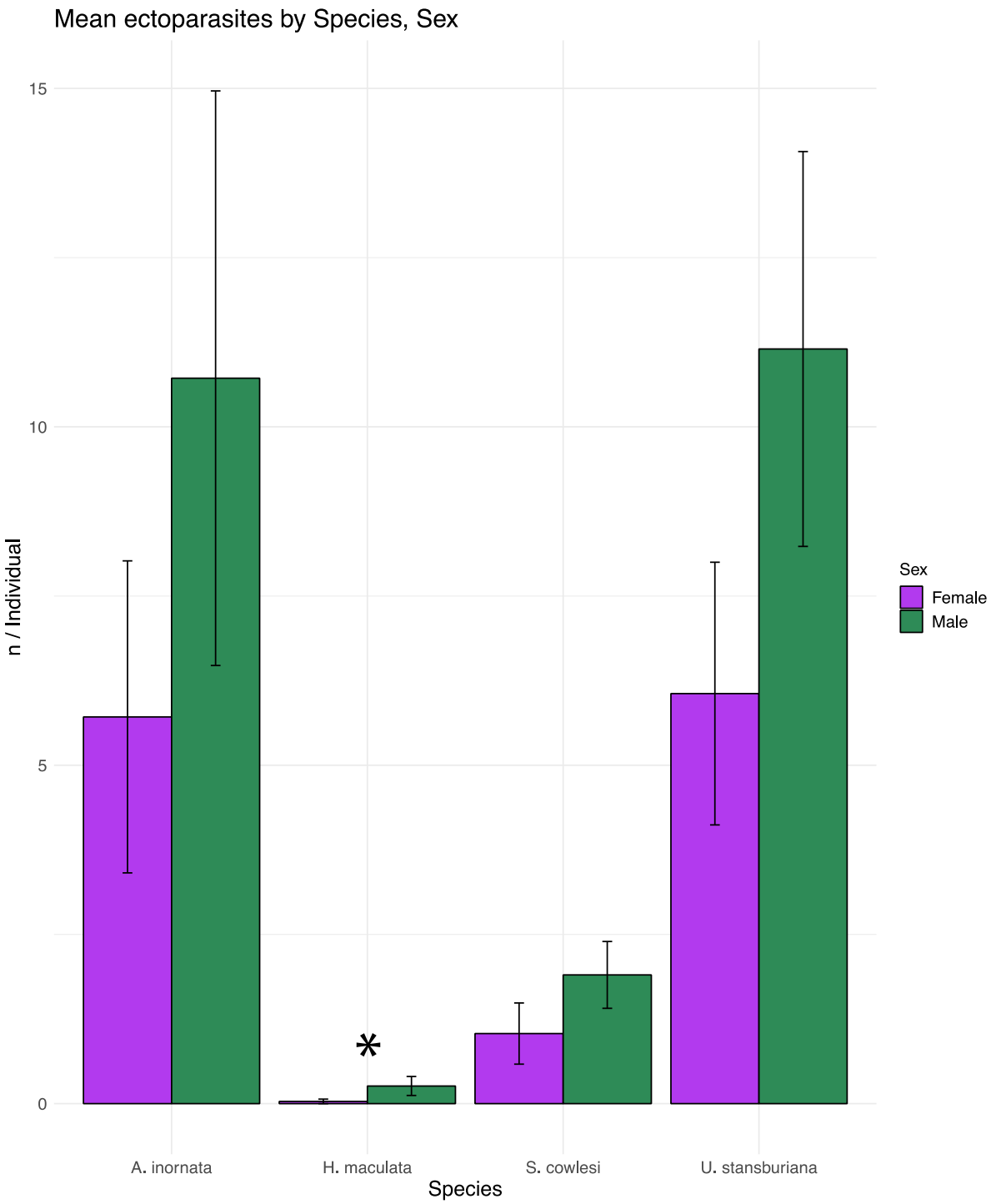

Fig 4.2. Mean number of ectoparasites per individual by sex by species. Error bars represent the standard error of the mean. Asterisk indicates the cases where the difference between sexes had $p < 0.1$ when subset by species. Males had significantly more Ixodidae than females for *S. cowlesi*, but not all ectoparasites or Trombiculidae.

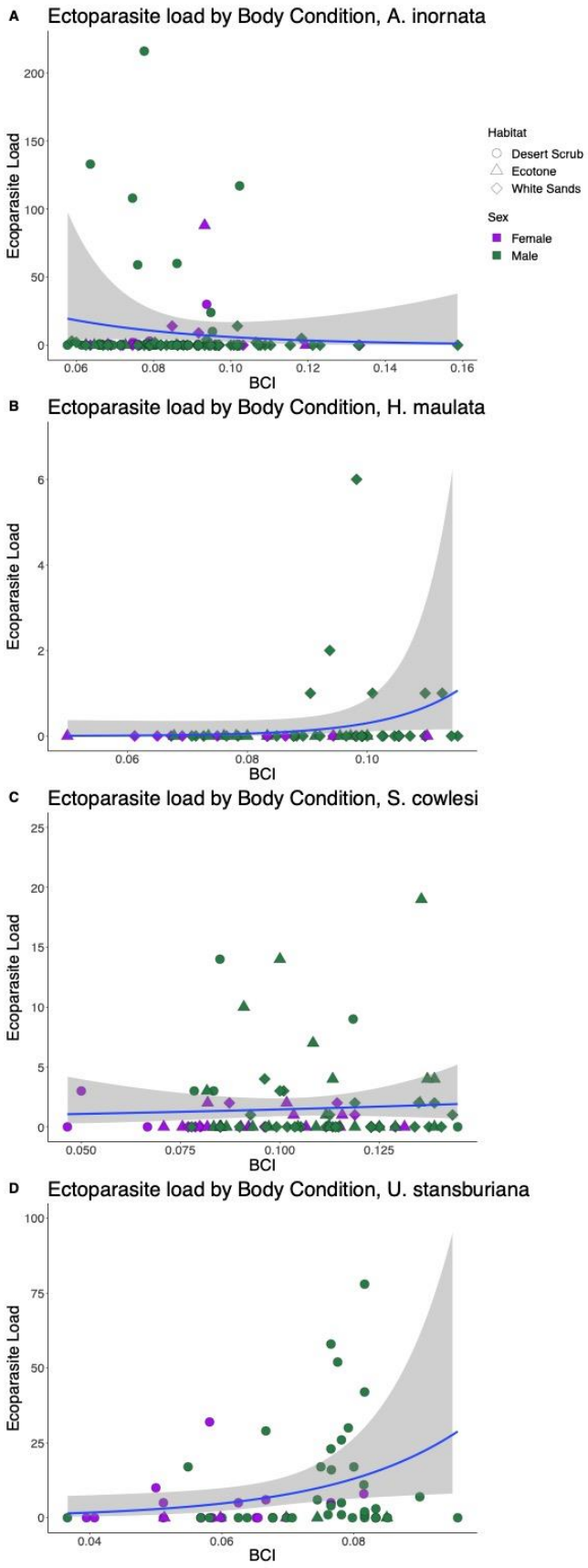

Fig 4.3. Relationship between ectoparasite loads (counts) and BCI (mass/SVL), across individuals. Blue line represents fitted GLM (family = negative binomial), shading the standard error of the estimate.

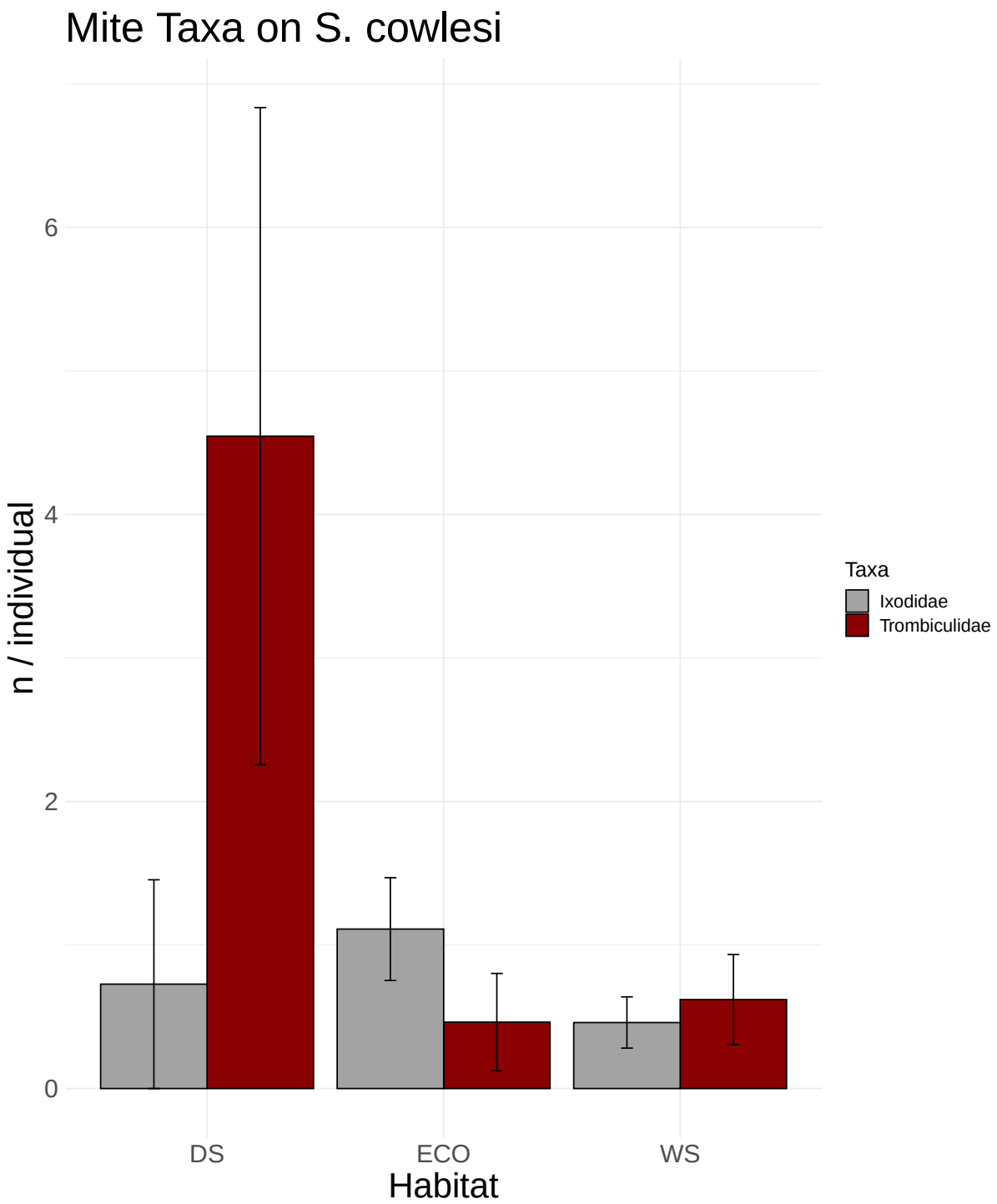

Fig 4.4. Mean number of ectoparasites per taxa (Ixodidae – ticks, Trombiculidae – mites) by habitat (desert scrub, ecotone and White Sands). All but two Ixodidae were caught on *S. cowlesi*. Error bars represent the standard error of the mean. Males had significantly more Ixodida than females, but not all ectoparasites or Trombiculidae.

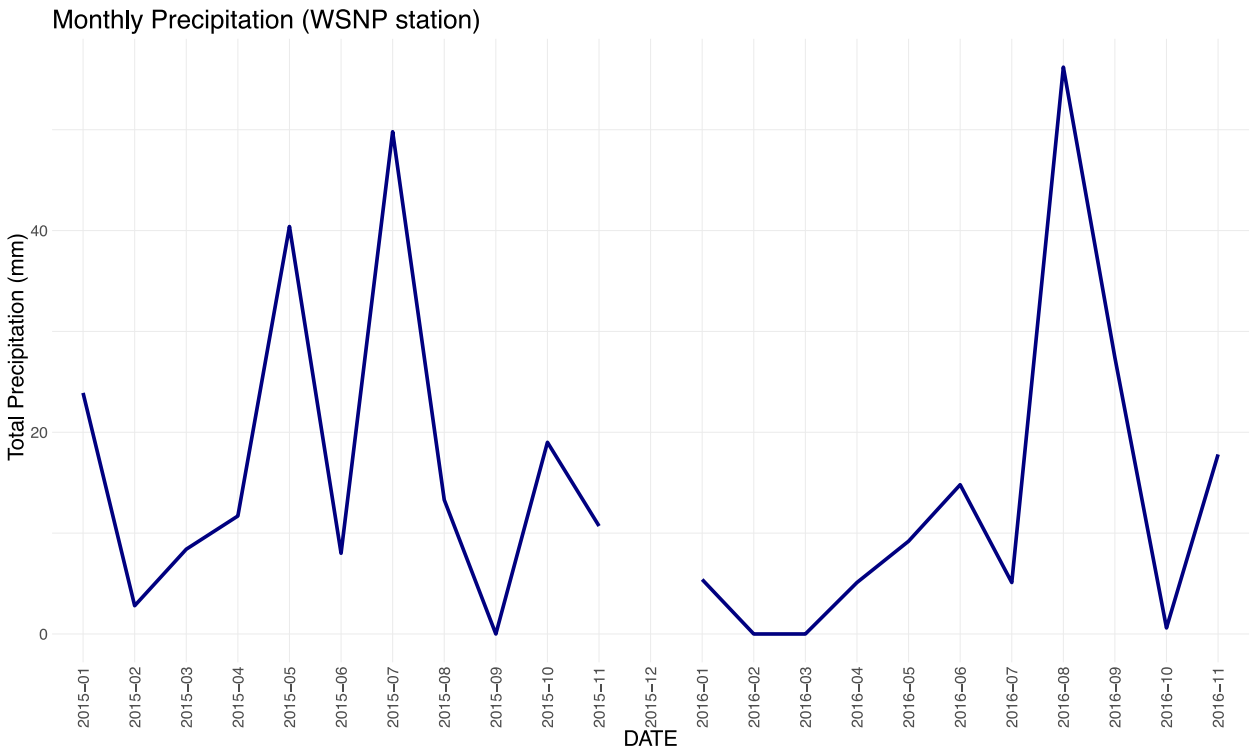

Figure 4.5. Total monthly precipitation records at White Sands National Park headquarters (near multiple study sites) from January 2015 to November 2011. Lizard sampling occurred from 6/17-8/12 in 2015 and 6/10-7/30 in 2016. Note that no recording was made in December 2015.

CHAPTER 5
CONCLUSIONS

Understanding the community scale ramifications of ecological release is challenging. Ecological release is characterized by multiple processes changing in tandem. My dissertation takes advantage of multiple species occurring on an ecological gradient across White Sands, the surrounding desert scrub and their ecotone to understand these consequences.

In Chapter 2, examining lizard trophic niche along this gradient revealed substantial differences in population niche width, individual specialization and trophic position within a relatively small area. Echoing prior work on convergence in the White Sands lizards, I found that these patterns were generally conserved between species and years. Resource diversity, intra and interspecific competition and predation intersect to shape all trophic niche metrics. One result of this is that individual specialization and population niche width can be surprisingly decoupled. My experimental work in Chapter 3 demonstrated that White Sands lizards can exert strong top down effects on arthropods that cascades to herbivory. In this system where lizards are one guild in a diverse community including carnivorous arthropods like spiders, compensatory predation was likely important for dampening these effects. We conclude that ecologists need to consider top down forcing by carnivores in other desert systems, including more diverse communities where lizards have not undergone ecological release. Finally, in Chapter 4 I found that increased mite ectoparasitism was not a consequence of ecological release from predators and competitors in White Sands. Unlike predators and competitors, however, the relative release from ectoparasites was highly mediated by year. More work is needed to understand mechanisms behind lower parasitism in White Sands. Our results are consistent with hypotheses that density (encounter-dilution effects), species diversity (diverse hosts as reservoirs) and abiotic differences could influence mite ectoparasitism in lizards.

I used a mixture of observational and experimental approaches grounded in natural history to examine White Sands lizards and the broader ecological community in the context of ecological release. My dissertation demonstrates that it is essential to consider multiple ecological processes in conjunction to understand the consequences of shifts in species diversity and composition.

REFERENCES

1 Terborgh, J. & Estes, J. A. *Trophic cascades: predators, prey, and the changing dynamics of nature*. (Island press, 2013).

2 Yoder, J. *et al.* Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology* **23**, 1581-1596 (2010).

3 Herrmann, N. C., Stroud, J. T. & Losos, J. B. The evolution of 'Ecological Release'into the 21st century. *Trends in Ecology & Evolution* **36**, 206-215 (2021).

4 Schluter, D. *The ecology of adaptive radiation*. (OUP Oxford, 2000).

5 Muldavin, E., Chauvin, Y., Schulz, K., Neville, T., Neville, P., Smith, J. & Fettes, A. A Vegetation Classification and Map, White Sands National Monument. Natural Resource Report NPS/WHSA/NRR - 2019/1906, National Park Service (2019).

6 Roches, S. D., *et al.* Ecological release in White Sands lizards. *Ecology and Evolution* **1**, 571-578 (2011).

7 Burkett, D. *Amphibians and Reptiles of White Sands Missile Range*. 2nd Edition. (ECO Inc., 2016).

8 Degenhardt, W. G., Painter, C. W. & Price, A. H. *Amphibians and reptiles of New Mexico*. (UNM Press, 2005).

9 Rosenblum, E. B. & Harmon, L. J. "Same same but different": replicated ecological speciation at White Sands White Sands. *Evolution* **65**, 946-960 (2011).

10 Roches, S. D., Harmon, L. J. & Rosenblum, E. B. Colonization of a novel depauperate habitat leads to trophic niche shifts in three desert lizard species. *Oikos* **125**, 343-353 (2016).

11 Robertson, J. M. *et al*. Colonization of novel White Sands habitat is associated with changes in lizard anti-predator behaviour White Sands. *Biological journal of the Linnean Society* **103**, 657-667 (2011).

12 Roches, S. D. *et al*. Ecological release and directional change in White Sands lizard trophic ecomorphology White Sands. *Evolutionary Ecology* **29**, 1-16 (2015).

13 Refsnider, J. M., Des Roches, S. & Rosenblum, E. B. Evidence for ecological release over a fine spatial scale in a lizard from the White Sands formation. *Oikos* **124**, 1624-1631 (2015).

14 Bolnick, D. I. *et al.* Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* **26**, 183-192 (2011).

15 Bolnick, D. I. *et al.* The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist* **161**, 1-28 (2003).

16 Post, D. M. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703-718 (2002).

17 Costa-Pereira, R., Araújo, M. S., Souza, F. L. & Ingram, T. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20190369 (2019).

18 Van Valen, L. Morphological variation and width of ecological niche. *The American Naturalist* **99**, 377-390 (1965).

19 Jones, A. W. & Post, D. M. Does intraspecific competition promote variation? A test via synthesis. *Ecology and Evolution* **6**, 1646-1655 (2016).

20 Roughgarden, J. Niche width: biogeographic patterns among Anolis lizard populations. *The American Naturalist* **108**, 429-442 (1974).

21 Vamosi, S. M. On the role of enemies in divergence and diversification of prey: a review and synthesis. *Canadian Journal of Zoology* **83**, 894-910 (2005).

22 Araújo, M. S., Bolnick, D. I. & Layman, C. A. The ecological causes of individual specialisation. *Ecology Letters* **14**, 948-958 (2011).

23 Costa-Pereira, R. *et* al. Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology* **87**, 1452-1464 (2018).

24 Eloranta, A. P. *et al.* Species interactions, environmental gradients and body size shape population niche width. *Journal of Animal Ecology* **91**, 154-169 (2022).

25 Estes, J. A. *et al.* Trophic Downgrading of Planet Earth. *Science* **333**, 301-306 (2011).

26 Pacioretty, M. T. *et al.* Experimental exclusion of insectivorous predators results in no responses across multiple trophic levels in a water-limited, sagebrush-steppe ecosystem. *Journal of Arid Environments* **160**, 74-81 (2019).

27 Oksanen, L., Fretwell, S. D., Arruda, J. & Niemela, P. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**, 240-261 (1981).

28 Noy-Meir, I. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**, 25-51 (1973).

29 Murdoch, W. W. " Community Structure, Population Control, and Competition"-A Critique. *The American Naturalist* **100**, 219-226 (1966).

30 Borer, E. *et al.* What determines the strength of a trophic cascade? *Ecology* **86**, 528-537 (2005).

31 Borer, E. T., Halpern, B. S. & Seabloom, E. W. Asymmetry in community regulation: effects of predators and productivity. *Ecology* **87**, 2813-2820 (2006).

32 Heske, E. J., Brown, J. H. & Mistry, S. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition Chihuahuan Desert Desert Trophic Intera. *Ecology* **75,** 438-445 (1994).

33 Brown, J. H., Whitham, T. G., Morgan Ernest, S. & Gehring, C. A. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* **293**, 643-650 (2001).

34 Castle, G. *et al.* Top-predator removal does not cause trophic cascades in Australian rangeland ecosystems. *Food Webs* **31,** e00229 (2022).

35 Wiens, J. A. *et al.* Arthropod dynamics on sagebrush (Artemisia tridentata): effects of plant chemistry and avian predation. *Ecological Monographs* **61**, 299-322 (1991).

36 Bang, C., Faeth, S. H. & Sabo, J. L. Control of arthropod abundance, richness, and composition in a heterogeneous desert city. *Ecological Monographs* **82**, 85-100 (2012).

37 Jessop, T. S. *et al.* Komodo dragons are not ecological analogs of apex mammalian predators. *Ecology* **101**, e02970 (2020).

38 Schoener, T. W. & Spiller, D. A. Trophic cascades on islands. in *Trophic Cascades: Predators, prey, and the changing dynamics of nature*, 179-202 (2010).

39 Sutherland, D. R., Glen, A. S. & de Tores, P. J. Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? *Proceedings of the Royal Society B: Biological Sciences* **278**, 641-648 (2011).

40 Prugh, L. R. *et al.* The rise of the mesopredator. *Bioscience* **59**, 779-791 (2009).

41 Frye, F. L. *Biomedical and surgical aspects of captive reptile husbandry*. (Veterinary Medicine Publishing Co., 1981).

42 Sorci, G., Massot, M. & Clobert, J. Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. *The American Naturalist* **144**, 153-164 (1994).

43 Levine, J. F. *et al.* Lizards as hosts for immature Ixodes scapularis (Acari: Ixodidae) in North Carolina. *Journal of Medical Entomology* **34**, 594-598 (1997).

44 Spence, A. R. *et al*. Physiological correlates of multiple parasitic infections in side-blotched lizards. *Physiological and Biochemical Zoology* **90**, 321-327 (2017).

45 Godfrey, S. S., Nelson, N. J. & Bull, C. M. Microhabitat choice and host-seeking behaviour of the tuatara tick, Amblyomma sphenodonti (Acari: Ixodidae). *New Zealand Journal of Ecology*, 52-60 (2011).

46 Klukowski, M. Seasonal changes in abundance of host-seeking chiggers (Acari: Trombiculidae) and infestations on fence lizards, Sceloporus undulatus. *Journal of Herpetology* **38**, 141-144 (2004).

47 Mugabo, M. *et al*. Density-dependent immunity and parasitism risk in experimental populations of lizards naturally infested by ixodid ticks. *Ecology* **96**, 450-460 (2015).

48 Ostfeld, R. S. & Keesing, F. Biodiversity and disease risk: the case of Lyme disease. *Conservation biology* **14**, 722-728 (2000).

49 Tälleklint-Eisen, L. & Eisen, R. J. Abundance of ticks (Acari: Ixodidae) infesting the western fence lizard, Sceloporus occidentalis, in relation to environmental factors. *Experimental & applied acarology* **23**, 731-740 (1999).

50 Smolinský, R., Hiadlovska, Z. & Martinkova, N. Ectoparasite load increase in reproductively active sand lizards. *Journal of Vertebrate Biology* **70**, 20128.20121(2021).

51 Pollock, N. B. & John-Alder, H. B. Sex-and Age-Specific Effects are Superimposed on Seasonal Variation in Mite Parasitism in Eastern Fence Lizards (Sceloporus undulatus). *Journal of Herpetology* **54**, 273-281 (2020).

52 Argaez, V., Solano-Zavaleta, I. & Zúñiga-Vega, J. J. Do ectoparasites affect survival of three species of lizards of the genus Sceloporus? *Zoology* **138**, 125723 (2020).

53 Rosenblum, E. B., Römpler, H. & Schöneberg, T. Molecular and functional basis of phenotypic convergence in white lizards at White Sands White Sands. *Proceedings of the National Academy of Science* **107**, 2113-2117 (2010).

54 Roulin, A., Riols, C., Dijkstra, C. & Ducrest, A.-L. Female plumage spottiness signals parasite resistance in the barn owl (Tyto alba). *Behavioral Ecology* **12**, 103-110 (2001).

55 Moya-Laraño, J. Genetic variation, predator–prey interactions and food web structure. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 1425-1437 (2011).

56 Svanbäck, R., Quevedo, M., Olsson, J. & Eklöv, P. Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia* **178**, 103-114 (2015).

57 Wilson, E. O. The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist* **95**, 169-193 (1961).

58 Stroud, J. T. & Losos, J. B. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **47**, 507-532 (2016).

59 MacArthur, R. H., Diamond, J. M. & Karr, J. R. Density compensation in island faunas. *Ecology* **53**, 330-342 (1972).

60 Bolnick, D. I. *et al.* Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B: Biological Sciences* **277**, 1789-1797 (2010).
61 Bolnick, D. I. *et al.* Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 10075-10079 (2007).
62 Hairston, N. G., Smith, F. E. & Slobodkin, L. B. Community structure, population control, and competition. *The American Naturalist* **94**, 421-425 (1960).
63 Svanbäck, R. & Bolnick, D. I. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings. Biological Sciences* **274**, 839-844 (2007).
64 Bolnick, D. I. Intraspecific competition favours niche width expansion in Drosophila melanogaster. *Nature* **410**, 463-466 (2001).
65 Costa, G. C. *et al*. Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages? *The American Naturalist* **172**, 868-877 (2008).
66 Peacor, S. D., Schiesari, L. & Werner, E. E. Mechanisms of nonlethal predator effect on cohort size variation: ecological and evolutionary implications. *Ecology* **88**, 1536-1547 (2007).
67 Belgrad, B. A. & Griffen, B. D. Predator–prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160408 (2016).
68 Sánchez-Hernández, J. *et al*. Beyond ecological opportunity: Prey diversity rather than abundance shapes predator niche variation. *Freshwater Biology*, fwb.13606-fwb.13606 (2021).
69 Layman, C. A. *et al.* Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews* **87**, 545-562 (2012).
70 Silvy, N. J. *The Wildlife Techniques Manual: Volume 1: Research. Volume 2: Management*. (JHU Press, 2020).
71 Gamble, L. R. Comparative effectiveness of two trapping techniques for surveying the abundance and diversity of reptiles and amphibians along drift fence arrays. *Herpetological Review* **34**, 39 (2003).
72 Costa, G. C. *et al*. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* **17**, 670-677 (2008).
73 Legler, J. M. & Sullivan, L. J. The application of stomach-flushing to lizards and anurans. *Herpetologica*, 107-110 (1979).
74 Vander Zanden, M. J. *et al*. Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PloS one* **10**, e0116182 (2015).
75 Post, D. M. *et al.* Getting to the fat of the matter: models, methods and assumptions for dealign with lipids in stable isotope analyses. *Oecologia* **152**, 179-189 (2007).
76 Ruiz-Cooley, R., Garcia, K. & Hetherington, E. Effects of lipid removal and preservatives on carbon and nitrogen stable isotope ratios of squid tissues: implications for ecological studies. *Journal of Experimental Marine Biology and Ecology* **407**, 101-107 (2011).
77 Zuur, A. F., Ieno, E. N. & Smith, G. M. *Analysing ecological data*. Vol. 680 (Springer, 2007).

78 Benhadi-Marín, J. & Sven Schmeller, D. A conceptual framework to deal with outliers in ecology. *Biodiversity and Conservation* **27**, 3295-3300 (2018).
79 Quinby, B. M., Creighton, J. C. & Flaherty, E. A. Stable isotope ecology in insects: a review. *Ecological Entomology* **45**, 1231-1246 (2020).
80 Gibb, H. & Cunningham, S. A. Habitat contrasts reveal a shift in the trophic position of ant assemblages. *Journal of Animal Ecology* **80**, 119-127 (2011).
81 Lagerlöf, J., Maribie, C. & John, J. M. Trophic interactions among soil arthropods in contrasting land-use systems in Kenya, studied with stable isotopes. *European Journal of Soil Biology* **79**, 31-39 (2017).
82 Jackson, A. L. *et al*. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**, 595-602 (2011).
83 Shaner, P. J. L., Chen, Y. K. & Hsu, Y. C. Niche–trait relationships at individual and population level in three co-occurring passerine species. *Ecology and Evolution* **00**, ece3.7569-ece7563.7569 (2021).
84 Littleford-Colquhoun, B. L. *et al*. City life alters the gut microbiome and stable isotope profiling of the eastern water dragon (*Intellagama lesueurii*). *Molecular Ecology* **28**, 4592-4607 (2019).
85 Nunes, S. F. *et al.* Trophic niche changes associated with the eradication of invasive mammals in an insular lizard: an assessment using isotopes. *Current Zoology* **68**, 211-219 (2021).
86 Bolnick, D. I. *et al*. Measuring Individual-Level Resource Specialization. *Ecology* **83**, 2936-2936 (2002).
87 Araújo, M. S. *et al*. & dos Reis, S. F. Using δ13C stable isotopes to quantify individual-level diet variation. *Oecologia* **152**, 643-654 (2007).
88 Refsnider, J. M. *et al*. Is dietary or microhabitat specialization associated with environmental heterogeneity in horned lizards *Phyrnosoma*? *Ecology and Evolution* **9**, 5542-5550 (2019).
89 Takimoto, G., Spiller, D. A. & Post, D. M. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. *Ecology* **89**, 3001-3007 (2008).
90 Pringle, R. M. *et al.* Predator-induced collapse of niche structure and species coexistence. *Nature* **570**, 58-64 (2019).
91 R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/ (2022).
92 Biaggini, M. *et al.* The taxonomic level order as a possible tool for rapid assessment of Arthropod diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment* **122**, 183-191 (2007).
93 Zuur, A. *et al*. *Mixed effects models and extensions in ecology with R*. (Springer Science & Business Media, 2009).
94 Bates, D. *et al*. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**, 1-48 (2015).
95 Fox, J. & Monette, G. Generalized collinearity diagnostics. *Journal of the American Statistical Association* **87**, 178-183 (1992).
96 Barton, K. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn (2020).

97 Anderson, D. & Burnham, K. *Model selection and multi-model inference*. (Springer-Verlag, 2004).

98 Fox, J. & Weisberg, S. *An R companion to applied regression*. (Sage publications, 2018).

99 Maria, A. *et al.* Feeding Strategies of Co-occurring Newt Species across Different Conditions of Syntopy: A Test of the "Within-Population Niche Variation" Hypothesis. *Diversity* **12**, 181 (2020)

100 Warne, R. W. & Wolf, B. O. Nitrogen stable isotope turnover and discrimination in lizards. *Rapid Communications in Mass Spectrometry* **35**, e9030 (2021).

101 Taper, M. L. & Chase, T. J. Quantitative genetic models for the coevolution of character displacement. *Ecology* **66**, 355-371 (1985).

102 Ackermann, M. & Doebeli, M. Evolution of niche width and adaptive diversification. *Evolution* **58**, 2599-2612 (2004).

103 Sjödin, H., Ripa, J. & Lundberg, P. Principles of niche expansion. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20182603 (2018).

104 Warne, R. W., Pershall, A. D. & Wolf, B. O. Linking precipitation and C_3—C_4 plant production to resource dynamics in higher-trophic- level consumers. *Ecology* **91**, 1628-1638 (2010).

105 Kark, S. & Van Rensburg, B. J. Ecotones: marginal or central areas of transition? *Israel Journal of Ecology and Evolution* **52**, 29-53 (2006).

106 Schoener, T. W. Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* **185**, 27-39 (1974).

107 Post, D. M. *et al*. Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* **89**, 2019-2032 (2008).

108 Polis, G. A. & Strong, D. R. Food web complexity and community dynamics. *The American Naturalist* **147**, 813-846 (1996).

109 Polis, G. A. *et al*. When is a trophic cascade a trophic cascade? *Trends in ecology & evolution* **15**, 473-475 (2000).

110 Power, M. E. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* **73**, 733-746 (1992).

111 McCluney, K. E. *et al.* Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews* **87**, 563-582 (2012).

112 Middleton, N. & Thomas, D. *World atlas of desertification. ed. 2*. (Arnold, Hodder Headline, PLC, 1997).

113 Li, D. *et al*. Vulnerability of the global terrestrial ecosystems to climate change. *Global change biology* **24**, 4095-4106 (2018).

114 Oksanen, L. & Oksanen, T. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist* **155**, 703-723 (2000).

115 Fretwell, S. D. & Barach, A. L. The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine* **20**, 169-185 (1977).

116 Fischer, C., Gerstmeier, R. & Wagner, T. C. Seasonal and temporal patterns of rainfall shape arthropod community composition and multi-trophic interactions in an arid environment. *Scientific reports* **12**, 1-9 (2022).

117 Peters, D. P. *et al.* Plant Species Richness in Multiyear Wet and Dry Periods in the Chihuahuan Desert. *Climate* **9**, 130 (2021).
118 Reynolds, J. F. *et al.* Modifying the 'pulse–reserve'paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* **141**, 194-210 (2004).
119 Ward, D. *The biology of deserts*. (Oxford University Press, 2016).
120 Brown, J. H., Valone, T. J. & Curtin, C. G. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences* **94**, 9729-9733 (1997).
121 Báez, S. *et al.* Bottom-up regulation of plant community structure in an aridland ecosystem. *Ecology* **87**, 2746-2754 (2006).
122 Gibb, H. *et al.* Testing top-down and bottom-up effects on arid zone beetle assemblages following mammal reintroduction. *Austral Ecology* **43**, 288-300 (2018).
123 Collins, S. L. *et al.* A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems. *Annu. Rev. Ecol. Evol. Syst* **45**, 397-419 (2014).
124 Grime, J. P. & Pierce, S. *The evolutionary strategies that shape ecosystems*. (John Wiley & Sons, 2012).
125 Schoener, T. W. Leaf damage in island buttonwood, Conocarpus erectus: correlations with pubescence, island area, isolation and the distribution of major carnivores. *Oikos*, 253-266 (1988).
126 Heath, M. R., Speirs, D. C. & Steele, J. H. Understanding patterns and processes in models of trophic cascades. *Ecology Letters* **17**, 101-114 (2014).
127 Ayal, Y. Trophic structure and the role of predation in shaping hot desert communities. *Journal of Arid Environments* **68**, 171-187 (2007).
128 Chase, J. M. Strong and weak trophic cascades along a productivity gradient. *Oikos* **101**, 187-195 (2003).
129 Letnic, M., Feit, A. & Forsyth, D. M. Strength of a Trophic Cascade Between an Apex Predator, Mammalian Herbivore and Grasses in a Desert Ecosystem Does Not Vary with Temporal Fluctuations in Primary Productivity. *Ecosystems* **21**, 153-165 (2018).
130 Rodríguez-Castañeda, G. The world and its shades of green: A meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography* **22**, 118-130 (2013).
131 Ernest, S. M., Brown, J. H. & Parmenter, R. R. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* **88**, 470-482 (2000).
132 Letnic, M., Tamayo, B. & Dickman, C. R. The responses of mammals to La Nina (El Nino Southern Oscillation)–associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689-703 (2005).
133 Lima, M., Stenseth, N. C. & Jaksic, F. M. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. *Ecology Letters* **5**, 273-284 (2002).
134 Ferrante, M. *et al.* Invertebrate and vertebrate predation rates in a hyperarid ecosystem following an oil spill. *Ecology and Evolution* **11**, 12153-12160 (2021).
135 Sagi, N. & Hawlena, D. Arthropods as the engine of nutrient cycling in arid ecosystems. *Insects* **12**, 726 (2021).
136 Polis, G. A. Complex trophic interactions in deserts: an empirical critique of food-web theory. *The American Naturalist* **138**, 123-155 (1991).

137 McCluney, K. E. & Sabo, J. L. Water availability directly determines per capita consumption at two trophic levels. *Ecology* **90**, 1463-1469 (2009).
138 Morris, T. & Letnic, M. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proceedings of the Royal Society B: Biological Sciences* **284**, 284.1854 (2017).
139 Contos, P. & Letnic, M. Top-down effects of a large mammalian carnivore in arid Australia extend to epigeic arthropod assemblages. *Journal of Arid Environments* **165**, 16-27 (2019).
140 Lyons, M. B., Mills, C. H., Gordon, C. E. & Letnic, M. Linking trophic cascades to changes in desert dune geomorphology using high-resolution drone data. *Journal of The Royal Society Interface* **15**, 144 (2018).
141 Turkington, R. Top-down and bottom-up forces in mammalian herbivore–vegetation systems: an essay review. *Botany* **87**, 723-739 (2009).
142 Mackay, D.A. The effects of ants on herbivory and herbivore numbers on foliage of the mallee eucalypt, Eucalyptus incrassata Labill. *Australian Journal of Ecology* **16**, 471-483 (1991).
143 Megías, A. G., Sánchez-Piñero, F. & Hódar, J. A. Trophic interactions in an arid ecosystem: From decomposers to top-predators. *Journal of Arid Environments* **75**, 1333-1341 (2011).
144 Pacala, S. & Roughgarden, J. Control of arthropod abundance by Anolis lizards on St. Eustatius (Neth. Antilles). *Oecologia* **64**, 160-162 (1984).
145 Schoener, T. W. & Toft, C. A. Spider populations: extraordinarily high densities on islands without top predators. *Science* **219**, 1353-1355 (1983).
146 Piovia-Scott, J., Yang, L. H., Wright, A. N., Spiller, D. A. & Schoener, T. W. Pulsed seaweed subsidies drive sequential shifts in the effects of lizard predators on island food webs. *Ecology Letters* **22**, 1850-1859 (2019).
147 Spiller, D. A. & Schoener, T. W. An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs* **58**, 57-77 (1988).
148 Spiller, D. A. & Schoener, T. W. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* **83**, 150-161 (1990).
149 Spiller, D. A. & Schoener, T. W. Climatic control of trophic interaction strength: the effect of lizards on spiders. *Oecologia* **154**, 763-771 (2008).
150 Feit, B., Dempster, T., Jessop, T. S., Webb, J. K. & Letnic, M. A trophic cascade initiated by an invasive vertebrate alters the structure of native reptile communities. *Global Change Biology*, 2829-2840 (2020).
151 Read, J. L. & Scoleri, V. Ecological implications of reptile mesopredator release in arid South Australia. *Journal of Herpetology* **49**, 64-69 (2015).
152 Strong, D. R. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**, 747-754 (1992).
153 Newton, B. T. & Allen, B. Hydrologic Investigation at White Sands National Monument. Open-file Report 559. New Mexico Bureau of Geology and Mineral Resources, Aquifer Mapping Program (2014).
154 National Integrated Drought Information Sytstem. National Oceanic and Atmospheric Administration. www.drought.gov (2022).
155 Manicom, C. *et al*. Self-made shelters protect spiders from predation. *Proceedings of the National Academy of Sciences* **105**, 14903-14907 (2008).

156 Blackmer, J. L., Byers, J. A. & Rodriguez-Saona, C. Evaluation of color traps for monitoring Lygus spp.: design, placement, height, time of day, and non-target effects. *Crop Protection* **27**, 171-181 (2008).
157 Frank, D. A. & McNaughton, S. J. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. *Oikos*, 57-60 (1990).
158 Stotz, H. U. *et al.* Induced plant defense responses against chewing insects. Ethylene signaling reduces resistance of Arabidopsis against Egyptian cotton worm but not diamondback moth. *Plant Physiology* **124**, 1007-1018 (2000).
159 Johnson, M. T., Bertrand, J. A. & Turcotte, M. M. Precision and accuracy in quantifying herbivory. *Ecological Entomology* **41**, 112-121 (2016).
160 Singmann, H. *et al.* afex: Analysis of factorial experiments. R package version 0.13–145 (2015).
161 Hothorn, T. *et al.* Package 'multcomp'. Simultaneous inference in general parametric models. R package version 1.4-19. http://mulcomp.R-forge.R.R-project.org (2022).
162 Hartig, F. & Hartig, M. F. Package 'DHARMa' Residual diagnostics for hierarchical (Multi - Level / Mixed). R package version 0.3.0. http://florianhartig.github.io/DHARMa (2020).
163 Maestre, F. T. *et al.* Structure and Functioning of Dryland Ecosystems in a Changing World. *Annual Review of Ecology, Evolution, and Systematics* **47**, 215-237 (2016).
164 Nordberg, E. J., Edwards, L. & Schwarzkopf, L. Terrestrial invertebrates: An underestimated predator guild for small vertebrate groups. *Food Webs* **15**, e00080 (2018).
165 Reyes-Olivares, C. *et al.* Lizard predation by spiders: A review from the Neotropical and Andean regions. *Ecology and Evolution* **10**, 10953-10964 (2020).
166 McCormick, S. & Polis, G. A. Arthropods that prey on vertebrates. *Biological Reviews* **57**, 29-58 (1982).
167 Valdez, J. W. Arthropods as vertebrate predators: A review of global patterns. *Global Ecology and Biogeography* **29**, 1691-1703 (2020).
168 Polis, G. A. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, 3-15 (1999).
169 Oksanen, T. *et al.* The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. *Ecography* **43**, 1859-1877 (2020).
170 Durtsche, R. D. Feeding time strategies of the fringe-toed lizard, Uma inornata, during breeding and non-breeding seasons. *Oecologia* **89**, 85-89 (1992).
171 Maute, K. *et al.* Surviving drought: a framework for understanding animal responses to small rain events in the arid zone. *Ecology* **100**, e02884 (2019).
172 Whitford, W. G. & Ettershank, G. Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environmental Entomology* **4**, 689-696 (1975).
173 Kamill, B. W., Steinberger, Y. & Whitford, W. Soil microarthropods from the Chihuahuan desert of New Mexico. *Journal of Zoology* **205**, 273-286 (1985).
174 Znari, M. & Nagy, K. A. Field metabolic rate and water flux in free-living Bibron's agama (*Agama impalearis*, Boettger, 1874) in Morocco. *Herpetologica*, 81-88 (1997).
175 Nagy, K. A. Seasonal patterns of water and energy balance in desert vertebrates. *Journal of Arid Environments* **14**, 201-210 (1988).
176 Schmitz, O. J., Krivan, V. & Ovadia, O. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**, 153-163 (2004).

177 Harrower, W. L. *Changes in trophic structure along a gradient of water availability in temperate montane grasslands*, University of British Columbia, (2017).
178 Rusek, J. Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity & Conservation* **7**, 1207-1219 (1998).
179 Santos, P. F. & Whitford, W. G. The Effects of Microarthropods on Litter Decomposition in a Chihuahuan Desert Ecosystem. *Ecology* **62**, 654-663, (1981).
180 Uetz, G. W. & Unzicker, J. D. Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology*, 101-111 (1975).
181 Lang, A. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. *Anzeiger für Schädlingskunde= Journal of Pest Science* **73**, 99-106 (2000).
182 Maschinski, J. & Whitham, T. G. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The American Naturalist* **134**, 1-19 (1989).
183 González-Juárez, D. E. *et al.* A review of the Ephedra genus: distribution, ecology, ethnobotany, phytochemistry and pharmacological properties. *Molecules* **25**, 3283 (2020).
184 Niklas, K. J. A biophysical perspective on the pollination biology of Ephedra nevadensis and E. trifurca. *The Botanical Review* **81**, 28-41 (2015).
185 Meeuse, A. *et al*. Entomophily in the dioecious gymnosperm Ephedra aphylla Forsk.(= E. alte CA Mey.), with some notes on Ephedra campylopoda CA Mey. III. Further anthecological studies and relative importance of entomophily. *Israel Journal of Botany* **39**, 113-123 (1990).
186 Lee, D. B., Ferdowsi, B. & Jerolmack, D. J. The Imprint of Vegetation on Desert Dune Dynamics. *Geophysical Research Letters* **46**, 12041-12048 (2019).
187 Segoli, M., Groner, E. & Ayal, Y. The importance of plant cover and predation in shaping a desert community. *Journal of Arid Environments* **135**, 33-38, (2016).
188 Marussich, W. A. & Faeth, S. H. Effects of urbanization on trophic dynamics of arthropod communities on a common desert host plant. *Urban Ecosystems* **12**, 265-286 (2009).
189 Polis, G. A., Hurd, S. D., Jackson, C. T. & Sanchez-Pinero, F. Multifactor Population Limitation: Variable Spatial and Temporal Control of Spiders on Gulf of California Islands. *Ecology* **79**, 490-490, (1998).
190 Stroud, C. P. A Survey of the Insects of White Sands National Monument, Tularosa Basin, New Mexico. *American Midland Naturalist* **44**, 659-659, (1950).
191 Ives, A. R., Cardinale, B. J. & Snyder, W. E. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters* **8**, 102-116 (2005).
192 Finke, D. L. & Denno, R. F. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* **8**, 1299-1306 (2005).
193 Abrams, P. A., Menge, B. A., Mittelbach, G. G., Spiller, D. A. & Yodzis, P. The role of indriect effects in Food Webs. in *Food webs* 371-395 (Springer, 1996).
194 Harmon, L. J. *et al.* Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167-1170 (2009).

195 Ingram, T., Stutz, W. E. & Bolnick, D. I. Does intraspecific size variation in a predator affect its diet diversity and top-down control of prey? *PLoS one* **6**, e20782 (2011).
196 Poulin, R. in *Evolutionary ecology of parasites* (Princeton university press, 2011).
197 Bower, D. S. *et al.* A review of the role of parasites in the ecology of reptiles and amphibians. *Austral Ecology* **44**, 433-448 (2019).
198 Frainer, A., McKie, B. G., Amundsen, P.-A., Knudsen, R. & Lafferty, K. D. Parasitism and the biodiversity-functioning relationship. *Trends in Ecology & Evolution* **33**, 260-268 (2018).
199 Richards, R. L., Drake, J. M. & Ezenwa, V. O. Do predators keep prey healthy or make them sicker? A meta-analysis. *Ecology Letters* **25**, 278-294 (2022).
200 Lozano-Fernandez, J. *et al.* Increasing species sampling in chelicerate genomic-scale datasets provides support for monophyly of Acari and Arachnida. *Nature Communications* **10**, 1-8 (2019).
201 Goldberg, S. R. & Bursey, C. R. Integumental lesions caused by ectoparasites in a wild population of the side-blotched lizard (Uta stansburiana). *Journal of Wildlife Diseases* **27**, 68-73 (1991).
202 Goldberg, S. R. & Holshuh, H. Histopathology in a captive Yarrow's spiny lizard, Sceloporus jarrovii (Phrynosomatidae), attributed to the mite Hirstiella sp.(Pterygosomatidae). *Transactions of the American Microscopical Society*, 234-237 (1993).
203 Domrow, R. A small lizard stifled by phoretic deutonymphal mites (Uropodina). *Acarologia* **22**, 247-252 (1981).
204 Dunlap, K. D. & Mathies, T. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia*, 1045-1048 (1993).
205 Lanser, D. M., Vredevoe, L. K. & Kolluru, G. R. Tick parasitism impairs contest behavior in the western fence lizard (Sceloporus occidentalis). *Behavioral Ecology and Sociobiology* **75**, 1-15 (2021).
206 Camin, J. H. Mite transmission of a hemorrhagic septicemia in snakes. *The Journal of Parasitology* **34**, 345-354 (1948).
207 Main, A. R. & Bull, C. M. The impact of tick parasites on the behaviour of the lizard Tiliqua rugosa. *Oecologia* **122**, 574-581 (2000).
208 Johnson, N., Lymburner, A. & Blouin-Demers, G. The impact of ectoparasitism on thermoregulation in Yarrow's Spiny Lizards (Sceloporus jarrovii). *Canadian Journal of Zoology* **97**, 1004-1012 (2019).
209 Taggart, P. L. *et al.* Endure your parasites: Sleepy Lizard (Tiliqua rugosa) movement is not affected by their ectoparasites. *Canadian Journal of Zoology* **96**, 1309-1316 (2018).
210 Bull, C. M. & Burzacott, D. The impact of tick load on the fitness of their lizard hosts. *Oecologia* **96**, 415-419 (1993).
211 Durden, L. A. *et al.* Parasitism of lizards by immature stages of the blacklegged tick, Ixodes scapularis (Acari, Ixodidae). *Experimental & Applied Acarology* **26**, 257-266 (2002).
212 Lukefahr, W. D. *Comparison of ectoparasitic mite loads between gonochoristic (Aspidoscelis marmorata) and parthenogenic (A. tesselata) syntopic whiptail lizards (Teiidae) from the northern Chihuahuan desert of Trans-Pecos, Texas*. (The University of Texas at El Paso, 2013).
213 Reed, J. C. *Analysis of the Function and Evolution of Mite Pockets in Lizards*, (2014).

214 Goldberg, S. R. & Bursey, C. R. Duration of attachment by mites and ticks on the iguanid lizards Sceloporus graciosus and Uta stansburiana. *Journal of Wildlife Diseases* **27**, 719-722 (1991).

215 Álvarez-Ruiz, L. *et al*. Fire reduces parasite load in a Mediterranean lizard. *Proceedings of the Royal Society B* **288**, 20211230 (2021).

216 Hamilton, K. *et al.* Decline in lizard species diversity, abundance and ectoparasite load across an elevational gradient in the Australian alps. *Austral Ecology* **46**, 8-19 (2021).

217 Hurst, H. *et al*. Characterizing tick microhabitat preferences in relation to lizard hosts at Angelo Coast Range Reserve, California. *California Ecology and Conservation Research* (2019)

218 Padgett, K. A. & Lane, R. S. Life cycle of Ixodes pacificus (Acari: Ixodidae): timing of developmental processes under field and laboratory conditions. *Journal of Medical Entomology* **38**, 684-693 (2001).

219 Bull, M. & Smyth, M. The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* Neumann, and *Amb. limbatum* Neumann II. Water balance of nymphs and adults in relation to distribution. *Australian Journal of Zoology* **21**, 103-110 (1973).

220 Chilton, N. B. & Bull, C. M. Interspecific differences in microhabitat choice by two species of Australian reptile tick. *International Journal for Parasitology* **23**, 1045-1051 (1993).

221 Schall, J. J., Prendeville, H. R. & Hanley, K. A. Prevalence of the tick, Ixodes pacificus, on western fence lizards, Sceloporus occidentalis: trends by gender, size, season, site, and mite infestation. *Journal of Herpetology* **34**, 160 (2000).

222 Ogden, N. H. *et al.* Evidence for geographic variation in life-cycle processes affecting phenology of the Lyme disease vector Ixodes scapularis (Acari: Ixodidae) in the United States. *Journal of Medical Entomology* **55**, 1386-1401 (2018).

223 Mooring, M. S. & Hart, B. L. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* **123**, 173-193 (1992).

224 Anderson, R. M. & May, R. M. Regulation and stability of host-parasite population interactions: I. Regulatory processes. *The Journal of Animal Ecology*, 219-247 (1978).

225 Dobson, A. Models for multi-species parasite-host communities. in *Parasite communities: patterns and processes*, 261-288 (Springer, 1990).

226 Krasnov, B., Khokhlova, I. & Shenbrot, G. The effect of host density on ectoparasite distribution: an example of a rodent parasitized by fleas. *Ecology* **83**, 164-175 (2002).

227 Arneberg, P. *et al*. Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 1283-1289 (1998).

228 Swei, A. *et al*. Impact of the experimental removal of lizards on Lyme disease risk. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2970-2978 (2011)

229 Svensson, E., Sinervo, B. & Comendant, T. Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences* **98**, 12561-12565 (2001).

230 Raffel, T. R., Martin, L. B. & Rohr, J. R. Parasites as predators: unifying natural enemy ecology. *Trends in Ecology & Evolution* **23**, 610-618 (2008).

231 Norman, R. *et al*. Persistence of tick-borne virus in the presence of multiple host species: tick reservoirs and parasite mediated competition. *Journal of Theoretical Biology* **200**, 111-118 (1999).
232 Krasnov, B. R., Stanko, M. & Morand, S. Host community structure and infestation by ixodid ticks: repeatability, dilution effect and ecological specialization. *Oecologia* **154**, 185-194 (2007).
233 Holt, R. D. & Lawton, J. H. Apparent competition and enemy-free space in insect host-parasitoid communities. *The American Naturalist* **142**, 623-645 (1993).
234 Cox, C. L. *et al.* Ectoparasite extinction in simplified lizard assemblages during experimental island invasion. *Biology Letters* **16**, 20200474 (2020).
235 Shaw, D., Grenfell, B. & Dobson, A. Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* **117**, 597-610 (1998).
236 Heredia, V. J. *et al*. Mites in the neotropical lizard Liolaemus pacha (Iguania: Liolaemidae): Relation to body size, sex and season. *South American Journal of Herpetology* **9**, 14-19 (2014).
237 Cox, R. M. & John-Alder, H. B. Increased mite parasitism as a cost of testosterone in male striped plateau lizards Sceloporus virgatus. *Functional Ecology*, 327-334 (2007).
238 Oppliger, A. *et al*. Effect of testosterone on immunocompetence, parasite load, and metabolism in the common wall lizard (Podarcis muralis). *Canadian Journal of Zoology* **82**, 1713-1719 (2004).
239 Salvador, A. *et al.* The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behavioral Ecology* **7**, 145-150 (1996).
240 García-De la Peña, C., Castañeda, G. & Barrows, C. W. Infestation by chigger mites in two lizard species from a dune habitat of Northern Mexico. *Texas Journal of Science* **59**, 23-32 (2007).
241 Hager, S. B. Microhabitat use and activity patterns of Holbrookia maculata and Sceloporus undulatus at White Sands National Monument, New Mexico. *Journal of Herpetology* **35**, 326-330 (2001).
242 Baeckens, S. & Van Damme, R. Immunocompetence and parasite infestation in a melanistic and normally-coloured population of the lacertid lizard, *Podarcis siculus*. *Amphibia-Reptilia* **39**, 471-478 (2018).
243 Megia-Palma, R. *et al.* Multiple color patches and parasites in *Sceloporus occidentalis*: differential relationships by sex and infection. *Current Zoology* **64**, 703-711 (2018).
244 Václav, R., Prokop, P. & Fekiač, V. Expression of breeding coloration in European green lizards (*Lacerta viridis*): variation with morphology and tick infestation. *Canadian Journal of Zoology* **85**, 1199-1206 (2007).
245 Dudek, K. *et al.* Distribution pattern and number of ticks on lizards. *Ticks and Tick-borne Diseases* **7**, 172-179 (2016).
246 Curtis, J. L. & Baird, T. A. Within-population variation in free-living adult and ectoparasitic larval Trombiculid mites on collared lizards. *Herpetologica* **64**, 189-199 (2008).
247 Baak-Baak, C. *et al.* Four species of under-reported parasitic arthropods in Mexico and their potential role as vectors of pathogens. *The Journal of Parasitology* **106**, 835-842 (2020).

248 Bostic, D. Parasites of the teiid lizard, *Cnemidophorus hyperythrus beldingi*. *The Southwestern Naturalist* **10**, 313-313 (1965).
249 Mayberry, L. F. *et al*. Bibliography of parasites and vertebrate hosts in Arizona, New Mexico and Texas (1893–1984). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology* (2000).
250 Goldberg, S. R. & Bursey, C. R. Duration of attachment of the chigger, Eutrombicula lipovskyana (Trombiculidae) in mite pockets of Yarrow's spiny lizard, Sceloporus jarrovii (Phrynosomatidae) from Arizona. *Journal of Wildlife Diseases* **29**, 142-144 (1993).
251 Paredes-León, R. in *Animal Diversity and Biogeography of the Cuatro Ciénegas Basin* 147-160 (Springer, 2019).
252 Paredes-Leon, R. *et al*. Metazoan parasites of Mexican amphibians and reptiles. *Zootaxa* **1904**, 1–166-161–166 (2008).
253 Durden, L. A. & Keirans, J. E. *Nymphs of the genus Ixodes (Acari: Ixodidae) of the United States: taxonomy, identification key, distribution, hosts, and medical/veterinary importance*. (Entomological Society of America, 1996).
254 Oliver Jr, J. H., Cummins, G. A. & Joiner, M. S. Immature Ixodes scapularis (Acari: Ixodidae) parasitizing lizards from the southeastern USA. *The Journal of Parasitology* **79**, 684-689 (1993).
255 Castro, M. B. & Wright, S. A. Vertebrate hosts of Ixodes pacificus (Acari: ixodidae) in California. *Journal of Vector Ecology* **32**, 140-149 (2007).
256 Slowik, T. J. & Lane, R. S. Feeding preferences of the immature stages of three western North American ixodid ticks (Acari) for avian, reptilian, or rodent hosts. *Journal of Medical Entomology* **46**, 115-122 (2009).
257 Sion, G., Watson, M. J. & Bouskila, A. Measuring body condition of lizards: a comparison between non-invasive dual-energy X-ray absorptiometry, chemical fat extraction and calculated indices. *Frontiers in Zoology* **18**, 1-9 (2021).
258 Peig, J. & Green, A. J. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**, 1883-1891 (2009).
259 McBrayer, L. D. *Lizard ecology*. (Cambridge University Press, 2007).
260 Ripley, B. *et al.* Package 'MASS'. R package version 7.3-57. http://www.stats.ox.ac.uk/pub/MASS4/ (2022)
261 Lenth, R.V. *et al.* Package 'emmeans'. R package version 1.7.5. https://github.com/rvlenth/emmeans (2022)
262 Sorci, G., de Fraipont, M. & Clobert, J. Host density and ectoparasite avoidance in the common lizard (Lacerta vivipara). *Oecologia* **111**, 183-188 (1997).
263 Hawlena, D., Abramsky, Z. & Bouskila, A. Bird predation alters infestation of desert lizards by parasitic mites. *Oikos* **119**, 730-736 (2010).
264 Krause, J. *et al*. *Living in groups*. (Oxford University Press, 2002).
265 Shatrov, A. B. & Kudryashova, N. I. Taxonomic ranking of major trombiculid subtaxa with remarks on the evolution of host-parasite relationships (Acariformes: Parasitengona: Trombiculidae). *Annales Zoologici* **58,** 279-287 (2008)
266 Wharton, G. Observations on *Ascoschongastia indica* (Hirst 1915)(Acarinida: Trombiculidae). *Ecological Monographs* **16**, 152-184 (1946).
267 Heylen, D. J. & Matthysen, E. Experimental evidence for host preference in a tick parasitizing songbird nestlings. *Oikos* **120**, 1209-1216 (2011).

268 Wilder, S. M., Raubenheimer, D. & Simpson, S. J. Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Functional Ecology* **30**, 108-115 (2016).