Wild bee responses to land use change: investigating the role of bee body size

BY

Daphne M. Mayes

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Chairperson: Dr. Deborah Smith

Dr. Helen Alexander

Dr. Ben Sikes

Dr. Robert Hagen

Dr. J. Christopher Brown

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The dissertation committee for Daphne M. Mayes certifies that this is the approved version of the following dissertation:

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Dissertation Abstract

Land use change impacts biodiversity through many facets including an alteration of habitat and the resources required to sustain species and populations. Wild bees (Hymenoptera: Apoidea) are essential pollinators for many wild and cultivated flowering plants, and exhibit marked differences in life history traits. The consequences of land use change may therefore affect wild bees differently, but this remains poorly understood for many taxa. Body size is a trait that can vary widely across and within bee species, and has important ramifications for several aspects of bee fitness including foraging range. To better understand wild bee responses to land use change, I focused on bee body size from the scale of the community (interspecific) and within a species (intraspecific).

In Chapter 1, I examined tallgrass prairie remnants and restorations across eastern Kansas and found that both types of prairie hosted a similar abundance, diversity, and body size of trap-nesting bees over both study years. The bee community composition differed between prairie types in the first study year but not the second. Regardless of prairie type, bee diversity increased with increasing forb diversity but did not have significant associations with landscape composition. Trap-nesting bee abundance and interspecific body size did not vary in relation to local forb diversity or landscape composition. In Chapter 2, I again used the context of the tallgrass prairie to focus on the response (i.e., total offspring produced, intraspecific body size, and sex ratio) of a single bee species, *Heriades carinata,* to prairie type, forb diversity, and landscape composition. My results indicate that within this species, foraging mothers provision a greater number albeit smaller size of offspring (both male and female) in prairies with increasing forb diversity. These trends were not extended to the landscape scale, however, indicating that the resources immediately surrounding nest sites may have a greater influence on bees in these sites. In Chapter 3, I extend the question of interspecific bee body size to stingless bee communities collected across a deforestation gradient in Rondônia, Brazil. Stingless bees are diverse and important pollinators in tropical systems, but little is known about how they respond to habitat loss and fragmentation from a trait-based perspective. I found that larger bees were collected more often in areas with less forest and within landscapes that had greater isolation between remaining forest patches, while smaller bees were found in areas with a greater amount of forest and shorter distances between forest patches. In Chapter 4, I find that Africanized honey bees were observed more frequently in open (i.e., deforested) areas but still rely on some amount of forest in the landscape. Taken together, my results suggest that body size differently affects wild bee responses to land use change.

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General Introduction

Pollinators are essential for ecosystem function and agricultural production, contributing to the pollination of an estimated 87.5% of the world's flowering plant species (Ollerton et al. 2011, FAO 2018). Pollination is the movement of pollen from the reproductive parts of one flower to another within a plant species and is accomplished by many organisms (Willmer 2011). Bees are notable pollinators because they require floral resources as larvae and adults, and they tend to forage among the same plant species within a flight trip (i.e., floral constancy) (Linsely 1958, Winfree 2010). Visiting the same plant species while foraging increases the chance that conspecific pollen will be transferred and result in pollination (Linsely 1958). Studies have found declines in pollinators are associated with declines in their associated flowering plant species (Biesmeijer et al. 2006, Carvell et al. 2006, Potts et al. 2010).

Declines of certain pollinator taxa have been attributed to human activity, such as habitat loss and introductions of pathogens from commercially used species (Steffan-Dewenter et al. 2005, Cameron et al. 2011). Other suspected contributors to pollinator declines include pesticide use, disease, and invasive species (Brittain et al. 2010, Goulson et al. 2015). Recently, 8 bee species were listed as federally endangered or threatened in the United States (Gorman 2017), and over a quarter of the bee fauna recorded across Europe is listed in Red data books (Steffan-Dewenter et al. 2005). Overall, experts agree that pollinators are suffering from anthropogenic disturbances and recommend more work to understand their requirements for conservation (Potts et al. 2010).

Human-caused land use change is occurring globally at a rapid pace, resulting in the alteration and fragmentation of many landscapes and habitats (Fahrig 2003). The consequences of land use changes affecting bees depends on the availability of resources remaining in the environment, and may differently impact taxa depending on their life history traits (Williams et al. 2010, Jauker et al. 2013) and dietary breadth (Bommarco et al. 2010, DePalma et al. 2015). Bees are diverse, with an estimated 20,000 species occupying the majority of terrestrial ecosystems around the globe (Michener 2000). This diversity is reflected in the manner in which bees nest (Linsley 1958, Michener 2000), the spaces used and resources needed for nest construction, the type(s) of pollen and nectar consumed as adults and larvae (Linsley 1958), social or solitary behavior (Batra 1984), as well as the body size (Roulston and Cane 2000) and (for social species) colony size (Michener 2000). The responses of bees to land use changes can thus be complicated and dependent on how those changes affect a particular bee's needs within their range of occupation.

Researchers have examined responses of bee populations, species and entire communities to land use change. Bee body size—at the level of both populations and communities—is predicted to differ under different environmental scenarios. Large-bodied bee species have greater foraging distances than small-bodied bees (Greenleaf et al. 2007), leading to predictions about the effect of habitat fragmentation on bee populations and communities. Some studies have found that smaller species are more vulnerable than large species to habitat fragmentation (Bommarco et al. 2010, DePalma et al. 2015, Chapter 3), presumably because they are unable to fly long distances among habitat patches. On the other hand, other studies have found larger species more negatively affected than smaller species (Rader et al. 2014); while smaller sized species may not have the ability to fly over large distances, they also require fewer resources (Radmacher and Strohm 2009) than larger bees and may find sufficient resources within a single patch.

Intraspecific variation in body size has also been observed within some bee populations (Warzecha et al. 2016). Since individual bee body size is primarily determined by the food resources provided by the mother (or sister in case of social species), changes in the availability of resources within their flight range may have consequences for the size of the progeny. Whether an increase or decrease is observed in bee body size in relation to land use change remains questionable and is likely context dependent (Williams and Kremen 2007). In tropical systems, a social stingless bee species (*Melipona quadrifisciata anthidioides* Lepeletier) had smaller and weaker colonies in association with less foraging resources (Ramalho et al. 1998). Oliveira et al (2016) examined museum specimens collected over a period of 147 years, and found that bee body size had decreased within species across time, which may be attributed to the reduction of habitat quality and quantity across the study region.

The type or quality of food that the larva feeds upon and rearing temperature (Roulston and Cane 2002, Radmacher and Strohm 2009), as well as nesting behavior (Roulston and Cane 2000) may influence the body size of the growing bee. Bee body size is largely driven by an adaptation to environmental conditions (Tepedino et al. 1984, Pignata and Diniz-Filho 1996). These studies are based on a small fraction of bee species, however, and more work examining this relationship is needed. In bees, increased body size has been associated with lower overwintering mortality rates (Tepedino and Parker 1986, Bosch and Kemp 2004), increased foraging provisioning efficiency (Kim and Thorp 2001), and greater competitive advantages over conspecifics for territory and mating (Barthell and Thorp 1995). The plasticity of bee body size in relation to changes in land use have been explored at the level of populations (Renauld et al. 2016) and communities (Gathmann 1994, Williams 2010, Kremen and M'Gonigle 2015), but few have addressed this relationship in the context of North America's tallgrass prairie (Evans

2016) or the Brazilian Amazon tropical forest (Carvalho-Zilse and Nunes-Silva 2012). This dissertation examines bee responses to land use change within these two systems, with a particular focus on bee body size in Chapters 1, 2, and 3.

Several approaches have been used to quantify bee body size. Some studies have defined bee body size by measurements of head width (Renauld et al. 2016), abdomen length (Gathmann et al. 1994), wing characteristics (Araújo et al. 2004), thorax width (Goulson et al. 2003), and specifically intertegular distance (Cane 1987, Greenleaf et al. 2007). These traits are predicted to be associated with each other due to allometric constraints and studies examining multiple traits have supported this (Araújo et al. 2004). The body size measurements in this dissertation were limited to the intertegular distance, which is often used in questions relating to the foraging ranges of bees of different sizes (Araújo et al. 2004, Greenleaf et al. 2007). Using a mean-weighted body size approach to characterize the body sizes within a community has been applied in other studies (Wray et al. 2014), and includes information about the abundance and size of bees within the community. For solitary species, this seems to be an appropriate method to examine interspecific body size because foraging mothers are solely collecting and provisioning nests independently (unlike social bees).

The tallgrass prairie and Brazilian Amazon tropical forest have both been greatly affected by human-driven land use change (Freitas et al. 2009, Carvalho-Zilse and Nunes-Silva 2012, Harmon-Threatt and Chin 2016). Each system is home to diverse bee fauna; North America has an estimated 4,000 bee species with the majority being solitary (Moisset and Buchmann 2016) while the Neotropical forests harbor a tremendous diversity of social stingless bee species (Freitas et al. 2009) among others. This presents an opportunity to examine how bees with different life history strategies may respond to land use changes, with an emphasis on bee body size associations to local and landscape scale resources. In Chapter 1, I address this topic by examining trap-nesting (TN) bee communities in two tallgrass prairie systems—remnant and restored tallgrass prairies. I compared the abundance (i.e., total offspring reared), diversity, species composition, and body size of the bee communities in remnant versus restored prairies. I further examined the TN bee community relationships to local forb diversity and landscape composition. In Chapter 2, I examined intraspecific associations with land use of a single species in the tallgrass prairie systems. In Chapter 3, I explored changes in mean body size in multi-species stingless bee communities as a function of the effects of deforestation across the state of Rondônia, Brazil. And in Chapter 4, I explore the foraging behavior of Africanized honey bees across the deforestation gradient in Rondônia, Brazil. Below, I summarize the primary objectives and results of each chapter:

Chapter 1: Local and landscape level factors associated with trap-nesting bee communities in tallgrass prairies across eastern Kansas.

Bees are central place foragers, mobile organisms that make trips to and from a chosen nest site (Elliott 1988). The foraging range of bees is related to their size; larger individuals are capable of foraging over greater distances (Greenleaf et al. 2007). A larger body size may be advantageous to bees that occupy land that has been highly fragmented or simplified. The tallgrass prairie remaining today exists as either fragmented patches embedded within an agricultural landscape or in large preserves (Davis et al. 2008). Efforts to reinstate prairie to lands that were once used for agriculture indicate bees may respond positively, producing similar abundance and diversity to remnant prairies (Denning and Foster 2017, Griffin et al. 2017). Some studies have also found that the composition of bee communities differs among prairie restorations and remnants (Denning and Foster 2017), leading to questions of what bees are inhabiting these systems and whether particular traits (e.g., body size) can be useful predictors of observed species.

I used trap-nests to sample bee communities in remnant and restored tallgrass prairies across eastern Kansas in 2013 and 2014. Bee fitness can be assessed directly, in the type and number of offspring reared (hereafter, ‘abundance’) in each trap nest. I compared the abundance, species diversity, distribution of body sizes, and composition of bee communities in tallgrass prairie remnants and restorations for each study year. Second, I used a forb survey conducted by another researcher at shared study sites to examine the association of TN bee abundance, diversity, and body size in relation to local forb diversity. Because bees are mobile and may search for resources beyond the local scale, I also examined these relationships at the landscape scale. Here, I explore the TN bee abundance, diversity, and body size relationships to the percent of natural/semi-natural grassland, percent woodland, and percent cropland at 1000 m radius surrounding the study sites.

Previous studies found that tallgrass remnants harbor a greater diversity of flowering plants than restorations (Kindscher and Tieszen 1998). Thus, I predicted that (1) TN bees would have higher abundance and diversity in remnant than in restored prairies, and (2) TN bees would have a larger body size in restored prairies due to the need to forage greater distances in search of resources. I expected to see (3) a difference in the TN bee species composition between prairie types. In addition, I predicted to observe (4) a positive association between the TN bee abundance and diversity and the local forb diversity, and (5) decreased body size in relation to increased local forb diversity. Finally, I examined these relationships with landscape composition and expected to observe (6) a positive association between TN abundance and diversity and the amount of natural/semi-natural grassland and woodland in the landscape, and a negative association with the amount of cropland in the landscape. Again, predicting that larger bees would be able to access resources that are more patchily distributed I expected to observe (7) a larger body size of bees in relation to increased cropland at the landscape scale.

Contrary to our predictions, there were no differences in TN bee abundance, diversity, or body size between prairie remnants or restorations, strongly suggesting that prairie restoration projects do benefit bee communities. In 2013 the bee community differed between prairie types, but this was not observed for the 2014 study year. As expected, there was a positive association between TN bee diversity and local forb diversity, but not between TN bee abundance or body size and forb diversity. Contrary to predictions, there were no significant associations between TN bee abundance, diversity, or body size and landscape composition. In summary, tallgrass prairie remnants and restorations are providing the resources needed to support similar numbers of TN bees, and sites with higher forb diversity also showed higher TN bee diversity.

Chapter 2: Impacts of local forb diversity and landscape composition on body size, offspring production, and sex ratio of Heriades carinata Cresson *(Hymenoptera: Megachilidae) in tallgrass prairies*

Biotic pollination is an ecosystem service that is accomplished by many organisms (Willmer 2011), and bees are particularly important facilitators (Ollerton et al. 2011). Honey bees are often regarded as the primary pollinators of domesticated plants (McGregor 1976). Recent studies suggest that wild bees are more effective than previously realized (Greenleaf et al. 2006, Winfree et al. 2007) and for some crops can provide all of the pollination services needed provided sufficient natural area is located nearby fields (Kremen et al. 2004, Steffan-Dewenter 2006). Unlike honey bees, the majority of bees are solitary species that are largely unmanaged

(Murray et al. 2009, Moisset and Buchmann 2016) and little is known about their current status and how populations respond to land use changes (Murray et al. 2009).

The tallgrass prairie of North America has been reduced to a fraction of its former range, with less than 1 percent remaining in large preserves or as scattered fragments across the Midwest (Samson and Knopf 1994). Much of this loss is due to agricultural expansion, resulting in simplification of the landscape and an alteration of resources available for bees (Tschartnke et al. 2005). A reduction of natural and semi-natural areas has been shown to negatively impact wild bee populations (Kremen and Chaplin-Kramer 2007), with a reduced visitation to plants in areas with less natural habitat remaining in the landscape (Kremen et al. 2002).

Bees are mobile and able to transverse landscapes at scales related to their size (Greenleaf et al. 2007), thus may be able to tolerate some level of habitat loss and fragmentation associated with land use changes. Bees in the genus *Heriades* are one example of a solitary species that nests aboveground in hollowed-out spaces such as grass stems or beetle burrows in dead wood (Matthews 1965). They are presumably polylectic, based on observing multiple pollen types within their nests (Jensen 2001). They have been observed in studies examining bee fauna occupying disturbed areas (Jensen 2001, Prajzner 2016), however, little is known about the resources they use or their responses to land use change within tallgrass prairies.

In Chapter One, as mentioned above, bee communities were not found to differ between tallgrass prairie remnants or restorations, however, there was some evidence of compositional changes by prairie type in the first study year. I revisit these data and focus on a single species collected, *Heriades carinata*, to better understand the relationship of local and landscape scale resources affecting this bee. For many bee species males are often smaller in size than females (Moisset and Buchmann 2011). The difference in size is due in part to the amount of provisions that the mother provides to each cell, with a smaller amount given to male progeny (Phillips and Klostermeyer 1978, Torchio and Tepedino 1980). Studies that have examined Fisher's theory to explore sex ratios of bees have found that in some cases the expectation of a 2:1 male to female ratio is supported (Torchio and Tepedino 1980, Bosch and Vicens 2005), while others have not observed this pattern (Tepedino et al. 1994). Since males require smaller provisions, there may be situations when more males are produced due to scarce resources in the foraging ranges of the mother (Peterson et al. 2005), however this has been little explored.

To address this, I examined associations between the intraspecific body size, total offspring collected at each site, and sex ratio of *H. carinata* and (1) remnant versus restoration tallgrass prairies (2) local forb diversity (3) landscape composition (i.e., percent natural/semi-natural grassland, percent woodland, and percent cropland) at 250 m radius surrounding the study sites. I predicted a larger bee body size in restored prairies and sites with lower local forb diversity. I further predicted that body size would be larger in areas with less natural/semi-natural grassland and larger in association with increased amounts of cropland. I predicted a greater number of offspring produced in remnant versus restored prairies, and a strong association with the total number of offspring per site and local forb diversity. In addition, I expected to observe more offspring produced in relation to increased amounts of natural/semi-natural grassland and fewer produced in relation to increased cropland surrounding the study sites. Finally, I examined the sex ratios per sites in relation to prairie type, local forb diversity, and landscape composition.

The body size of *H. carinata* was similar between remnant and restored prairies however there was a significant negative association between body size and local forb diversity. I found a similar number of offspring produced in remnant versus restored prairies, but that the total offspring produced increased with increasing local forb diversity. I did not find any significant associations between the total offspring produced and landscape composition. Last, I did not find sex ratio to be associated with prairie type, local forb diversity, or landscape composition. These findings suggest that *H. carinata* make foraging decisions based on local resource availability, with fewer and larger offspring (independent of sex) in areas with lower forb diversity immediately surrounding the nest site.

Chapter 3: Body size influences stingless bee (Apidae: Meliponini) communities across a range of deforestation levels in Rondônia, Brazil

Behavioral attributes that influence the interaction of bees with their environments may also have in role in bee body size responses to land use change. Social species, for example, may respond differently than solitary species due to their ability to communicate information about resources to other foragers in the same colony (Williams et al. 2010). While social species have more individuals to provide for, they have also adapted a means to efficiently exploit resources in their environment (Nieh and Roubik 1998, Aguilar et al. 2005) as well as utilize stored supplies in times of resource scarcity (Seeley 1995). Nonetheless, many studies indicate that social bee species are more sensitive to the effects of habitat loss and subsequent isolation from natural habitat than solitary species (Williams et al. 2010). Deforestation is a growing threat in the world's largest rainforest—the Amazon (Freitas et al. 2009), negatively impacting many species including stingless bees (Brown and Oliveira 2013). Stingless bees are particularly diverse in the Neotropics and are vital contributors to the pollination of many wild plant species (Slaa et al. 2006). Despite their important role in pollination and cultural uses (Gonzalez et al. 2018), few large-scale systematic studies have taken place in this region making inferences pertaining to their ecology and responses to disturbance limited.

In this chapter, I used a dataset from a study that took place in Rondônia, Brazil nearly 20 years ago which examined bee communities across a deforestation gradient (Brown and Albrecht 2001, Brown and Oliveira 2013). To address the topic of bee body size relationships, I narrowed my focus on the stingless bees (Hymenoptera: Apidae: Meliponini) collected, and used museum specimens to collect body size measurements for each species recorded. Here, I measured only females and used these measurements to examine associations of body size and total forest area, total forest edge, and the average distance between forest patches at three spatial scales surrounding sample points (i.e., 500 m, 1000 m, 1500 m). Again, referencing the body size-foraging distance relationship in which larger bees are capable of foraging greater distances (Greenleaf et al. 2007); I predicted a negative association between bee body size and the percent forest. Further, I predicted as forest patch isolation increased that bee body size would also increase. Lastly, I expected to see an increase in species richness with the amount of forest edge regardless of body size.

I found that bee body size increased in areas with less forest area, and also increased in relation to increasing forest inter-patch distance. Species richness also increased with increased amount of forest edge, but did not favor smaller or larger sized bees. Taken together, these results provide additional evidence supporting the hypothesis that small social bees are particularly sensitive to habitat loss. While species richness increased with the amount of forest edge, the ability of these bees to tolerate increasing levels of deforestation may be limited. This work is in-press at the *Journal of Insect Science*.

Chapter 4: Observations of Africanized honey bee Apis mellifera scutellata absence and presence within and outside forests across Rondônia, Brazil

The spread of Africanized honey bees (AHB), *Apis mellifera scutellata*, across the Neotropics has raised concerns about the impacts they will have on native bee species (Freitas et al. 2009). Deforestation in Brazil has negatively impacted wild native bees species (Brown and Oliveira 2013, Chapter 3), but the response of AHB to deforestation is little explored (but see Cairns et al. 2005).

In Chapter 4, I revisit the dataset used in Chapter 3 to examine observations of AHB within and outside of forest interiors, and in relation to forest area at multiple spatial scales surrounding sample points. I predicted that AHB would be found largely outside of forest interiors, and that they would respond positively to deforestation. These predictions are based on the generalist foraging behavior of Africanized honey bees (Roubik 2000).

I found that AHBs presence was recorded most often outside of forests, in open canopy areas. At the landscape scale, AHBs presence increased with deforestation, but this relationship was limited to smaller spatial scales. As deforestation increased at larger spatial scales, AHB presence decreased. These observations may be in part due to the nesting requirements by AHB (needing trees for nesting), and the alteration of the landscape over time. Areas that were deforested over longer time scales may have fewer foraging options for AHBs, thereby affecting the presence of these bees depending on local versus landscape level scales. This work has been published in the journal *Insectes Sociaux*.

Chapter 1: Local and landscape level factors associated with trap-nesting bee communities in tallgrass prairies across eastern Kansas

Abstract

Nesting behavior and body size are attributes that may help shed light on wild bee responses to land use change at local and landscape scales. We studied trap-nesting solitary bees colonizing remnant and restoration prairie sites in an agricultural landscape located across eastern Kansas for two years, and assessed the abundance, diversity, composition and body size of nest occupants reared in response to site type, local forb diversity, and landscape composition surrounding each field site. Tallgrass prairie remnants and restorations hosted a similar diversity, abundance, and community body size of trap nesting bees. We found that trap-nesting bee diversity increased with local forb diversity, but did not observe significant relationships between abundance or body size in the bee community and local forb diversity. The bee community composition differed between remnants and restorations in 2013, but we did not observe a significant difference in 2014. Contrary to our expectations, trap-nesting bees were not more abundant or diverse in areas with a greater percentage of natural/semi-natural grasslands or woodlands, and did not differ in their response to landscape resources based on body size. Our work provides additional data focusing on a subset of the bee fauna in tallgrass prairie systems showing similar responses to the larger community of bees in these areas.

Introduction

Bees are the primary pollinators of flowering plant species (Cane 2008), therefore their presence in natural and cultivated areas is an important consideration for providing this key ecosystem and agricultural service (Klein et al. 2007). Habitat loss and fragmentation are the primary drivers of wild bee declines (Brown and Paxton 2009; Potts et al. 2010), therefore studies examining wild bees in ecosystems that have been greatly reduced or altered, such as the tallgrass prairie, are needed.

Tallgrass prairie is the most endangered ecosystem in North America (Samson and Knopf 1996) and is home to a diverse assemblage of flower-visiting insects. An estimated 1-5 % of the former range of tallgrass prairie remains across the Midwest, embedded in a mosaic of agricultural, cool season and warm season grasslands. In addition, the eastern portion of Kansas holds the westernmost edge of the eastern deciduous forest range, resulting in woodlands adjacent to tallgrass prairies (Anderson 1983). Studies that have examined insect pollinators in restored tallgrass prairie systems have found that these systems can successfully support diverse pollinator communities, but that they may differ in community composition (Denning and Foster 2017, Griffin et al. 2017). The nesting requirements or body sizes of bees may be important factors contributing to these differences, but require greater exploration.

Trap-nesting bees include species that utilize hollowed stems or reeds, and beetle burrow tunnels or cavities for their nesting needs (Krombein 1967, Loyola and Martins 2006). In addition, these (i.e., nonparasitic) bees are central place foragers that make several trips to and from their chosen nest site to collect the provisions needed (i.e., pollen, nectar, nesting materials) for offspring growth and survival. Bees are mobile insects that consume and collect nesting resources that are located within their respective foraging range, whereby larger-bodied bees are capable of foraging at greater distances (Greenleaf et al. 2007). The differences in local and landscape scale resources coupled with body size creates an opportunity to better understand the consequences of land use change on these important insects.

Trap-nesting bees can utilize forest resources for their nesting needs, however their relationship to forested areas within mixed use landscapes remains unclear. In a study utilizing trap nests within European grassland systems, the presence of old growth trees supported increased numbers of bee species in comparison to meadows without trees (Tschartnke et al. 1998), while in tropical forest systems, Klein et al. (2002) found a positive relationship between bee richness and abundance in relation to land use intensity. Studies in tropical forested landscapes have found that trap nesting bee species are often collected with higher richness and abundance in non-forested or disturbed areas (Klein et al. 2002; Buschini 2005). While the utility of trap-nests to sample bee and wasp diversity has been demonstrated in other studies (Buschini 2006; Loyola and Martins 2008; Sheffield et al. 2008) and used for monitoring local bee communities (Tscharntke and Brandl 2003), we are not aware of any study that has used this method in mixed landscapes with tallgrass prairie and forested areas in this region.

Studies focusing on land use change in agricultural landscapes indicate a positive relationship between bee richness with and the surrounding extent of semi-natural habitat (Holzschuh et al. 2010, Diekötter et al. 2014, Steckel et al. 2014). These responses may vary according to the life history of select bee species. For example, Williams et al. (2010) found that in comparison to ground-nesting species, above-ground nesting bees show greater sensitivity to the effects of agricultural intensification, with fire and mowing negatively affecting their abundance. In the context of the tallgrass prairie, these factors may present greater challenges for wild above-ground nesting bees since management practices such as mowing and prescribed burning are commonly used to manage and sustain this ecosystem.

In this study, we aimed to assess the abundance, diversity, species composition, and body size of trap-nesting solitary bees in remnant and restored tallgrass prairies. We expected to find a higher abundance and increased diversity of bees in remnant prairies in comparison to restored prairies. We also predicted a positive relationship between bee abundance and diversity with local forb diversity, based on increased resource availability in close proximity to nest sites. We predicted a positive relationship at the landscape scale between both bee traits and amount of natural/semi-natural grasslands, as well as woodland, with the richness and abundance of trap-nesting bees due to greater food and nesting resources surrounding nest sites. Finally, we investigated whether any possible differences in bee community composition was related to changes in bee body size. Because body size is related to foraging distance (Greenleaf et al. 2007), we expected to find a greater abundance of larger-bodied bees in sites with lower local floral diversity, as well as sites with less natural/semi natural grassland surrounding the sites.

Materials and Methods

Study sites

In total, 17 sites across eastern Kansas were used during the 2 years of this study (Figure 1.1). Not all sites could be used each year; 15 were used in 2013 and 10 in 2014. The sites (size range 3–7 ha, mean = 4.2 ha) represented two types of tallgrass prairie, remnant (never tilled) or restoration and were situated in a landscape mosaic that included agricultural fields, conservation reserve program (CRP) fields, grassland, and woodland. Study sites were classified as either tallgrass prairie remnants or restorations based on the historical use of the site. Sites that have never been plowed and converted for agricultural use were classified as remnant. We classified restorations as sites that had a history of agricultural use and were under a management system that incorporated restoration, such as a Conservation Reserve Program (CRP) or utilized practices to restore land to former prairie by the addition of native seed mixes (Table S1.1).

Trap nests

Trap-nesting bees were sampled using wood-block trap-nests. Each trap-nest unit consisted of 4 pine boards, with 5 holes drilled 130 mm into each board; traps were placed within a sheltered frame attached to a metal fence post (Figure S1.1). Each unit included 10 holes 5 mm in diameter, and 10 holes 10 mm in diameter. Holes were lined with parchment paper to allow collection of finished nests.

In 2013 three trap-nest units, and in 2014 five trap-nest units were placed 1-1.5 m aboveground facing in a southeast orientation, ten meters apart, across the center of each field site (Figure S1.2). Sites were checked twice per month from May–September in 2013, and May–August, 2014; completed nests were collected and replaced with new paper liner to ensure continuous availability of nesting sites. Collected nests were stored in clear test tubes with a breathable lid at ambient temperatures, and monitored for emergence of nest occupants. Emerged insects were collected and later prepared for identification.

Bees were identified to species level using Mitchell (1960) and Discover Life (www.discoverlife.org) and a subset of specimen identifications were confirmed by Dr. Victor Gonzalez, University of Kansas, to ensure accuracy. Voucher specimens will be deposited at the Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Trap-nesting community variables

Trap-nesting bees were characterized by measures of total number of bees reared (hereafter, “abundance”) of bees, effective number of species, and mean community body size. Effective number of species is an index that accounts for the number and evenness of species in a community using the exponential Shannon’s diversity (e^H) allowing frequency to be included without favoring more or less common species (Jost 2006). We measured the intertegular distance (IT) of bees reared from study sites. The IT is commonly used in studies examining body size relationships to environmental factors (Cane 2001, Wray et al. 2014, Williams et al. 2010), and is related to the foraging distance of bees (Greenleaf et al. 2007). For each site, we used a modified version of the weighted mean IT approach following Wray et al. (2014):

$$\sum_{i=1}^{n} \frac{(\mathrm{IT}_i \times \mathrm{N}_i)}{\underline{\mathrm{N}}_t}$$

where IT_i represents the mean intertegular distance (mm) of species *i*, N_i corresponds to the number of individuals of species *i* reared at a site, and N_t is the total abundance of all individuals reared per site. In our measures of body size, we estimated the mean IT value for each species separately, for each site, because we previously observed evidence of intraspecific variation due to site effects (Chapter 2).

Local floral diversity

Local floral diversity was collected by a researcher concurrently sampling a portion of the field sites used in this study. During each survey, four parallel 20 x 2.6-m belt transects were established near the center of each site. All currently-flowering forbs within each transect were recorded. Sites were sampled 3–4 times annually. Therefore, richness values were rarefied to three samples using sample-based rarefaction (R package “rich”; Rossi 2011). Detailed information about forb sampling can be found in Denning and Foster (2017). Sites that did not overlap with the other study were sampled using the same method but had fewer sampling events per season. In the analyses examining the effects of local floral diversity, only sites with the same number of sampling events per study year were included.

Landscape composition

The landscape composition surrounding each site was estimated using data provided using the 2005 Kansas Land Cover Patterns Level IV data (KLCP; Kansas Applied Remote Sensing Program 2010), and entered into ArcGIS v.10 for final quantifications of the area of various types of land use within a radius of 1000 m surrounding the center of the study site. A final raster layer of 30 x 30 m resolution was created using the KLCP raster. We used this distance to include the typical foraging ranges of the species found in our study based on estimates in Greenleaf et al. (2007) and comparable with other studies (Kremen et al. 2004; Hines and Hendrix 2005). Land use types included woodland, cool and warm season grassland, CRP land, and cropland. For our study, we combined CRP land and cool and warm season grassland into a single category of land use, hereafter "natural/semi-natural grassland", and separately examined the extent of woodland and combined cropland (all subcategories of crop cover).

Statistical analyses

Abundance, diversity, and body size

We used linear mixed effects models with the packages lme4 and LmerTest (LmerTest tutorial; Brockhoff, 2015) in R (R Core Team 2015) to separately assess differences in the abundance, diversity (e^H), and body size of trap nesting bees due to site type (fixed effect: remnant, restoration), year (fixed effect: 2013, 2014) and their interaction. Because we expected each site to have variation, we modelled “site” as a random effect. Next, we used linear mixed effects models to separately model the effects of local forb diversity, study year, and their interaction on the abundance, diversity (e^H), and body size of trap nesting bees, and included “site” as a random effect term. Finally, we examined the effects of land use at 1000 m surrounding the sites using three separate linear mixed effects models. Here we modeled percent land use (percent natural/semi-natural land; percent woodland; percent cropland) as a fixed effect on the abundance, diversity (e^H), and body size of trap nesting bees. “Site” was included as a random term in the models. Cleptoparasitic bees were not included in our measures of body size due to the differences in foraging needs and behaviors.

Community composition of trap-nesting bees

We used non-metric multi-dimensional scaling (NMDS) to visually examine the community composition of bees reared from the study sites. The NMDS approach allows visual comparison of communities in multidimensional space using measures of dissimilarity. We used the Bray-Curtis measure of distance to compare the raw abundances of each species reared from our sample sites. We used PERMANOVA to examine whether bee composition differed between remnant and restored prairies separately for each study year. Each matrix type (remnant versus restoration) was compared using *F*-ratios from the sums of squared distances within and between groups (matrix type), based on permutations of the observations. We used 5000 permutations for our analysis. Last, we tested for homogeneity of dispersions within bee communities in remnant versus restored sites using PERMDISP (R package ‘vegan’, Oksanen et al. 2016).

Results

In total we reared 749 bees (19 bee species) from trap nests in both study years. These species include *Heriades carinata, H. leavitii, Megachile brevis, M. exilis, M. georgica, M.*

policaris, *M. rugifrons*, *Dianthidium simile*, *Chelostoma sp.*, *Osmia caerulescens*, *O. georgica*, *O. illinoensis*, *O. albiventris*, *O. cordata*, *O. pumila*. In addition, we reared 2 cleptoparasitic bee species *Coelioxys texana* and *C. octodentata*. The mean body size of bees collected from all sites was 1.84 mm (range: 1.25 mm – 2.66 mm). For a list of trap nesting bees within each site, site type, and their body size see Table S1.2.

Bee abundance, diversity, and body size in prairie remnants versus restorations

Bee abundance did not differ between remnant and restoration prairie types ($t_{(20)} = 0.543$; $P = 0.143$; Figure S1.2). Bee diversity also did not differ according to site type, but was marginally nonsignificant ($F_{(1,14)} = 3.74$; $P = 0.073$; Figure S1.3). There was no significant difference in the body size of bees collected between the two prairie types ($F_{(1, 20)} = 0.034$; $P = 0.853$; Supplement Table S1.7).

Bee communities and local and landscape level resources

We found that bee diversity was significantly and positively associated with local forb diversity ($F_{(1,13.26)} = 6.679$; $P = 0.022$; Figure 1.2), but did not observe significant relationships between bee abundance and forb diversity ($F_{(2, 16)} = 1.020$; $P = 0.603$) or body size and forb diversity ($F_{(15, 5.998)} = 0.466$; $P = 0.892$; Table 1.1). We did not find bee diversity, abundance, or body size to be significantly associated with the percent of natural-semi natural, combined cropland, or woodland at 1000 m radius surrounding the study sites (Table 1.2).

Bee community composition

We found significant differences in the bee community composition between remnant and restoration sites sampled in 2013 (PERMANOVA: $F_{(1,13)} = 2.34$, $P = 0.019$; Figure 1.3). Provided the differences in the bee community composition were not driven by within group dispersion (PERMDISP: $F_{(1,12)} = 0.383$, $P = 0.536$), the PERMANOVA differences were not attributable to either site type (remnant v. restored) being more variable in species composition. This result was driven by differences in the species collected by site type. For example, we collected *Heriades carinata* in greater numbers (n = 113) within remnant prairies the 2013 study year. Unlike the 2013 season, we did not find a significant difference in bee community composition between the two prairie types sampled in 2014 (PERMANOVA: $F_{(1,9)} = 0.325$, $P = 0.588$; Figure 1.4).

Discussion

We did not find significant differences between the prairie remnants and restorations in the abundance, diversity, or body size of the bee communities sampled. These results in part agree with a concurrent study sampling the entire forb-visiting insect community using aerial net collections, which supports the conclusion that both types of prairie are providing some key resources for bee communities in this study region (Denning and Foster 2017). This is also in agreement with other studies demonstrating that prairie restoration sites can reinstate a similar number and diversity of bee communities as remnant areas (Griffin et al. 2017).

Higher local forb diversity, regardless of site management history, supported a higher diversity of trap-nesting bees in our study sites. This difference in potential food resource diversity is expected to be reflected in the bee communities (Roulston and Goodell 2011, Hanula et al. 2016, Denning and Foster 2017). In contrast to our predictions, the bee body size was not related to local forb diversity, suggesting that a range of body sizes are supported in these sites. This implies that resource needs are being met within the differing foraging ranges of the species observed in our study, though species-specific responses have shown a different relationship (Chapter 2).

In our study, we did not observe significant relationships between the number, diversity, or body size of trap-nesting bees in relation to landscape composition. We were surprised that the bee species collected in our nests were not responsive to the percent of land use types surrounding our study sites, because others have observed positive relationships between trap-nesting bees and percent natural areas in the landscape (Holzschuh et al. 2010; Steckel et al. 2014). The sites in our study range 0 to 29 percent cropland (Supplement S1.9) within 1000 m of each of the prairie types. Future studies would benefit by examining prairie landscapes that have greater differences in the surrounding land use to better understand the consequences of landscape level resource availability on these species. In addition, we did not find body size relationships between the bees collected and landscape level resources. Others examining the broader bee community have observed larger bee species inhabiting areas with greater amounts of habitat loss or fragmentation (Kambach et al. 2012; Jauker et al. 2013; ch 4), and in some cases observing that larger bees are more sensitive (Benjamin et al. 2014; Rader et al. 2014).

Bees are expected to respond to changes in land use differently due to their varied life histories and requirements for offspring provisioning. In the current study, even though we narrowed our focus to above-ground nesting solitary bee species, there were marked differences in the resources used to build their respective nests. For example, the leafcutter bees (e.g., *Megachile brevis*) use leaf and sometimes flower petals to line and separate the brood cells in their nests (Eickwort et al., 1981; Michener 2000). Other species, such as *Heriades carinata,* use resins to separate the cells in their nests (Krombein 1967). In addition to the different resources these two species use for nesting, they differ in body size (Supplementary material). While some areas may offer both types of resources and nesting hole size requirements, others may not, and this is a challenging but important piece of information that is difficult to collect and quantify in the field. One limitation of our study was the use of two diameter hole sizes for nest occupation, which may have restricted certain species from utilizing those sizes. Nonetheless, our trap-nest method collected over half of the species that would be expected to utilize this type of structure based on comparisons of community wide aerial net surveys in the same sites (Supplement S1.10). The use of trap-nests to collect bees provides important information about offspring production and resource use (i.e., nesting materials; pollen provisioning behavior) that other methods do not provide (e.g., aerial nets collection, malaise trapping; pan trapping). In the future, a comprehensive comparison of different sampling methods would be beneficial for understanding the suitability of using trap-nests in monitoring bee communities in tallgrass prairies.

Conclusions

Our results indicate that trap-nesting bee communities in fragmented tallgrass prairie ecosystems are occupying and nesting similarly in remnant and restoration sites and benefit from local forb diversity. The compositional differences, however, suggest that these species may be affected differently by aspects of their immediate and/or surrounding environment that have yet to be explored. Contrary to our expectations, body size did not reveal relationships showing a sensitivity of larger or smaller bee species to land use change in this system. Future work will examine species-specific (intraspecific) body size responses to land use change.

Figures and Tables

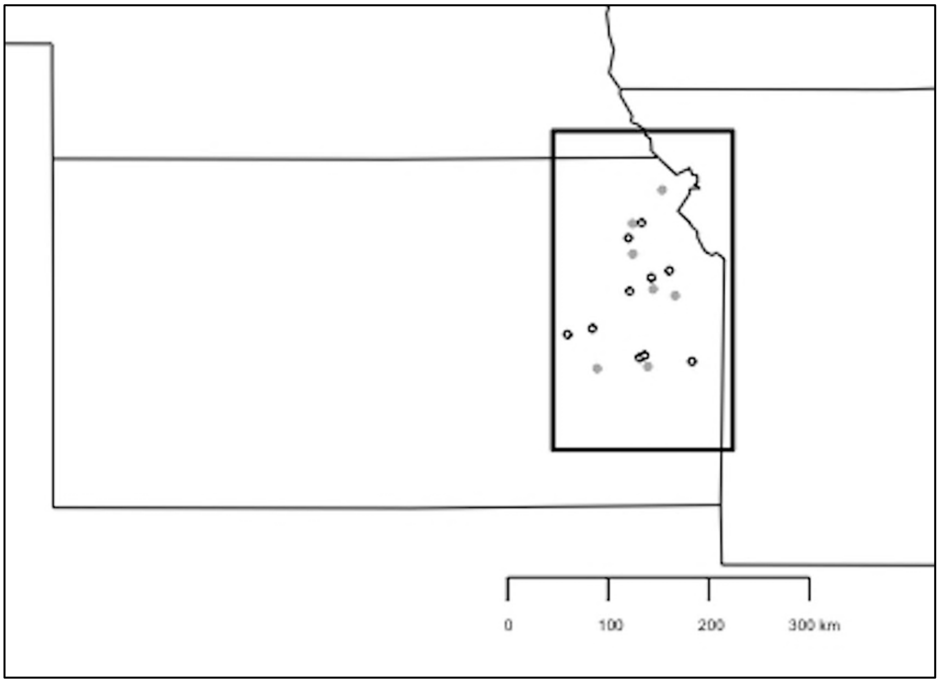

Figure 1.1. Map of study sites in eastern Kansas. Prairie remnant sites are in open circles, and restored sites are in grey filled circles.

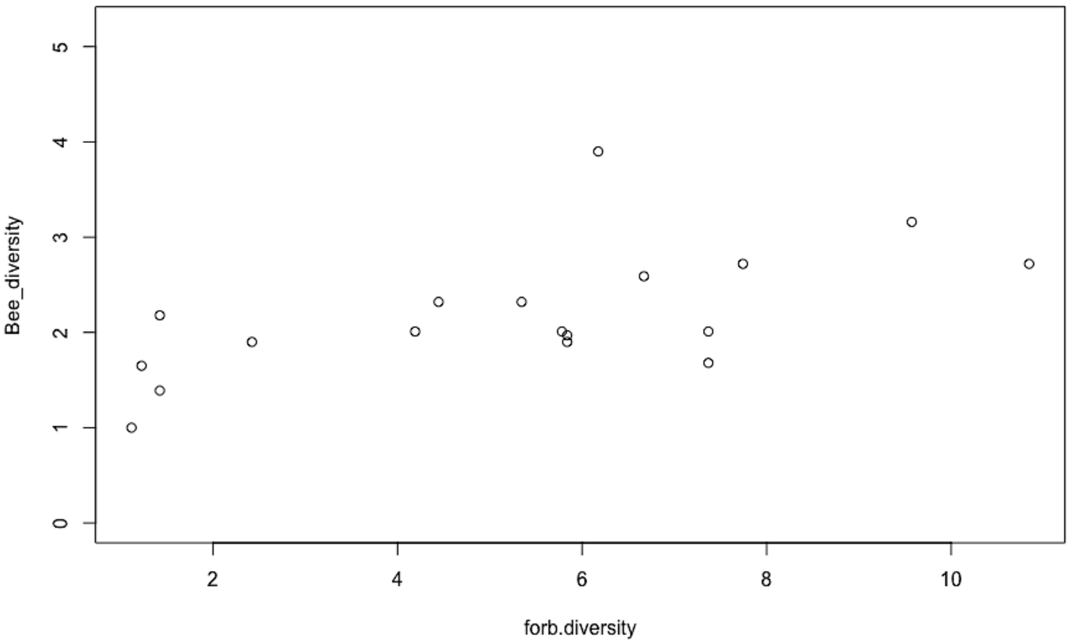

Figure 1.2. Significant positive association between bee diversity (e^H) and local forb diversity ($F_{(1,13.26)} = 6.679$; $P = 0.022$).

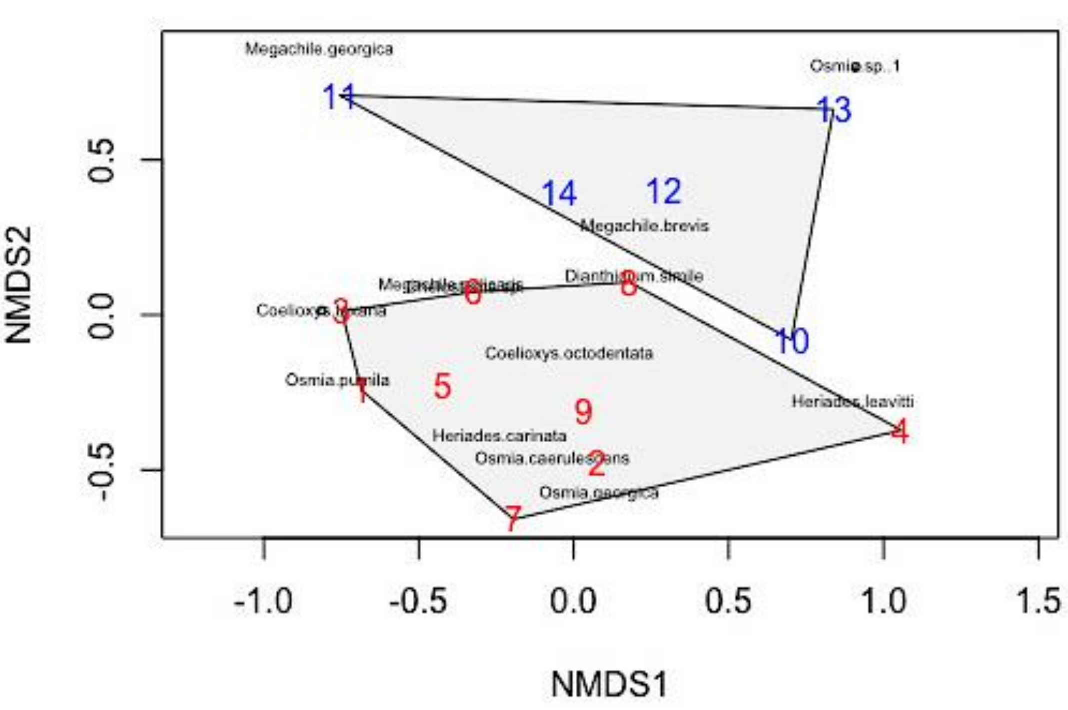

Figure 1.3. NMDS ordination of trap-nesting bee community composition across nine prairie remnants (red) and five restored prairies (blue) in study year 2013.

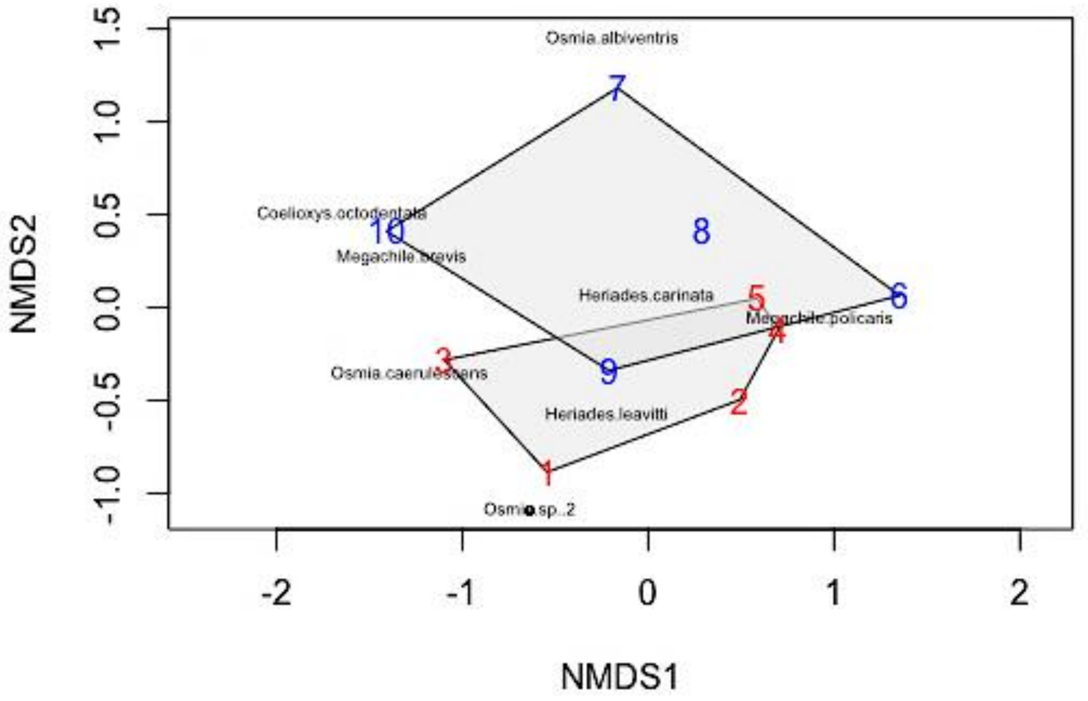

Figure 1.4. NMDS ordination of trap-nesting bee community composition across five prairie remants (red) and five restored prairies (blue) in study year 2014.

Chapter 2: Impacts of local forb diversity and landscape composition on body size, offspring production, and sex ratio of *Heriades carinata* Cresson (Hymenoptera: Megachilidae) in tallgrass prairies

Abstract

Native bees provide important pollination services to wild and cultivated plants, yet little is known about the current status and factors that affect particular species in their natural habitats. We used trap-nests to investigate how local forb diversity and surrounding landscape composition affected the body size, total number of offspring produced, and sex ratio of a native, solitary polylectic bee species, *Heriades carinata* Cresson. The study took place in tallgrass prairie remnant and restoration sites located within a largely agricultural landscape across eastern Kansas, USA. We reared a total of 196 individuals from 17 sites across both study years. We found a significant negative relationship between body size and local forb diversity, but did not find a relationship with body size and landscape composition. Total number of offspring per site was positively related to local forb diversity regardless of site type, but not significantly associated with landscape composition. We did not find any significant relationships between the sex ratio per site and local forb diversity or landscape composition. Our results suggest that *H. carinata* responds to local forb diversity by altering their provisioning behaviors, which may have consequences to both body size and population size.

Introduction

Bees (Hymenoptera: Apoidea) are integral contributors to ecosystem functioning and agricultural pollination services (Michener 2000). Adults and developing larvae depend on floral resources for survival, emphasizing the need for these resources to be present during the active flight season and within the foraging ranges of bees (Roulston and Goodell 2011). Wild bees inhabit diverse environments and are subjected to periods of floral resource scarcity due to a variety of factors including poor weather conditions (Tuell and Isaacs 2010) and land use management practices (Kremen et al. 2002). Bees are able to respond to changes in their environment by altering their foraging behavior including shifting the amount of pollen provisions per cell, subsequently affecting progeny size (Kim and Thorp 2001, Bosch 2008), the number of offspring produced, and/or sex ratio of offspring (Peterson et al. 2006a).

Bee body size, specifically intertegular distance (ITD), is related to the foraging range such that larger bees have a greater foraging distance (Greenleaf et al. 2007). Consequently, we might expect selective pressure for larger size allowing animals to reach greater distances in search of resources or mates, or selection for smaller size allowing survival on fewer resources. For example, in central Germany, two medium-sized solitary bee species (*Andrena* spp.) showed increased body size in relation to increased fragmentation (Warzecha et al. 2016). Local floral diversity was also associated with body size of bee and wasp communities in an agricultural landscape, with the mean community body size increasing in fields with fewer floral resources (Gathmann et al. 1994). Other studies report changes in body size across time, with species tending to become smaller as landscapes became more heavily modified or fragmented (Oliveira et al. 2016). Offspring size has important implications for fitness in bees, with larger-bodied individuals having lower overwintering mortality rates (Tepedino and Parker 1986, Bosch and Kemp 2004), increased cell provisioning rates (Kim and Thorp 2001) and fewer nest usurpations (Barthell and Thorp 1995).

Solitary female bees provide all of the necessary resources for nesting and offspring sustenance, therefore provisioning behaviors by the foraging mother has important implications for population dynamics. One study examining a multivoltine bee, *Megachile apicalis*, found that season influenced the provisioning behaviors of mother bees, with an increased number and smaller body size of offspring in spring emerging females and fewer, larger offspring produced later in the summer when resources were diminished (Kim and Thorp 2001). Increasing the distance of suitable host plants from nest sites resulted in fewer offspring produced by two specialist univoltine bee species in the family Megachilidae (Zurbuchen et al. 2010). Others have found similar relationships between foraging distance and offspring production for other solitary bee species (Peterson & Roitberg 2006a, Williams and Kremen 2007).

Females of many bee species are larger than males (Shreeves and Field 2007). The size difference between the sexes may be influenced by a number of factors including parental provisioning behavior and female fecundity (Rosenheim et al 1996, Shreeves and Field 2007). Bee body size is related to the amount of food consumed during the larval stage (Klostermeyer et al 1973, Johnson 1988), and because bees are haplodiploid and able to control the sex of progeny (Michener 2000), the availability of resources may influence the number or size of sons or daughters a foraging mother produces (Tepedino and Parker 1986, Kim 1999; Peterson and Roitberg 2005). Fisher’s theory of parental investment and sex allocation (1930) predicts a 1:1 ratio of females and males if there is no difference in the parental investment cost per sex produced. Studies that have examined solitary bee sex ratios in natural systems have found some support for this theory (Bosch and Vicens 2005), however this relationship is also likely influenced by changes in resource availability (Tepedino and Torchio 1982, Rosenheim et al. 1996, Kim 1999, Bosch 2008). However, Persson et al (2018) did not find any significant effects of floral resources on the proportion of female offspring in a predominately agricultural landscape in Sweden. To our knowledge, these relationships have not been explored in the context of the tallgrass prairie ecosystem.

The tallgrass prairie (TGP) is a North American ecosystem that dominated the central plains prior to European-American settlement 170 years ago (Sampson and Knopf 1994); but has been largely lost to agricultural expansion resulting in small, isolated remnants scattered throughout the Great Plains region (Bock and Bock 1998). TGP restoration projects began in the upper Midwest in the 1930's with selected seeds transplanted from nearby remnant areas (Cottam and Wilson 1966). Goals and management practices used to re-create former TGP continues to be a growing area of inquiry and discussion with many unique challenges in the present day dominantly agricultural landscape (Howe 1994). Prairie restorations tend to have lower species richness than remnant prairies (Sluis 2002); however, recent studies have found that pollinators, especially bees, have similar abundance and diversity in these two prairie types but with marked differences in composition (Denning and Foster 2017, Tonietto et al. 2017, Chapter 1). These studies indicate that prairie restorations are benefitting wild bee communities in an increasingly fragmented landscape, however, the compositional differences suggest that species-specific responses, such as dispersal ability and foraging range (i.e., body size) may differ.

In this study, we explored the response of *H. carinata* populations nesting in remnant and restoration tallgrass prairies located across eastern Kansas. More specifically, we examined four hypotheses: (i) the body size, total offspring produced, and sex ratio will differ by prairie type (remnant versus restoration), (ii) differences in local forb diversity will be associated with changes in the body size, number of offspring produced, and sex ratio (iii) landscape composition will be associated with changes in the body size, number of offspring produced, and sex ratio (iv) the interaction of local forb diversity and landscape composition will lead to differences in the body size, total offspring produced, and sex ratio.

Methods

Site selection

In total, 17 sites across eastern Kansas were used during the 2 years of this study (Figure 1.1). Not all sites could be used each year; 15 were used in 2013 and 10 in 2014, with 8 sites sampled both years (Table 2.1). The sites represented two types of tallgrass prairie, remnant (never tilled) or restoration. Restoration sites varied in management history (Table S1.1). All prairie sites chosen were similar in size (mean = 4.2 ha; range = 3 – 7 ha; Table S1.1), situated in a landscape that included cropland, grasslands, and woodland.

Study species

Bees in the genus *Heriades* are widely distributed across North America, nesting in narrow burrows and stems provisioned by a single female bee (Matthews 1965). Like other bee species, *H. carinata* are central place foragers, requiring several foraging trips to and from the nest site to provision brood cells with pollen and nectar resources. *Heriades* are small (4–7 mm length) (Michener 2000), which limits their foraging distance to locate necessary resources surrounding nest sites. For example, a similarly sized specialist bee, *Chelostoma florisomne*, foraged at distances no greater than 150 m from the nest site (Gathmann and Tscharntke 2002). Little is known about the diet breadth of *H. carinata*, but one study observed collections of multiple pollen types within their nests (Jensen 2001). We therefore presume that *H. carinata* is able to forage on multiple forb species in our study area.

Bee collection and identification

In 2013 three trap-nest units, and in 2014 five trap-nest units were placed 1-1.5 m aboveground in a southeast orientation, ten meters apart, across the center of each field site (Figures S1.2, S1.3). Each trap-nest unit consisted of 20 holes drilled 130 mm into pine boards. Ten holes were 5 mm in diameter, and 10 holes were 10 mm in diameter. Holes were lined with parchment paper to allow collection of finished nests. Sites were checked bimonthly from May–September in 2013 and May–August in 2014. Occupied nests were collected and replaced with new paper liner. Collected nests were stored in clear test tubes with a breathable lid at ambient temperatures and monitored for emergence of nest occupants. A subset of species identifications was confirmed by Dr. Victor Gonzalez, University of Kansas. D. Mayes and S. Anderson identified the remaining specimens using the individuals confirmed by Dr. Gonzalez in addition to keys found in Mitchell (1960) and Discover Life (www.discoverlife.org). The ITD of individuals was measured using a Leica dissecting microscope and Moticam1 camera with Motic Images Plus 2.0 software (Motic China Group Co., Ltd.).

Forb Richness Surveys

Ten of the 17 study sites were being concurrently used for a survey of forb and insect flower visitor communities (see Denning and Foster 2017). During each survey, four parallel 20 x 2.6-m belt transects were established near the center of each site. All currently-flowering forbs within each transect were recorded. Sites were sampled 3-4 times annually. Therefore, richness values were rarefied to three samples using sample-based rarefaction (R package “rich”; Rossi 2011). Detailed information about forb sampling can be found in Denning and Foster (2017). Sites that did not overlap with the other study were sampled using the same method but had fewer sampling events per season. In the analyses examining the effects of local floral diversity, only sites with the same number of sampling events per study year were included.

Landscape Composition

We used a combination of visual surveys and landcover mapping data to quantify the extent of natural/semi-natural land within 500 m surrounding (but exclusive of) the sites (Denning 2018). This spatial scale was used to include an estimated foraging range of our study species using Greenleaf et al. (2007) and the R package *BeeIT*, version 0.1.0. We defined natural/semi-natural land as the combined extent of woodlands and warm-season grasslands within each study site area. The 2005 Kansas Land Cover Patterns-Level IV raster layer (Kansas Applied Remote Sensing Program 2010) was used to provide baseline land use data. We updated this raster layer to account for land use changes subsequent to 2005 using the 2014 Cropland Data Layer (USDA National Agricultural Statistics Service 2014) to update agricultural lands surrounding the sites. We also visually surveyed the grasslands surrounding each site (depending on accessibility) to confirm (or, when needed, to update) the KLCP designations. Proportion natural/semi-natural land was calculated by dividing the sum of woodland and warm-season grassland area by the total extent of terrestrial land cover within the study areas. Finally, we also separately examined the percent woodland alone to explore this area as potentially valuable nesting habitat. Landscape characterization was performed in ArcMap (ArcGIS version 10.2, ESRI, Redlands, CA, USA).

Statistical analyses

Statistical analyses were carried out in R (R Core Team 2015). We compared the ITD of females versus males to account for possible sexual size dimorphism using a two-sample t-test prior to further analysis. We compared the ITD of bees collected in remnant versus restoration tallgrass prairie sites using a two-sample t-test. Linear mixed effects models were fit using the nmle package to examine the relationship between body size and local forb diversity, with local forb diversity and sex as fixed effects and site and year as nested random effects. We further explored whether there was a significant interaction between sex and forb diversity in response to body size to account for possible differences in how males and females respond in body size to forb diversity. In separate analyses, we used generalized linear models (GLM) to examine whether the total number of offspring (assuming a quasipoisson distribution) and sex ratio (females/ individuals; assuming binomial distribution) per site were related to local forb diversity or to percent natural/semi-natural, highly modified, or woodland area at the 500 m scale. We also examined total offspring production and sex ratio in response to interactions between local forb diversity and landscape composition.

Results

We reared a total of 196 *H. carinata* individuals from the two study years (Table 2.1). The average ITD of *H. carinata* females was significantly greater than the males (Table 2.2, Figure S2.1). We therefore included sex as a fixed effect in subsequent analyses exploring relationships between body size and local and landscape variables.

In 2013 we collected *H. carinata* nests primarily from remnant prairie sites; thus, our examination of body size differences in remnants versus restorations only includes data collected in 2014. We found no significant difference between the body sizes of *H. carinata* individuals collected in remnants versus restoration study sites (t = -0.542, df = 10, *P* = 0.598; Figure S2.2).

We found that body size was significantly negatively related to forb diversity ($\chi^2(1)$ = 5.163, *P* = 0.023, Table 2.3, Figure 2.1). We did not find a significant response of body size to interactions between sex and forb diversity ($\chi^2(1)$ = 0.0005, *P* = 0.98). We found no significant relationships between the body size of individuals collected per site and percent highly modified land or percent woodland (Table 2.3) or to interactions between forb diversity and landscape composition (Table 3).

The total number of offspring per site was positively associated with local forb diversity (Table 2.4; Figure 2.2). Because the percent of highly modified land and percent of natural/semi-natural grassland are inversely correlated, we report only the relationship between total offspring produced and percent highly modified land. There were no significant relationships found between the total offspring produced to the percent highly modified land or percent woodland (Table 2.4). We found no significant effect of local forb diversity or landscape composition (neither percent highly modified land or percent woodland) on the sex ratio (proportion of female offspring) in our study sites (Table 2.4).

Discussion

Understanding how wild solitary bees respond to resources in their immediate and surrounding environment is an important first step in protecting their populations and the ecological services they provide. Our study examined the intraspecific variation in body size, total offspring production, and sex ratio of a widely distributed solitary bee, *H. carinata*, in tallgrass prairie remnant and restoration sites within landscapes comprising agricultural and semi-natural fields and forested areas, to better understand effects of local and landscape factors on this species. Our findings suggest that both prairie restorations and remnant fields that were sampled are accessible to *Heriades*, and that local forb diversity regardless of field type may be a more influential factor on the body size and total number of offspring of these bees.

Resource availability, habitat loss and land use changes differently impact wild bees according to their body sizes (Gathmann et al. 1994; Jauker et al. 2013). In our study, decreased local forb diversity was associated with an increase in the body size of *H. carinata* individuals.

We did not find a greater proportion of females in relation to local forb diversity or landscape composition, which suggests that foraging mothers are producing females and males similarly regardless of resource availability and that our findings of body size response to local forb diversity was not skewed due to sex ratio decisions. It is possible that foraging mothers altered their provisioning behavior in the sites with fewer resources to maximize offspring body size, rather than provisioning a greater number of (smaller, or male biased) progeny. In areas with fewer local resources, larger bees should be better equipped to forage over a larger range in fragmented landscapes (Lichtenberg 2017; Chapter 3).

Incorporating traits such as body size and sociality is an important consideration in understanding how wild bees may differ in their responses to landscape composition. The percent of semi-natural habitat has been found to positively affect large social generalists (i.e., bumblebees), while small social and solitary bees were unaffected (Hopfenmüller et al. 2014). For solitary bee species, Warzecha et al. (2016) found that medium-sized *Andrena* species increased in body size as fragmentation in the surrounding landscape increased but did not observe this relationship for smaller or larger species. In contrast, Renauld et al. (2016) observed a reduction in the body size of *Andrena nasonii* bees in relation to increased agricultural use, with smaller individuals carrying less pollen. In our landscape-level analyses, we found no relationship between the percentage of highly modified land and body sizes of *H. carinata* in either study years. It is possible that since *Heriades* bees are smaller, they may be more responsive to local factors with foraging females altering provisioning behaviors in response to resources that are in closer proximity to their nest sites.

The number of solitary bee offspring produced is influenced by the resources that are available for the foraging mother. Under three different resource treatments, diminishing floral resources led to a reduction of size and number of offspring produced by *Megachile rotundata* (Peterson and Roitberg 2006b). Our findings partially agree, with fewer offspring produced in areas with decreased forb diversity; however, we found that body size increased in those environments, suggesting a trade-off between offspring production and body size. Under conditions of high floral resources available to spring emerging females, *M. apicalis* altered their provisioning behavior to increase the number of offspring produced, but they were smaller in size (Kim and Thorp 2001). Our work agrees with these findings, with increased offspring production and smaller-bodied individuals in resource-rich sites.

Figures and Tables

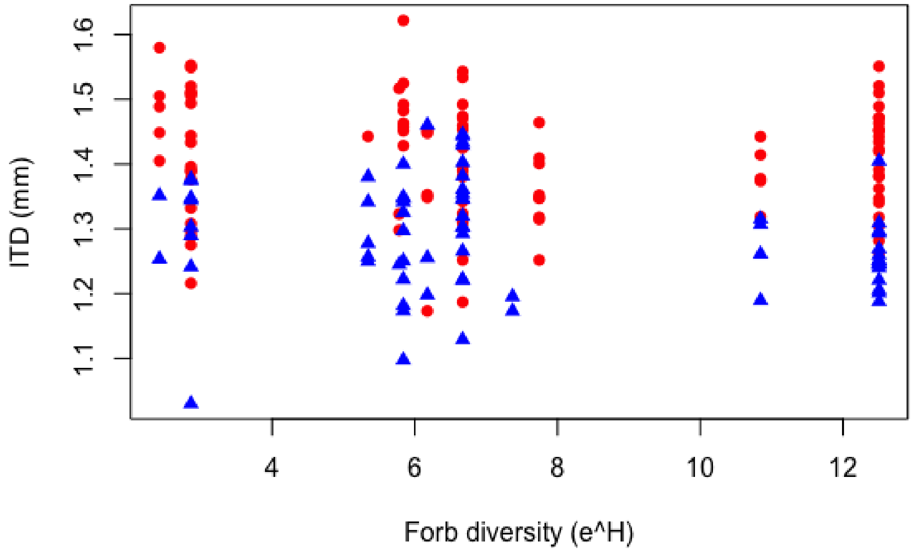

Figure 2.1. Significant negative association between bee body size (ITD) and local forb diversity ($\chi^2(1) = 5.163$, $P = 0.023$). Red circles are female bees, blue triangles are male bees.

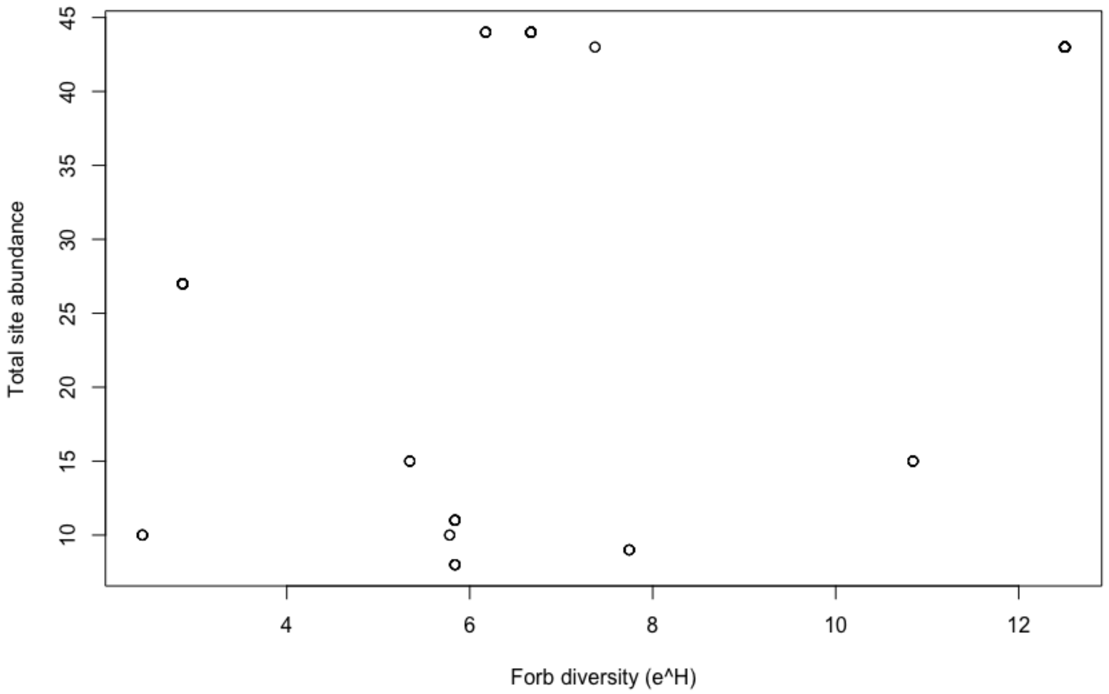

Figure 2.2. Significant positive association between total offspring and local forb diversity (*P* = 0.046).

Table 2.1. Study sites, site type, location, and the total number of *Heriades carinata* individuals reared from tallgrass prairies sites located across eastern Kansas in 2013 and 2014. NS = Site not sampled for that year.

Site	**Type**	**Latitude (N)**	**Longitude (W)**	**Total (2013)**	**Total (2014)**
BAK	Restoration	39.189	-95.610	0	0
BUS	Restoration	38.830	-95.141	0	8
COO	Restoration	39.451	-95.614	0	11
GUE	Remnant	38.984	-95.405	6	9
KET	Restoration	38.886	-95.385	0	0
MCE	Remnant	38.868	-95.646	44	8
MCK	Remnant	38.158	-94.571	18	NS
MEL-DO	Remnant	38.294	-95.536	0	NS
MEL-IH	Remnant	38.315	-95.480	6	NS
REA	Remnant	38.323	-96.036	9	NS
ROC	Remnant	39.045	-95.205	4	8
ROS	Remnant	38.299	-96.203	0	NS
SCO	Restoration	38.218	-95.444	0	NS
SLA	Restoration	38.202	-96.007	0	NS
SNY	Remnant	39.326	-95.660	44	2
AND	Remnant	39.458	-95.513	NS	27
PED	Restoration	39.741	-95.285	NS	10

Table 2.2. Body size (Mean ITD) and total number of *H. carinata* females and males collected from tallgrass prairie sites in eastern Kansas in 2013 and 2014.

Species	**Sex**	**Total (2013)**	**Total (2014)**	**Mean ITD (SE)**
H. carinata	female	71	51	1.404 (0.009)
	male	44	30	1.277 (0.010)

Table 2.3. Linear mixed-effects models describing the effects of local forb diversity, landscape composition (Percent highly modified land and Percent woodland in 500 m radius), and their interactions on bee body size (ITD).

Effect	**d.f.**	χ^2	***P***
Forb diversity	1	5.163	0.023
Percent highly modified land	1	0.483	0.487
Percent woodland	1	0.705	0.504
Forb diversity x Percent highly modified land	1	0.303	0.581
Forb diversity x Percent woodland	1	0	1

Table 2.4. Total offspring and sex ratio ANOVA table. Fixed effects are displayed from generalized linear models examining total offspring (quasipoisson distribution) and sex ratio (females/individuals; binomial distribution) per site in response to local forb diversity and landscape composition and their interaction from 17 tallgrass prairie study sites in eastern Kansas.

Response	**Effect**	**d.f.**	***P (chi-sq.)***
Total offspring	Forb diversity	1	0.046
	Percent highly modified land	1	0.831
	Percent woodland	1	0.191
	Forb diversity x Percent highly modified land	1	0.254
	Forb diversity x Percent woodland	1	0.793
Sex ratio	Forb diversity	1	0.815
	Percent highly modified land	1	0.639
	Percent woodland	1	0.390

Chapter 3: Body size influences stingless bee (Hymenoptera: Apidae: Meliponini) communities across a range of deforestation levels in Rondônia, Brazil

Abstract

Developments in understanding bee responses to habitat loss indicate that body size is a trait with important consequences for conservation. Stingless bees are a diverse group of eusocial bees providing pollination services in tropical landscapes, exhibiting a large range in body size across species. We tested the effects of deforestation on the body sizes of stingless bee communities by using museum specimens and revisiting a previous effort that sampled stingless bee communities across varying levels of deforestation at 183 sites in Rondônia, Brazil, in 1996-1997. Body size measurements (intertegular distance) from 72 species collected were included as dependent variables in response to forest area, forest edge, and connectivity of forest patches at several spatial scales. We find that stingless bee body size is negatively related to forest cover: mean community body size was larger in areas with greater amounts of deforestation, and smaller in areas with less deforestation. Second, stingless bee species richness was positively associated with forest edge regardless of body size. Lastly, we find that as forest patch isolation increased, the stingless bee community body size also increased. These findings support hypotheses that small stingless bee species might be more negatively affected by deforestation, adding to the growing body of evidence that stingless bees require areas of intact forest in near proximity to other forest patches to conserve these diverse pollinator communities.

Introduction

Habitat loss and decreased connectivity of suitable habitat have been associated with declines in wild pollinator diversity (Ricketts 2008, Winfree et al. 2009). In tropical regions, deforestation has been related to a decrease in species richness of native wild bees (Brosi et al. 2007, Brown and Oliveira 2013), however, some species seem less affected by forest loss or disturbance (Klein et al. 2002, Pioker-Hara et al. 2014, Giannini et al. 2015). In efforts to parse these responses, studies have included traits such as diet breadth, nesting requirements, foraging behavior, and intraspecific and interspecific variation in body size (Winfree et al. 2007, Bommarco et al. 2010, Williams et al. 2010, Lichtenberg et al. 2017).

Body size is an important trait to consider in understanding wild bee responses to land use change. Foraging range is positively related to body size of bees, with larger species capable of foraging greater distances (Araújo et al. 2004, Greenleaf et al. 2007). Bees are central place foragers and must collect nest resources within the limitations of their foraging ranges (Michener 2000), which may present greater challenges for smaller species as resources become locally scarce or increasingly disconnected. Including life history traits and body size of bees in analyses have provided insight regarding patterns of wild bees across landscapes with varying amounts of habitat loss, with some indications that smaller-bodied, social species are particularly sensitive (Jauker et al. 2013), however these patterns are not always consistent. Williams et al. (2010) did not find body size to be a reliable predictor of bee responses to land use change, but habitat isolation negatively affected above-ground nesting and social species while ground nesting species responded more negatively to soil tillage. At the intraspecific level, Renauld et al. (2016) found that the average body size of a solitary ground-nesting bee species (*Andrena nasonii* Robertson) decreased as the percent of agricultural land increased. In contrast, Warzecha et al.

(2015) found that medium sized *Andrena spp*. increased in body size with fragmentation with no discernable patterns for larger and smaller sized species. Bee body size has important implications for dispersal, as well as pollination efficiency (Stout 2000), therefore additional work is needed to better understand how bee body size responses may vary in response to land use changes.

Stingless bees (Hymenoptera: Apidae: Meliponini) are a species rich group of eusocial bees and are ecologically important as pollinators in tropical systems (Vit et al. 2013). In addition, they make important economic contributions via the pollination of many tropical crops, including coffee (Ricketts et al. 2004), and they exhibit a great range of interspecific variation in body size (Araújo et al. 2004, Pedro and Camargo 2009), colony size (Michener 2000), and foraging behaviors (Lichtenberg et al. 2017) across several hundred described species (Michener 2000). Studies examining how land use change driven by human activities affects stingless bee communities have found complicated responses. In general, forest area is positively associated with increased species richness (Brosi 2009, Brown and Oliveira 2013), with changes in the species observed at forest edges versus open areas (Brosi et al. 2007, 2008; Lichtenberg 2017). Eltz et al. (2002) found that in northern Borneo stingless bee nest densities tended to be higher in sites located in close proximity to mangroves and plantations than in continuous forests, benefitting from collection of non-forest pollen resources. While many studies have examined the impact of land use change on stingless bees (Roubik 2006, Brosi 2009, Frankie et al. 2009 and references therein; Vit et al. 2013), few have addressed trait-based responses to land use change.

This analysis tests the hypothesis that stingless bee communities respond differently to deforestation depending on body size and measures of habitat loss and fragmentation. In the present study, we measured the body size of 72 stingless bee species collected in Rondônia, Brazil in 1996-1997 using museum specimens and a dataset which included a major systematic inventory of stingless bees (Brown and Oliveira 2013). Specifically, we examined how body size in stingless bee communities is related to forest habitat fragmentation, as measured by total forest area, the amount of forest edge, and distance of forest patches to nearest patches (i.e., isolation) at several spatial scales surrounding sample points where bees were collected. Because body size is related to foraging distance (Greenleaf et al. 2007), we predict that smaller species will be more negatively affected by deforestation and increasing forest patch distance, and that these relationships will differ by landscape scale (Lichtenberg 2017). Further, because many stingless bee species depend on forests for nesting but may also forage outside of the forest we predict a positive relationship between richness and forest edge regardless of body size (Eltz et al. 2002).

Methods

Study area

This study took place in the state of Rondônia, Brazil, which has undergone heavy deforestation due to agricultural expansion since the 1970's (Frohn and Hao 2006). Sample points occurred across varying levels of deforestation, which is positively correlated with the length of time of modern human settlement (Brown and Albrecht 2001). One hundred eighty-three locations were sampled across the state from September 1996 to September 1997. To avoid resampling bees from the same colony, sampling locations were a minimum distance of 1.5 km apart.

Bee collections and identifications

Bees were collected using a standardized method in which three sub-locations (when possible, one forested and two non-forested) per location were sampled. Within each sub-location, three collectors each located a bush 50 m apart (parallel to the nearest forest edge located 250-500 m away) and then sprayed 15 pumps of a 1:1 mixture of honey and water on 0.25 m surface area of the bush and waited 60 m to attract and capture arriving bees (after methods of Wille, 1962). All bee species collected at each sub-location per location were combined for the purpose of this analysis. Because a nest's distance from the sampling areas could influence the number of foraging nestmates that come to the bait, and because stingless bee species are eusocial and differ in their recruitment to resources, we based our analyses on presence rather than abundance of each species in our samples. Previous work has examined the influence of sub-locations (i.e., forest and non-forest) on bee species richness and foraging behavior (Brown and Oliveira 2013, Brown et al. 2016). A full description of the sampling protocol can be found in Brown and Oliveira (2013).

The species collected by Brown and Oliveira (2013) included those individuals identified to species-level by the late Dr. João M.F. Camargo and Dr. Sílvia R.M. Pedro at the University of Sao Paulo-Ribeirao Preto, with additional representatives from the study region located in the Snow Entomological Museum at the University of Kansas, Lawrence, Kansas, USA.

We assessed body size by measuring the intertegular distance (ITD) of each species following the method of Cane et al. (1987) by measuring the shortest distance between the tegulae using an Olympus SZ60 stereo microscope (Supplemental Figure S3.1). We chose to use ITD as our body size measurement due to its correlation with stingless bee wing dimensions (Araújo et al. 2004) and foraging distance (Greenleaf et al. 2007). To account for possible differences in intraspecific variation, we measured five individuals of each species (all females) collected from the study region whenever possible. We divided all samples bee species into two categories, large and small. We used 1.44 mm, the median ITD of all species sampled, as the dividing point; “Small” bees had ITDs lower than the median (0.60-1.44 mm) and “Large” bees had ITDs greater than the median (1.45-3.81 mm) (Supplement Table S3.1). At each collection location, species were scored as “present” or “absent”. To make comparisons with other studies examining bee body size responses to disturbance, we included both the species richness of size classes and the mean body size of the community as response variables in our analyses.

Forest parameters

In this study deforestation is characterized from several aspects, including forest area and connectivity, patch isolation and increased fragmentation. The forest parameters—such as forest area, forest edge, and average distance of a forest patch to its nearest neighboring forest patch—that characterize deforestation properties were computed based on geo-referenced data with the aid of GIS (Geographic Information System, ArcGIS, ESRI). The geographic coordinates of sample locations were generated using GPS (See Brown and Oliveira 2013 for full description of field methods). Vegetation coverage information in 1997 was collected from PRODES (Amazon Deforestation Calculation Program) from INPE (National Institute of Space Research) (Câmara et al. 2006) with 30-meter spatial resolution. The sample locations were imposed on the vegetation layer depicting forest and non-forest cover in ArcGIS.

Our study aims to investigate how body size reflects the response of bee communities to deforestation at different spatial levels. The forest parameters and models were generated and constructed at three scales (radii of 500 m, 1000 m, and 1500 m) surrounding each study site. At each scale the total forest area, total forest edge, and distance between forest patches were computed using FRAGSTATS software (McGarigal et al. 2012). We classified areas of human disturbance based on Brown & Olivera (2013) and Fearnside (1989), where "new" refers to land that was deforested from 1981 to 1996, "old" refers to deforestation that took place prior to 1980, and "protected" includes those areas that were under preservation during the time the collections took place.

Statistical analysis

Before examining whether body size of stingless bee species is related to the landscape variables of interest, a Mantel test was performed to check for spatial autocorrelation among sites using the dist function in R version 3.2.2 (R Development Core Team 2015). Based on these results, we accept the null hypothesis that the two matrices (Site and Species) are not related due to geographic location (P = 0.4155).

To investigate associations between forest landscape variables and stingless bee species richness, we used generalized linear models with a Poisson distribution at each scale (500 m, 1000 m, 1500 m) surrounding sample points; landscape variables include forest area (ha), total edge (m), and average forest patch to nearest forest patch distance (m) as a measure of forest patch isolation (Tables 1, 3, 5). Response variables include total species richness, and species richness within each bees' size category ("Small", "Large"). To examine the response of the mean community ITD, we used a linear regression with the lm function in R. Finally, we categorized sample sites according to of the length of time since settlement to visualize the average ITD of those areas due to the positive relationship between settlement and deforestation (Brown & Oliveira 2013). Visual inspection of residual plots did not reveal obvious deviations from homoscedasticity or normality. All statistical analyses were carried out using R version 3.2.2 (R Development Core Team 2015).

Results

In total, we measured the ITD of 72 stingless bee species (range of individuals per species = 1-5, mean individuals per species = 4.7; Supplementary Table S3.1). Total stingless bee species richness was positively related to forest area at the 500 m, 1000 m, and 1500 m scales, and it was not significant when placed into small and large size categories (Table 3.1). Mean community ITD was negatively related to forest area at 500 m ($F_{(1,\,164)} = 6.171$, $P = 0.014$), 1000 m ($F_{(1,\,179)} = 4.741$, $P = 0.031$, Figure 3.1) and nearly significant at 1500 m (Table 3.2).

Stingless bee species richness was positively related to amount of forest edge at all scales (Table 3.3; $P < 0.001$, Figure 3.2), and also for both categories of body sizes ("Small"; $P < 0.001$; "Large"; $P < 0.001$). Mean community ITD was not significantly related to total forest edge at any scale surrounding sample points (Table 3.4).

Stingless bee species richness was positively related to average forest patch distance at 500 m and 1000 m, but not at 1500 m (Table 3.5). Species richness of "Small" bees was positively related to patch distance at 500 m and 1000 m ($P < 0.029$), but not 1500 m (Table 3.5). Species richness of the "Large" bee category was positively related to patch distance at 500 m ($P < 0.004$), but not for the other distances. Mean community ITD was positively related to patch distance at 500 m, 1000 m but not at 1500 m (Table 3.6, Figure 3.3). We found no significant differences in the mean community ITD when grouped by time since settlement ("old," 'new," and "protected", Figure 3.4).

Discussion

The total species richness of stingless bees was positively related to forest area at all scales, which agrees with earlier findings examining this relationship (Brown and Oliveira 2013).

When divided into two body size categories (i.e., “Small” and “Large”), the relationship of species richness to forest area was nonsignificant. Interestingly, however, when examining the mean ITD of the stingless bee community there was a significant negative relationship between body size and forest area. Bee body size responses to disturbance or habitat loss have been analyzed using the species richness or abundance individuals within a specified size class (Cane et al. 2006, Bommarco et al. 2010, Hopfenmüller et al. 2014), or by taking the average body size of individuals or species in a community (Steffan-Dewenter and Tscharntke 1999, Jauker et al. 2013). We include both approaches to make comparisons to other findings. The distribution in body sizes across all species included in our study was unimodal, thus no clear division of body size classes separated smaller-sized from larger-sized species (Supplementary Table S3.1; Supplementary Figure S3.1). Focusing on mean ITD community response to deforestation supports observations that smaller sized bees may be more susceptible to the effects of deforestation (Araújo et al. 2004, Kambach et al. 2012; Lichtenberg 2017).

In our study, forest edge was significantly related to total species richness, and species richness of both small and large sized stingless bee species. The direction of the relationship was positive for all groups, indicating that increased amounts of forest edge supports a greater richness of stingless bees regardless of body size. Others have found the presence of edge to be beneficial for bees (Eltz et al. 2002), with some observations that bees respond differently in relation to forest edges (Brosi et al. 2008) and disturbance (Kambach et al. 2012).

The severity of fragmentation and amount of natural habitat remaining differently affects wild bees (Winfree et al. 2009). The site history and landscape composition may influence stingless bee responses to disturbance events. Kambuch et al (2012) found increased species richness in areas that were fire degraded when compared to intact forest interiors. Areas that have been deforested may provide some added foraging opportunities for those species able to access the resources (Eltz et al. 2002). However, the beneficial aspects of disturbance to stingless bees should be considered with a clear understanding of the species needs for survival including availability of suitable nesting and foraging resources.

Few studies have examined the effects of connectivity on wild bees across fragmented habitats in tropical forest systems. In a Costa Rican landscape largely converted for agricultural production, Brosi et al. (2008) did not find forest fragment isolation to significantly affect bee richness or abundance, however, there were marked differences in the community composition based on landscape attributes with stingless bees comprising the majority (75 %) of bees sampled in forest interiors and less frequent (50 %) in adjacent pasture areas . Similarly, Calvillo et al. (2010) did not find forest fragment connectivity to be significantly related to bee richness or diversity, however they found overall increased species richness and diversity in relation to fragment size. In our study, stingless bees had mixed responses to forest patch connectivity. The total species richness was positively related to forest inter-patch distance at 500 m, but negatively related at 1000 m. A similar trend was found for the small bee category, and large bee species responded positively at 500 m, but there were no other distances with a significant relationship. Because smaller-sized bees have shorter foraging distances (Greenleaf et al. 2007), it is likely that the smaller stingless bee species are negatively affected by increasing forest patch distances in fragmented landscapes. For example, Araújo et al. (2004) estimated that larger stingless bee species are capable of foraging over distances up to 2 km, while smaller species foraged at a range of 621 to 951 m. Larger-bodied stingless bees have been found more frequently in pasture areas in Costa Rica (Lichtenberg et al. 2017), which may be due to the ability of larger bees to forage greater distances in search of resources. Our study found the mean community body size increased with increasing forest patch distances, supporting findings that larger species are present more in areas with greater forest patch distances compared to fewer smaller sized species.

These results support our prediction that smaller bee species may rely on large forested areas and forest patches that are closely connected. Body size influences foraging range in many bee species; in addition, stingless bees initiate new colonies by moving resources from the maternal nest site to a newly established nest (Roubik 2006, Vit et al. 2013) which may place additional limits on smaller species. However, it must be noted that some larger stingless bee species in the genus *Melipona* have also been found to be sensitive to deforestation or disturbance (Brown and Albrecht 2001, Pioker-Hara et al. 2014).

Adult bee body size is related to the quantity of resources consumed during the larval growth period (Johnson 1988) and temperature (Radmacher and Strohm 2009). Some work examining the effects of larval food intake on *Melipona* adult worker body sizes have found that less food results in weaker colonies with smaller workers, but that smaller individuals had higher pollen load carrying capacities (Ramalho et al. 1998). Additionally, Kuhn-Neto et al. (2009) found that larger *Melipona* workers foraged and recruited at significantly greater distances than smaller workers. Our study did not examine intraspecific differences in stingless bee body sizes across the range of deforestation; rather, we used an average ITD measurement to represent each species within the communities sampled. We observed a range of ITD across species (min = 0.66 mm, max = 3.81 mm) with some variation within species (Supplementary Table 3.1). Stingless bees are capable of adjusting their body size and corbiculae during periods of resource scarcity (Veiga et al. 2013) which may provide some flexibility to disturbance events.

Stingless bees are central place foragers (Elliott 1988) and must collect their resources within a foraging distance that is related to their body size (Roubik and Aluja 1983, Araújo et al. 2004, Kuhn-Neto et al. 2009). While our models suggest that body size is an important trait to include when aiming to understand the effects of deforestation, there are many other factors to consider. For example, foraging strategies may also influence stingless bee community responses, with generalist species being more sensitive to forest loss (Lichtenberg et al. 2017). Literature examining bee body size generally supports the conclusion that heritability of body size within bee species is low (Tepedino et al. 1984, Pignata and Diniz-Filho 1996), emphasizing the need for resources to be available within the foraging ranges of bees to ensure their persistence in modified landscapes.

Our study provides important insights into the body size responses of a highly diverse and important community of bees native to the Brazilian Amazon forest. While we find stingless bees respond positively to increased forest edge, we highlight that smaller bees favor larger areas of forest located in close proximity to other forest patches; therefore, the ability of these bees to tolerate increasing levels of deforestation may be limited.

Acknowledgments

I appreciate the extensive field work by J.C. Brown, and his permission and collaboration with exploring his dataset with additional questions pertaining to stingless bee ecology. I also am grateful for the assistance of Chet Bhatta for help with statistics and discussion of this topic. I appreciate Di Shi for her help with FRAGSTATS. I thank Deb Smith for her thoughtful feedback pertaining to this topic and assistance with revisions.

Figures and Tables

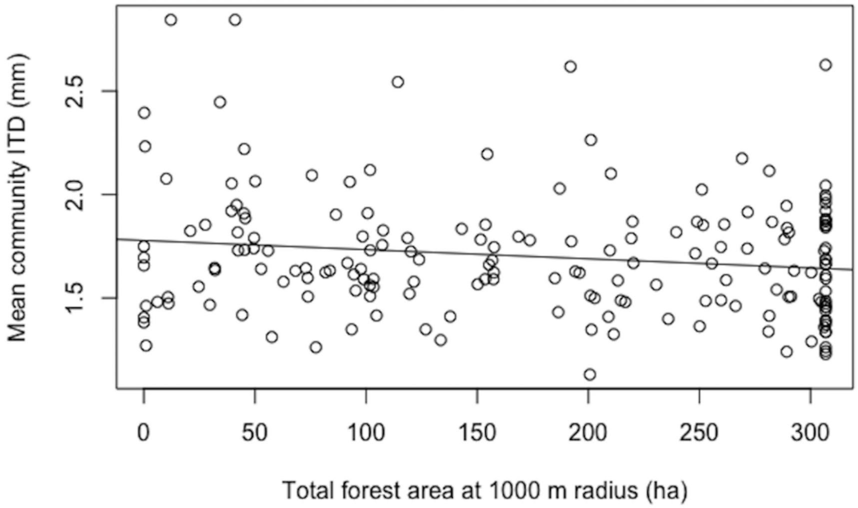

Figure 3.1. Single regression of mean community ITD against total forest area at 1000 m radius (R^2= 0.02, d.f. = 1, 179, *P* = 0.031).

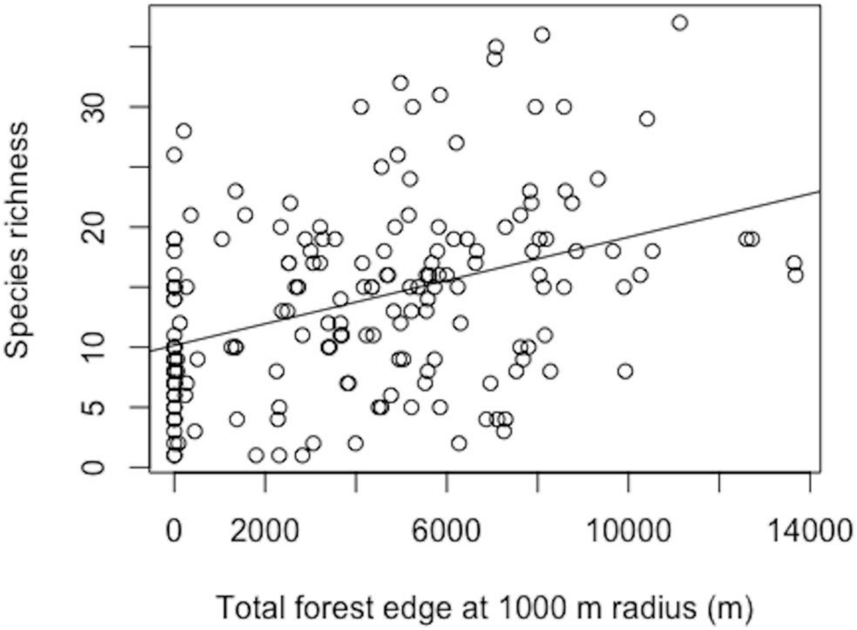

Figure 3.2. Single regression of total species richness against forest edge at 1000 m radius ($R^2 = 0.14$, d.f. = 1, 176, $P < 0.001$).

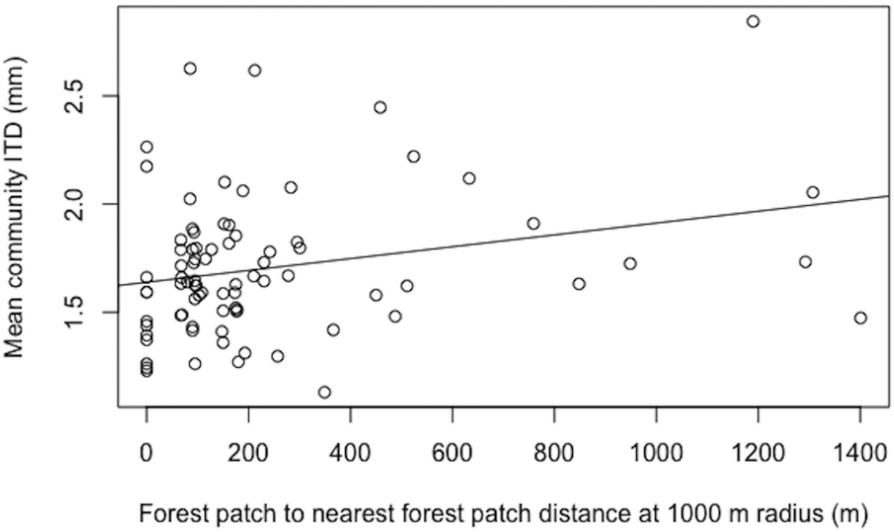

Figure 3.3. Single regression of mean community ITD against forest patch to nearest forest patch distance at 1000 m radius (R^2= 0.05, d.f. = 1, 79, *P* = 0.019).

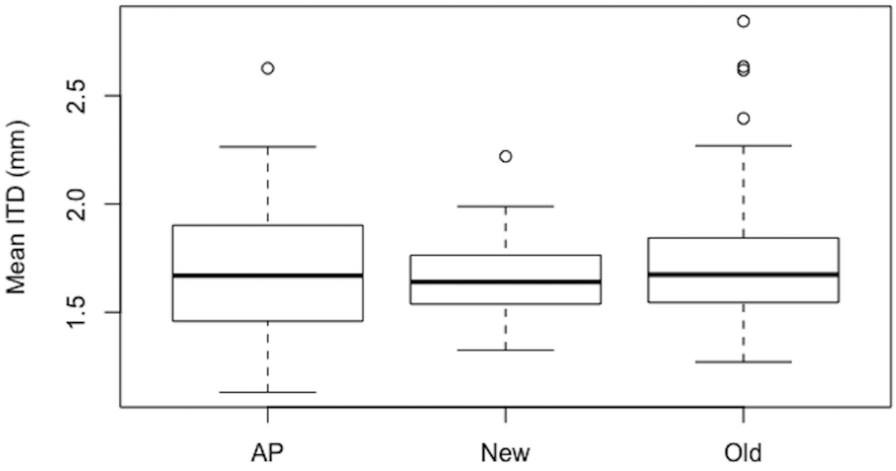

Figure 3.4. Box plot of Mean community ITD by settlement type (AP = Preservation area, New = deforested from 1981-1997, old = areas deforested prior to 1980).

Table 3.1. Results from linear models of mean community body size (ITD) against total forest edge at 500 m, 1000 m, and 1500 m radii of sample points.

Group	Distance (m)	Coefficient	SE	F-statistic	df	*P-value*
Mean body size of community (Mean ITD)	500	1.163e-05	1.845e-05	0.0253	1, 164	0.873
	1000	3.156e-06	6.818e-06	0.3879	1, 179	0.534
	1500	5.179e-07	3.421e-06	0.0138	1, 179	0.906

Table 3.2. Results from generalized linear models of stingless bee species richness and the species richness of two body size (ITD) categories (small = < 1.44 mm, large = > 1.44 mm) against average forest patch to nearest forest patch distance at 500 m, 1000 m and 1500 m radii of sample points.

Group	Distance (m)	Coefficient	SE	z value	df	*P-value*
Species richness (all)	500	0.0006	0.0002	3.24	1, 162	0.001
	1000	-0.0004	0.0001	-2.707	1, 77	0.006
	1500	-0.0003	0.0001	-0.607	1, 177	0.544
Species richness (small)	500	0.0007	0.0003	2.181	1, 159	0.029
	1000	-0.0005	0.0002	-2.567	1, 75	0.010
	1500	-0.0001	0.0001	-0.971	1, 174	0.331
Species richness (large)	500	0.0009	0.0003	2.91	1, 159	0.003
	1000	-8.553e-05	1.734e-04	-0.493	1, 75	0.622
	1500	4.224e-05	1.162e-04	0.364	1, 174	0.716

Table 3.3. Results from linear models of mean community body size (ITD) against average forest patch to nearest forest patch distance at 500 m, 1000 m, and 1500 m radii of sample points.

Group	Distance (m)	Coefficient	SE	F- statistic	df	*P-value*
Mean body size of community (Mean ITD)	500	0.0005	0.0002	6.661	1, 163	0.011
	1000	0.0003	0.0001	5.669	1, 79	0.019
	1500	-4.285e-06	8.097e-05	0.0101	1, 179	0.958

Chapter 4: Observations of Africanized honey bee *Apis mellifera scutellata* absence and presence within and outside forests across Rondônia, Brazil

Abstract

Researchers interested in the impacts of invasive species on native pollinators have conducted many studies dealing with the Africanized honey bee (AHB), ever since introduction of the African honey bee in Brazil some 60 years ago. Some have sought to determine how deforestation plays a role in mediating impacts. We present the largest-ever, systematic survey of AHB presence/absence in the Neotropics to test to what extent the AHB prefers to forage within forests vs. outside forests. AHB presence/absence within and outside forest fragments was recorded at 187 locations distributed across the state of Rondônia, Brazil. The landscapes at each location varied in terms of overall level of deforestation and the length of time since modern human settlement. AHB presence was significantly higher outside forest cover. These findings agree with previous studies documenting the spread of AHBs in the Amazon in their preference for deforested areas.

Introduction

Bees (Hymenoptera: Apoidea) are integral partners in the process of pollination, an ecosystem service imbedded within many terrestrial food webs including the human diet. Honey bees (*Apis spp*.) are notable because of their world-wide distribution driven largely by human-induced introductions (Goulson 2003). The escape and subsequent range expansion of Africanized honey bees (*A. mellifera sutellata*, hereafter, AHB) in Brazil and throughout the Neotropics and southern portions of the United States has taken place over the past 60 years (Kaplan 2007). While AHBs are generalist foragers capable of exploiting many types of floral resources, the patterns of AHB presence within and outside of forested areas across varying levels of deforestation warrants further insight.

The invasion of AHBs has been a model for better understanding invasive species dynamics, and continues to generate much concern for the impacts made both ecologically and economically. Many factors contribute to the success of AHBs rapid expansion, including their polylectic diet breadth (Cortopassi-Laurino and Ramalho 1988), forager and colony size and communication behavior for resources (Roubik 1980), colony establishment and long-distance dispersal (Gould and Gould 1988 cited by Brosi et al. 2008), and hybridization and eventual displacement of European honey bee alleles (Schneider et al. 2006). Indeed, this invasion has been described as one of the most rapid biological invasions ever recorded (Schneider et al. 2006).

Extensive work over the years on the interaction of AHBs with native bees (Roubik et al. 1986; Roubik and Villanueva-Gutierrez 2009; Roubik 1980, 2009), has revealed a picture that competition for floral resources is diminished by resource partitioning in forested environments. In long-term studies on Barro Colorado Island, Roubik and Wolda (2001) showed that the arrival of AHBs had no major effect on native bees. Brown and Oliveira 2014), and Cairns et al. (2005) suggest that stingless bees are affected both by a combination of habitat alteration and interaction with AHBs, with the latter seemingly thriving in deforested environments. Giannini et al. (2015) analyzed bee-plant network properties of two supergeneralist species (i.e., exotic *A. mellifera* and native *Trigona spinipes*) on flowers from numerous locations in Brazil, showing contrasting responses from the two focal species. *A. mellifera* responded indifferently to disturbance but was negatively effected by temperature, while *T. spinipes* responded positively to disturbance.

An important piece of understanding the relationships among AHBs, native bees, and disturbance is determining AHB preference for foraging outside vs. inside forested habitats. If AHBs showed no difference in preference, then one would expect that their impacts on native bees would be greater than if there were a strong preference for deforested environments. To this end, Oliveira and Cunha (2005), working in the area of the Biological Dynamics of Forest Fragments study near the National Institute for Amazonian Research (INPA) in Manaus, used numerous types of baits along transects within and outside forest fragments of various sizes and continuous forest to attract AHBs. They did not register even one occurrence of AHBs within the forest. While occurrences of AHBs outside the forest were confirmed, they were very low in number, perhaps because the density of colonies in the region of the experiment was low to begin with. Similarly, Brosi et al. (2008) examined the effects of forest fragmentation on tropical bee communities and found native bees to dominate forested areas, while honey bees were observed primarily in open pasture areas.

We report here observations of AHB presence/absence in Rondônia, Brazil, to test whether AHB have a preference for deforested over forested environments when foraging. This was an opportunistic, sideline study conducted during a major systematic inventory of stingless bees and orchid bees, part of an even larger inventory of fauna as part of the World Bank-funded studies conducted in support of the Second Approximation of the Socio-Economic-Ecological Zoning of the state in the 1990s. The AHB observations were made at the same time a research team carried out the methods for collecting stingless bees as published in Brown and Oliveira (2014). The present AHB study is significant in that it covers a much larger number of observation locations (187) than other studies, across an entire state in the Brazilian Amazon, which helps to avoid any potential bias introduced by the human or environmental characteristics of a particular place or region. Our study also relies on geo-referenced data, which allow for the calculation of deforestation levels around each sample location using satellite remote sensing and a geographic information system (GIS).

Cattle ranching and agriculture over the past half-century has led to significant deforestation in Rondônia (Brown 2001, Brown et al. 2004). The level of deforestation at the municipal or county-level in Rondônia is positively correlated with the length of time an area has been settled by farmers and ranchers (Brown and Albrecht 2001). The observation locations of the present study were distributed throughout 13 meso-regions, chosen to balance state-wide coverage with accessibility. The municipality of Ouro Preto do Oeste (1 of 13 meso-regions), in central Rondônia, was the base of operations of our study. It was surveyed each month at locations comprising a wide range of deforestation levels. Other meso-regions comprised a wide range of characteristics, differing in length of time since modern settlement, and some were within protected areas (biological stations, extractive reserves, national forests).

Methods

From September 1996 to September 1997 fieldwork was conducted in six locations each month in the Ouro Preto meso-region, and a separate meso-region of the state for a survey expedition, lasting from 5 to 10 days was selected and took place in the same month. The latitude/longitude of every sample location, most often at the border of a forest toward the back of a farm or ranch, was recorded with the aid of a Garmin 45 GPS. Each sample location was comprised of three sample sub-locations. Sub-location 1, outside forest cover, was approximately 250-500 m from the nearest forest. Land use/land cover included crops, savannas, pasture, or fallow. Sub-location 2, inside the nearest forest, was located approximately 250 m within the forest. Provided there are no standardized protocols for sampling bees in tropical forests (Brosi et al 2008), a variation on a technique by Wille (1962) in which at sub-locations 1 and 2, three observers sprayed a mixture of honey and water (1:1) on a bush, covering approximately .25 m^2. The bushes ran along a line parallel to the forest edge and were separated by 50 m. Observers noted the presence or absence of AHB at the honey baits over a 60-minute period. Abundance of AHB individuals was not recorded. Sub-location 3 was comprised of the area of flowers outside forest cover near the bait areas where observers recorded presence/absence of AHBs over an additional 60-minute period. Thus, in the most routine circumstances, for each sample location there are two outside forest and one inside observations. In some cases, however, there are only outside forest observations, and in others, only inside forest. All observations were made between 0700 h and 1800 h, and each sample location was at least 1.5 km apart in an effort to minimize the chances of observing bees from the same colony.

Associated with each sample location are variables measuring percent deforestation. These variables were determined with the aid of a GIS (Geographic Information System, ArcGIS, ESRI). The sample locations were imposed on a 1997 data layer depicting forest and non-forest cover available from PRODES (Amazon Deforestation Calculation Program) from INPE (National Institute of Space Research) (Câmara et al. 2006). Circular buffers were generated around each point with radii of numerous lengths (1, 2, 4, 6, and 10 km). Percent area deforested within each buffer was calculated.

A Chi-square test of independence for two nominal variables was used to determine whether the proportions of one variable (AHB presence/absence) are different for different values of the other variable (outside forest or inside forest observation), including all of the sub-locations, regardless of the fact that most locations had two outside forest observations and only one inside forest observation (Test 1). We then reconstructed the dataset in a few different ways by removing sub-location observations that potentially bias our results because they, in effect, are duplicate, non-independent observations (for example, AHB being observed at both the honey baits and at flowers in the two outside forest sub-locations of one location). We first removed repeated equal observations from sub-locations (Test 2). Finally, we excluded any location entirely that was not a standard two outside forest-, one inside forest-location, and we randomly removed one of the outside forest sub-location observations (Test 3).

We also sought to understand whether the percent deforestation around our sample locations was a significant predictor of AHB presence/absence. For this, we performed a logistic regression with percent deforestation as a continuous independent variable and AHB presence/absence as a binary response variable (present=1, absent = 0), using the generalized linear model (glm) function in R version 3.2.2 (R Development Core Team, 2015). We conducted 5 separate regressions, where the independent variable was 1 of 5 different circular areas drawn around each sample location (radii at 1, 2, 4, 6, and 10 km).

Results

All of the Chi-square tests reject the null hypothesis of independence (see table 1: tests 1, 2, and 3) at $p<0.01$. This is strong evidence that AHBs prefer to forage outside vs. inside forested environments. While such a finding has been stated before, we are unaware of any other study systematically covering such a large area with so many observations within and outside of forested environments. While Oliveira and Cunha (2005) found no honey bee presence at all within forested environments, our study observed AHB 20 (Test 1), 18 (Test 2), and 13 (Test 3) times within the forest, indicating that they may forage at least up to 250 m inside forest patches.

Our observations came at different times of the year. Seasonality could potentially affect our results. In order to account for this, we conducted observations in the meso-region of Ouro Preto do Oeste every month of the study in locations across a deforestation gradient from near total deforestation to near zero deforestation (see Brown and Albrecht 2001). When we limit our Chi-square test geographically to only the Ouro Preto do Oeste samples using our third statistic, we still get a similar, significant result (Table 4.1, Test 4). This result is expected, given that a large portion of our entire dataset comes from collections in that meso-region. Percent deforestation was a significant predictor of AHB observations only for radii at 2 km (Z =-2.067, p=0.0387) and 4 km (Z= -1.932, p=0.053). The relationship, in both cases, was negative.

Discussion

As deforestation levels increase, the likelihood of AHB presence decreases. At first, this seems to contradict our results from the Chi-square tests. Upon further consideration, we suggest this result is consistent, if we consider some other relationships. The time since modern settlement of each sample location is positively correlated with the level of deforestation (Brown and Albrecht 2001). As an area is first opened for settlement (low deforestation levels), pastures and croplands are established, and they are littered with a large number of fallen trees with cavities that make common nesting sites for AHBs. With time, these areas are repeatedly burned as part of common land management practices. With age, these areas eventually are removed of such logs, making AHB nests less common. Moreover, with increased deforestation, there is much more space over which AHBs can forage, and our honey baits may have been unable to compete with flowers that are especially abundant in fallowed fields and abandoned pastures. In contrast, in a newly deforested area, there are ample nesting sites, a smaller area over which to forage, and thus our baits were highly attractive.

In sum, AHBs clearly prefer foraging outside of forests, in the open. They are, however, capable of penetrating forests to forage, which could bring them into potential competition with pollinators that forage in forested environments. That said, it appears that only a certain amount of deforestation favors AHBs. At higher deforestation levels, they are less likely to occur, and this is correlated with the length of time since modern agricultural settlement. This may be because with time, potential nesting sites decrease due to common land management practices. This makes the AHB less abundant and, hence, it reduces the chances of any negative interactions with remaining native pollinators that forage within forests. Our study demonstrates the relevance of examining both local and landscape factors affecting AHBs and their relationships with other pollinators.

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Table 4.1. Results of Chi-square test of independence of AHB presence and absence inside *vs.* outside forests. Numbers in parentheses are expected cell totals. All tests reject the null hypothesis of independence, p<0.01

TEST 1	Present	Absent	Totals
Inside forest	20 (85.89)	143 (77.11)	163
Outside forest	205 (139.11)	59 (124.89)	264
Totals	225	202	427
Chi-square = 172.82			
TEST 2			
Inside forest	18 (68.13)	117 (66.87)	135
Outside forest	143 (92.87)	41 (91.13)	184
Totals	161	158	319
Chi-square = 129.12			
TEST 3			
Inside forest	13 (34.16)	86 (64.84)	99
Outside forest	56 (34.84)	45 (66.16)	101
Totals	69	131	200
Chi-square = 39.61			
TEST 4			
Inside forest	6 (16.13)	38 (27.87)	44
Outside forest	27 (16.87)	19 (29.13)	46
Totals	33	57	90
Chi-square = 19.66			

General Discussion

Wild bees are essential contributors to the functioning of terrestrial ecosystems and to the pollination of many crops that humans rely upon. Some evidence suggests that human induced land use changes are negatively affecting wild bees, therefore it is vital to improve our understanding of how populations and communities respond to these impacts. In this dissertation, I focused on bee body size changes as one possible mechanism that influences wild bee responses to habitat loss and fragmentation. In addition, I examined associations between bee abundance, diversity, and composition in response to land use change at local and landscape scales. In Chapters 1 and 2, I used the context of the tallgrass prairie to compare the abundance, diversity, community composition and body size of trap-nesting (TN) bees within prairie remnants and restorations for two study years. In addition, I explored the effects of local forb diversity and landscape composition on TN bees. In Chapters 3 and 4, I examine the responses of bee body size (Chapter 3) and foraging behavior (Chapter 4) to deforestation within context of the Brazilian Amazon forest.

Tallgrass prairie systems

While the majority of tallgrass prairie that once spanned across eastern Kansas has been replaced with agricultural land, some wild bee communities have continued to persist within the fragmented prairie sites. Bees are diverse in their nesting and resource needs, with some indications that aboveground nesting bees are particularly sensitive to the effects of agricultural intensification (Williams et al. 2010). At the community level, I found TN bees similarly in abundance, diversity, and body size between prairie remnants and restorations. Others have found prairie remnants and restorations supporting a comparable abundance and diversity of bees (Denning and Foster 2017), and restorations effectively reinstating pollinator communities over time (Griffin et al. 2017). Within my study sites, there was a positive association between TN bee diversity and local forb diversity. This observation is in agreement with others finding site-scale benefits to wild bees (Williams and Kremen 2007), which provides a management tool for land owners to use when aiming to improve pollinator habitat. Contrary to expectation, there were no significant associations between TN bee abundance, diversity, or body size and landscape composition. This may be due to a similar amount of remaining natural/semi-natural lands surrounding study sites (Supplemental Table 1.9), and future work examining landscape properties influencing tallgrass prairie fragments would benefit from sampling sites with a greater difference in surrounding composition.

In Chapter 1, the interspecific body size of TN bees was not associated with local or landscape level resources. Although these results were nonsignificant there was an opposing trend each study year where body size was larger in remnant prairies in 2013, and in 2014 the body size was larger in restored prairies (Supplemental Figure S1.3). These patterns may have been driven by collecting *Heriades* spp., a small-bodied bee, primarily in remnant study sites in 2013, but more equally from both site types in 2014. *Megachile policaris*, a larger-bodied bee was primarily collected in remnant prairies in 2014 which increased the overall mean body size of the community. Wild bee populations are known to fluctuate over space and time (Roubik 2001, Franzén and Nilsson 201**3**), therefore additional study years and sites would be helpful to better explore this question.

Few studies have examined intraspecific bee body size responses to land use change. In Chapter 2, I found a single species of bee, *Heriades carinata*, to vary in size in relation to local forb diversity, with larger-sized offspring produced in sites with lower forb diversity. Warzecha et al. (2016) found that a ground nesting species of *Andrena* increased in size with measures of habitat fragmentation; but another found that body size of another *Andrena* decreased with increasing agricultural areas in the landscape (Renauld et al. 2016). Contrary to these studies, *H. carinata* are above-ground nesting bees and may face different size-based constraints due to nest site characteristics (Roulston and Cane 2000), but more studies examining body size responses and nesting behaviors are needed. A second consideration to better understanding the findings concerning body size responses is how the data are analyzed. Body size is a continuous trait that is frequently applied as a dependent variable in some types of regression analyses. Studies have also examined the species richness of body size categories and binned body size classes (Cane et al. 2006, Bommarco et al. 2010, Hopfenmüller et al. 2014). This presents challenges to interpreting the findings of multiple studies when sizes are classified differently.

Controlled study designs have been used to investigate potential bee body size trade-offs with offspring production and sex ratios (Peterson et al. 2005). Studies that have examined Fisher's theory to explore sex ratios of bees have found that in some cases the expectation of a 2:1 male to female ratio is supported (Torchio 1980). Since males require smaller provisions, there may be situations when there are more males produced due to scarce resources in the foraging ranges of the mother (Peterson et al. 2006). I did not find the sex ratio of *H. carinata* to be associated with prairie type, local forb diversity, or landscape composition. Foraging mothers thus did not produce more males in areas with fewer resources, rather, maintained varying proportions of males and females across study sites (Supplemental Table S2.1).

The trap-nest method is uniquely suited for examining bee body size responses to land use, because the foraging range is clearly delimited to the central nest place within the study sites. This method provided information from a community (Chapter 1) and population (Chapter 2) perspective. A benefit provided by sampling with trap-nests is the ability to collect more details about offspring number, size, and sex; this provides helpful information to better understand population dynamics. Some have found that nest hole dimensions can affect the provisioning behavior of a foraging bee (Bosch and Vicens 2006), so this must also be carefully considered when designing and interpreting these studies. Sex ratios did not differ for *H. carinata* between prairie types or in relation to local forb diversity or landscape composition (Chapter 2), suggesting that the nest hole dimensions were suitable for exploring these questions. Trap-nests with two different diameter sized hole openings captured 41 % of the species found using aerial net surveys in the same study sites (Supplemental Table S1.10). In addition, six bee species were sampled in trap-nests that were not collected using aerial netting at flowers. The results from these studies suggest that trap-nests are a useful tool for future monitoring efforts in this ecosystem, and would complement other sampling methods.

Brazilian Amazon forest

The state of Rondônia in Brazil has experienced some of the greatest forest losses in the Amazon (Lindsey 2007). In Chapter 3, stingless bees were previously sampled (1996-1997) in an effort to understand the impact of deforestation affecting bees in Rondônia, Brazil. This dataset provided an ideal opportunity to examine additional relationships of wild bees to land use change because it was a year-long intensive sampling effort that provided a species-rich characterization of the bee fauna (Brown and Albrecht 2001, Brown and Oliveira 2013). Using the stingless bee dataset along with additional information characterizing the environment surrounding study sites, I examined community body size associations in the context of the Brazilian Amazon, and found smaller sized bee species more frequently in areas with more intact forest and shorter distances between forest patches.

In addition to body size constraints affecting stingless bee foraging ranges (Araújo et al. 2004), they may have additional pressures due to their nest founding behaviors. Unlike the swarming behavior that honey bees use, stingless bees move resources from the maternal nest to a daughter nest and may take many weeks to establish (Vit et al. 2013). In a deforested landscape, smaller-bodied species may have greater difficulties gathering resources and founding new nest sites, but this requires additional research. In addition, larger bodied bees have been shown to forage at higher temperatures than smaller sized bees, which may also impact the foraging behaviors of bees in a deforested environment (APS 2019). Together, the findings from Chapters 2 and 3 support other studies demonstrating bee size variation in response to land use changes.

We found a significant relationship between the mean body size of the stingless bee community and forest area, but not when examining the species richness of small and large size classes. One explanation for this result is the unimodal shape of the distribution, with no clear divisions separating large and small-sized species (Supplemental Figure S3.2). Future work examining bee body size relationships would benefit from incorporating multiple approaches to assessing size responses.

The findings from Chapter 3 suggest that small-bodied stingless bee species may be more sensitive to the effects of deforestation, and supports others that have examined this topic (Kambach 2017, Lichtenberg et al. 2017). While we observed interspecific body size variation in response to deforestation for this system, we did not examine possible differences within each species across the deforestation gradient. Some studies have found body size changes within stingless bee species in response to food availability, with smaller individuals capable of carrying larger pollen loads than larger individuals (Ramalho et al. 1998, Veiga et al. 2013). Future research on the impact of habitat loss and fragmentation affecting intraspecific body sizes within stingless bee species would be insightful.

Another factor suspected to negatively impact stingless bees is the invasion and subsequent competitive pressures by Africanized honey bees (AHB) (Freitas et al. 2009). The findings presented in Chapter 4 are in agreement with others that have noted an increase in presence of AHBs in primarily deforested areas (Brosi et al. 2008). Our study did not directly assess AHB displacing stingless bees using shared resources (food, nesting), however, our results suggest that interactions between species is less likely in forested areas and more likely outside of the forest. Deforestation may therefore provide greater opportunities for AHBs to establish and compete for resources outside of the forest, however this requires greater exploration.

Conclusion

Land use changes are likely to continue as the human population increases, which will subsequently impact wild bees and their valued pollination services. Bees are notably diverse in their ecological and life history traits, exhibiting complex responses to disturbance. This dissertation research finds that (1) tallgrass prairie remnants and restorations are providing similar requirements for solitary aboveground nesting bees to survive and reproduce but that (2) the overall body size of the TN community does not vary according to the resources within or surrounding either prairie type. Although community level body size responses were not observed in the context of the tallgrass prairie, there was (3) intraspecific body size variation within *H. carinata*, with a larger body size and lower number of offspring produced in sites with lower local forb diversity. In Brazil, there was (4) an increased mean community body size of stingless bees in areas with less forest area and greater distances between forest patches, and (5) an increased likelihood of observing AHBs in deforested areas. These findings suggest that local practices have the potential to benefit wild bee communities, and that bee body size is a useful trait to incorporate when aiming to assess bee responses to land use change.

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Appendix 1: Supplemental Figures and Tables for Chapter 1

Figure S1.1. Wood block trap-nest unit. Finished nests have been sealed with specific materials used by the occupant (e.g., mud, leaves, or resins).

Figure S1.2. Trap-nest units set up at Rockefeller prairie in 2013.

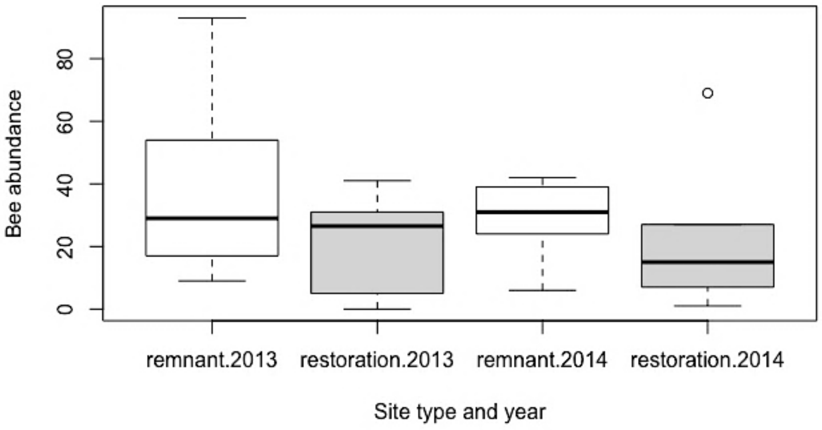

Figure S1.3. Boxplot of bee abundance within tallgrass prairie sites in 2013 and 2014.

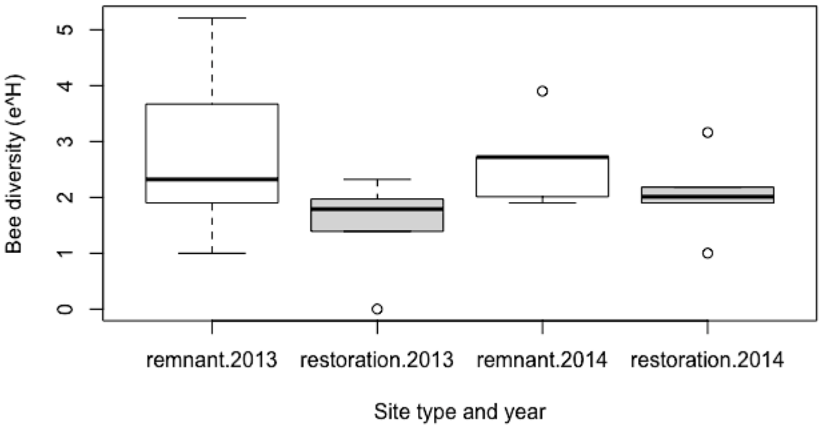

Figure S1.4. Boxplot of bee diversity (e^H) within tallgrass prairie sites in 2013 and 2014.

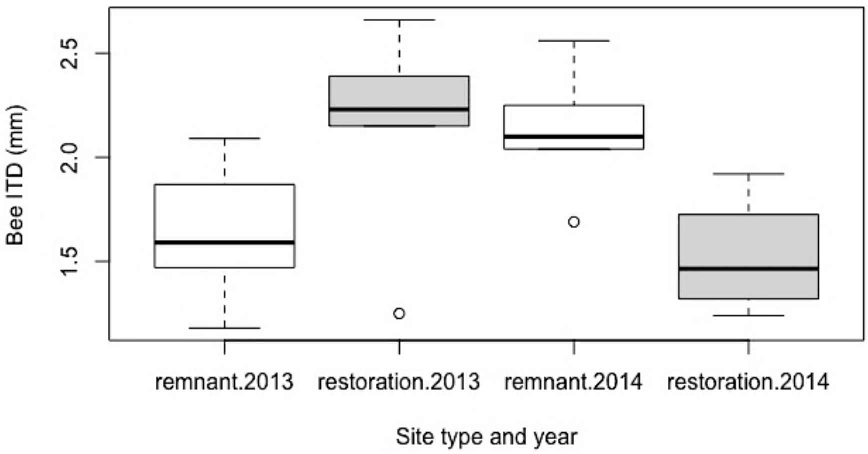

Figure S1.5. Boxplot of bee body sizes collected within tallgrass prairie sites in 2013 and 2014.

Table S1.1. Tallgrass prairie study sites located across eastern Kansas in 2013 and 2014. Rem = Remnant, Res = Restoration.

Site	Type	Lat (N)	Long (W)	Size (ha)	Year sampled	Management notes
BAK	Res	39.189	-95.610	3.1	2013, 2014	Burned and hayed periodically. Added native seed mixes.
BUS	Res	38.830	-95.141	5.2	2013, 2014	Burned every 3 years. Enrolled in CRP in 1999.
COO	Res	39.451	-95.614	5.2	2013, 2014	Burned and hayed periodically. Added native seed mixes.
GUE	Rem	38.984	-95.405	4.4	2013, 2014	Hayed annually. Burned periodically.
KET	Res	38.886	-95.385	7.0	2013, 2014	Hayed annually. Added native seed mixes.
MCE	Rem	38.868	-95.646	3.8	2013, 2014	Burned and hayed periodically.
MCK	Rem	38.158	-94.571	4.2	2013	Burned and hayed periodically.
MEL-DO	Rem	38.294	-95.536	3.1	2013	Burned and hayed periodically.
MEL-IH	Rem	38.315	-95.480	4.8	2013	Burned and hayed periodically.
REA	Rem	38.323	-96.036	3.5	2013	Burned periodically. Mowed periodically.
ROC	Rem	39.045	-95.205	3.5	2013, 2014	Burned and hayed periodically.
ROS	Rem	38.299	-96.203	3.2	2013	Burned and hayed periodically.
SCO	Res	38.218	-95.444	3.5	2013	Burned and hayed periodically. Enrolled in CRP.
SLA	Res	38.202	-96.007	4.8	2013	Hayed annually. Added native seed mixes.
SNY	Rem	39.326	-95.660	5.7	2013, 2014	Burned periodically.
AND	Rem	39.458	-95.513	5.8	2014	Hayed annually.
PED	Res	39.741	-95.285	3.5	2014	Burned periodically. Added native seed mixes.

Table S1.2. Complete list of trap-nesting bees reared from tallgrass prairie study sites in 2013 and 2014.

Species	**Site ID**	**Site type**	**Sex**	**ITD (mm)**	**Date collected**
Chelostoma sp.	Reading	remnant	m	1.93	2013
Chelostoma sp.	Reading	remnant	m	2.08	2013
Chelostoma sp.	Reading	remnant	m	2.03	2013
Dianthidium simile	Ross	remnant	m	2.33	2013
Dianthidium simile	Ross	remnant	f	2.32	2013
Dianthidium simile	Ross	remnant	f	2.47	2013
Dianthidium simile	Ross	remnant	m	2.42	2013
Dianthidium simile	Ross	remnant	f	2.68	2013
Heriades carinata	Guess	remnant	m	1.38	2013
Heriades carinata	Guess	remnant	f	1.44	2013
Heriades carinata	Guess	remnant	m	1.28	2013
Heriades carinata	Guess	remnant	m	1.25	2013
Heriades carinata	Guess	remnant	m	1.26	2013
Heriades carinata	Guess	remnant	m	1.34	2013
Heriades carinata	McElroy	remnant	m	1.43	2013
Heriades carinata	McElroy	remnant	m	1.22	2013
Heriades carinata	McElroy	remnant	m	1.22	2013
Heriades carinata	McElroy	remnant	f	1.31	2013
Heriades carinata	McElroy	remnant	m	1.35	2013
Heriades carinata	McElroy	remnant	m	1.32	2013
Heriades carinata	McElroy	remnant	m	1.38	2013
Heriades carinata	McElroy	remnant	f	1.45	2013
Heriades carinata	McElroy	remnant	f	1.53	2013
Heriades carinata	McElroy	remnant	f	1.54	2013
Heriades carinata	McElroy	remnant	f	1.47	2013
Heriades carinata	McElroy	remnant	m	1.43	2013
Heriades carinata	McElroy	remnant	f	1.34	2013
Heriades carinata	McElroy	remnant	f	1.40	2013
Heriades carinata	McElroy	remnant	m	1.27	2013
Heriades carinata	McElroy	remnant	f	1.46	2013
Heriades carinata	McElroy	remnant	f	1.42	2013
Heriades carinata	McElroy	remnant	m	1.35	2013
Heriades carinata	McElroy	remnant	f	1.47	2013
Heriades carinata	McElroy	remnant	m	1.36	2013
Heriades carinata	McElroy	remnant	f	1.39	2013
Heriades carinata	McElroy	remnant	f	1.49	2013

Heriades carinata	McElroy	remnant	f	1.19	2013
Heriades carinata	McElroy	remnant	f	1.32	2013
Heriades carinata	McElroy	remnant	m	1.44	2013
Heriades carinata	McElroy	remnant	f	1.38	2013
Heriades carinata	McElroy	remnant	m	1.45	2013
Heriades carinata	McElroy	remnant	f	1.25	2013
Heriades carinata	McElroy	remnant	f	1.35	2013
Heriades carinata	McElroy	remnant	f	1.35	2013
Heriades carinata	McElroy	remnant	m	1.30	2013
Heriades carinata	McKnight	remnant	f	1.25	2013
Heriades carinata	McKnight	remnant	f	1.40	2013
Heriades carinata	McKnight	remnant	f	1.32	2013
Heriades carinata	McKnight	remnant	m	1.22	2013
Heriades carinata	McKnight	remnant	m	1.09	2013
Heriades carinata	McKnight	remnant	m	1.15	2013
Heriades carinata	McKnight	remnant	f	1.10	2013
Heriades carinata	McKnight	remnant	m	1.23	2013
Heriades carinata	McKnight	remnant	f	1.35	2013
Heriades carinata	McKnight	remnant	m	1.25	2013
Heriades carinata	McKnight	remnant	f	1.22	2013
Heriades carinata	McKnight	remnant	f	1.42	2013
Heriades carinata	McKnight	remnant	m	1.36	2013
Heriades carinata	McKnight	remnant	f	1.36	2013
Heriades carinata	McKnight	remnant	f	1.41	2013
Heriades carinata	McKnight	remnant	m	1.28	2013
Heriades carinata	McKnight	remnant	m	1.18	2013
Heriades carinata	McKnight	remnant	f	1.47	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.45	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.35	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.43	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.47	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.47	2013
Heriades carinata	Melvern (Indian Hills)	remnant	f	1.33	2013
Heriades carinata	Reading	remnant	f	1.51	2013
Heriades carinata	Reading	remnant	f	1.45	2013
Heriades carinata	Reading	remnant	f	1.51	2013

Heriades carinata	Reading	remnant	f	1.42	2013
Heriades carinata	Reading	remnant	f	1.45	2013
Heriades carinata	Reading	remnant	f	1.41	2013
Heriades carinata	Reading	remnant	f	1.32	2013
Heriades carinata	Reading	remnant	m	1.12	2013
Heriades carinata	Reading	remnant	f	1.46	2013
Heriades carinata	Rockefeller	remnant	f	1.52	2013
Heriades carinata	Rockefeller	remnant	f	1.30	2013
Heriades carinata	Rockefeller	remnant	f	1.32	2013
Heriades carinata	Rockefeller	remnant	m	1.25	2013
Heriades carinata	Snyder	remnant	f	1.45	2013
Heriades carinata	Snyder	remnant	f	1.45	2013
Heriades carinata	Snyder	remnant	f	1.38	2013
Heriades carinata	Snyder	remnant	m	1.25	2013
Heriades carinata	Snyder	remnant	m	1.31	2013
Heriades carinata	Snyder	remnant	f	1.51	2013
Heriades carinata	Snyder	remnant	f	1.47	2013
Heriades carinata	Snyder	remnant	f	1.46	2013
Heriades carinata	Snyder	remnant	f	1.45	2013
Heriades carinata	Snyder	remnant	f	1.42	2013
Heriades carinata	Snyder	remnant	m	1.30	2013
Heriades carinata	Snyder	remnant	f	1.52	2013
Heriades carinata	Snyder	remnant	m	1.21	2013
Heriades carinata	Snyder	remnant	f	1.47	2013
Heriades carinata	Snyder	remnant	f	1.43	2013
Heriades carinata	Snyder	remnant	m	1.40	2013
Heriades carinata	Snyder	remnant	m	1.22	2013
Heriades carinata	Snyder	remnant	f	1.55	2013
Heriades carinata	Snyder	remnant	f	1.44	2013
Heriades carinata	Snyder	remnant	m	1.29	2013
Heriades carinata	Snyder	remnant	f	1.25	2013
Heriades carinata	Snyder	remnant	f	1.36	2013
Heriades carinata	Snyder	remnant	m	1.20	2013
Heriades carinata	Snyder	remnant	f	1.39	2013
Heriades carinata	Snyder	remnant	m	1.25	2013
Heriades carinata	Snyder	remnant	f	1.26	2013
Heriades carinata	Snyder	remnant	f	1.34	2013
Heriades carinata	Snyder	remnant	f	1.32	2013
Heriades carinata	Snyder	remnant	m	1.20	2013
Heriades carinata	Snyder	remnant	f	1.42	2013

Heriades carinata	Snyder	remnant	f	1.28	2013
Heriades carinata	Snyder	remnant	m	1.25	2013
Heriades carinata	Snyder	remnant	f	1.35	2013
Heriades carinata	Snyder	remnant	f	1.30	2013
Heriades carinata	Snyder	remnant	m	1.24	2013
Heriades carinata	Snyder	remnant	m	1.26	2013
Heriades carinata	Snyder	remnant	f	1.38	2013
Heriades carinata	Snyder	remnant	m	1.19	2013
Heriades carinata	Snyder	remnant	m	1.27	2013
Heriades carinata	Anderson	remnant	f	1.22	2014
Heriades carinata	Anderson	remnant	f	1.33	2014
Heriades carinata	Anderson	remnant	m	1.38	2014
Heriades carinata	Anderson	remnant	m	1.34	2014
Heriades carinata	Anderson	remnant	m	1.30	2014
Heriades carinata	Anderson	remnant	m	1.29	2014
Heriades carinata	Anderson	remnant	f	1.51	2014
Heriades carinata	Anderson	remnant	m	1.24	2014
Heriades carinata	Anderson	remnant	f	1.43	2014
Heriades carinata	Anderson	remnant	f	1.49	2014
Heriades carinata	Anderson	remnant	f	1.40	2014
Heriades carinata	Anderson	remnant	f	1.55	2014
Heriades carinata	Anderson	remnant	f	1.44	2014
Heriades carinata	Anderson	remnant	f	1.29	2014
Heriades carinata	Anderson	remnant	f	1.31	2014
Heriades carinata	Anderson	remnant	f	1.39	2014
Heriades carinata	Anderson	remnant	m	1.35	2014
Heriades carinata	Anderson	remnant	f	1.52	2014
Heriades carinata	Anderson	remnant	f	1.38	2014
Heriades carinata	Anderson	remnant	f	1.51	2014
Heriades carinata	Anderson	remnant	f	1.55	2014
Heriades carinata	Anderson	remnant	f	1.51	2014
Heriades carinata	Anderson	remnant	m	1.37	2014
Heriades carinata	Anderson	remnant	m	1.03	2014
Heriades carinata	Anderson	remnant	f	1.30	2014
Heriades carinata	Anderson	remnant	f	1.39	2014
Heriades carinata	Anderson	remnant	f	1.28	2014
Heriades carinata	Busby	restoration	m	1.30	2014
Heriades carinata	Busby	restoration	m	1.25	2014
Heriades carinata	Busby	restoration	f	1.43	2014
Heriades carinata	Busby	restoration	f	1.45	2014

Heriades carinata	Busby	restoration	m	1.10	2014
Heriades carinata	Busby	restoration	m	1.22	2014
Heriades carinata	Busby	restoration	f	1.46	2014
Heriades carinata	Busby	restoration	f	1.49	2014
Heriades carinata	Coombs	restoration	m	1.33	2014
Heriades carinata	Coombs	restoration	m	1.18	2014
Heriades carinata	Coombs	restoration	f	1.52	2014
Heriades carinata	Coombs	restoration	f	1.46	2014
Heriades carinata	Coombs	restoration	m	1.35	2014
Heriades carinata	Coombs	restoration	m	1.40	2014
Heriades carinata	Coombs	restoration	m	1.35	2014
Heriades carinata	Coombs	restoration	m	1.17	2014
Heriades carinata	Coombs	restoration	f	1.62	2014
Heriades carinata	Coombs	restoration	m	1.34	2014
Heriades carinata	Coombs	restoration	f	1.48	2014
Heriades carinata	Guess	remnant	f	1.38	2014
Heriades carinata	Guess	remnant	m	1.19	2014
Heriades carinata	Guess	remnant	m	1.26	2014
Heriades carinata	Guess	remnant	m	1.31	2014
Heriades carinata	Guess	remnant	f	1.32	2014
Heriades carinata	Guess	remnant	f	1.37	2014
Heriades carinata	Guess	remnant	f	1.41	2014
Heriades carinata	Guess	remnant	f	1.44	2014
Heriades carinata	Guess	remnant	m	1.32	2014
Heriades carinata	Kettle	restoration	f	1.17	2014
Heriades carinata	Kettle	restoration	f	1.34	2014
Heriades carinata	Kettle	restoration	f	1.27	2014
Heriades carinata	McElroy	remnant	m	1.26	2014
Heriades carinata	McElroy	remnant	f	1.45	2014
Heriades carinata	McElroy	remnant	f	1.35	2014
Heriades carinata	McElroy	remnant	f	1.35	2014
Heriades carinata	McElroy	remnant	f	1.17	2014
Heriades carinata	McElroy	remnant	m	1.46	2014
Heriades carinata	McElroy	remnant	f	1.45	2014
Heriades carinata	Pederson	restoration	m	1.20	2014
Heriades carinata	Pederson	restoration	f	1.32	2014
Heriades carinata	Pederson	restoration	f	1.31	2014
Heriades carinata	Pederson	restoration	f	1.35	2014
Heriades carinata	Pederson	restoration	f	1.40	2014
Heriades carinata	Pederson	restoration	f	1.35	2014

Heriades carinata	Pederson	restoration	f	1.46	2014
Heriades carinata	Pederson	restoration	f	1.35	2014
Heriades carinata	Pederson	restoration	f	1.25	2014
Heriades carinata	Pederson	restoration	f	1.41	2014
Heriades carinata	Rockefeller	remnant	f	1.49	2014
Heriades carinata	Rockefeller	remnant	f	1.51	2014
Heriades carinata	Rockefeller	remnant	f	1.41	2014
Heriades carinata	Rockefeller	remnant	f	1.45	2014
Heriades carinata	Rockefeller	remnant	m	1.25	2014
Heriades carinata	Rockefeller	remnant	f	1.58	2014
Heriades carinata	Rockefeller	remnant	m	1.35	2014
Heriades carinata	Snyder	remnant	m	1.17	2014
Heriades carinata	Snyder	remnant	m	1.20	2014
Heriades leavitti	Baker	restoration	m	1.26	2013
Heriades leavitti	Baker	restoration	f	1.12	2013
Heriades leavitti	Baker	restoration	m	0.99	2013
Heriades leavitti	Baker	restoration	f	0.99	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.23	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.23	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.29	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.28	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.07	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.21	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.23	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.14	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.32	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.21	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.30	2013
Heriades leavitti	Melvern (Docking)	remnant	f	1.22	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.09	2013

Heriades leavitti	Melvern (Docking)	remnant	f	1.28	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.10	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.07	2013
Heriades leavitti	Melvern (Docking)	remnant	m	1.08	2013
Heriades leavitti	Melvern (Docking)	remnant	m	0.83	2013
Heriades leavitti	Snyder	remnant	m	1.25	2013
Heriades leavitti	Snyder	remnant	f	1.34	2013
Heriades leavitti	Snyder	remnant	f	1.42	2013
Heriades leavitti	Ross	remnant	m	1.10	2013
Heriades leavitti	Ross	remnant	m	1.17	2013
Heriades leavitti	Ross	remnant	m	1.19	2013
Heriades leavitti	Ross	remnant	m	1.12	2013
Heriades leavitti	Ross	remnant	m	1.15	2013
Heriades leavitti	Ross	remnant	f	1.29	2013
Heriades leavitti	Ross	remnant	f	1.21	2013
Heriades leavitti	Ross	remnant	m	1.10	2013
Heriades leavitti	Anderson	remnant	f	1.25	2014
Heriades leavitti	Anderson	remnant	f	1.17	2014
Heriades leavitti	Anderson	remnant	f	1.32	2014
Heriades leavitti	Anderson	remnant	f	1.16	2014
Heriades leavitti	Anderson	remnant	m	1.23	2014
Heriades leavitti	Anderson	remnant	m	1.23	2014
Heriades leavitti	Anderson	remnant	m	1.22	2014
Heriades leavitti	Anderson	remnant	m	1.15	2014
Heriades leavitti	Anderson	remnant	f	1.32	2014
Heriades leavitti	Anderson	remnant	m	1.09	2014
Heriades leavitti	Anderson	remnant	f	1.28	2014
Heriades leavitti	Anderson	remnant	m	1.06	2014
Heriades leavitti	Anderson	remnant	m	1.28	2014
Heriades leavitti	Anderson	remnant	m	1.25	2014
Heriades leavitti	Anderson	remnant	m	1.15	2014
Heriades leavitti	Anderson	remnant	m	1.25	2014
Heriades leavitti	Anderson	remnant	m	1.25	2014
Heriades leavitti	Anderson	remnant	m	1.26	2014
Heriades leavitti	Anderson	remnant	m	1.22	2014
Heriades leavitti	Anderson	remnant	m	1.18	2014

Heriades leavitti	Anderson	remnant	f	1.26	2014
Heriades leavitti	Anderson	remnant	m	1.19	2014
Heriades leavitti	Anderson	remnant	m	1.14	2014
Heriades leavitti	Anderson	remnant	m	1.21	2014
Heriades leavitti	Anderson	remnant	f	1.30	2014
Heriades leavitti	Anderson	remnant	f	1.28	2014
Heriades leavitti	Anderson	remnant	f	1.46	2014
Heriades leavitti	Guess	remnant	m	1.03	2014
Heriades leavitti	Guess	remnant	m	1.07	2014
Heriades leavitti	Guess	remnant	m	1.78	2014
Heriades leavitti	Guess	remnant	f	1.40	2014
Heriades leavitti	Guess	remnant	f	1.33	2014
Heriades leavitti	Guess	remnant	f	1.34	2014
Heriades leavitti	Guess	remnant	f	1.29	2014
Heriades leavitti	Guess	remnant	m	1.11	2014
Heriades leavitti	Guess	remnant	m	0.98	2014
Heriades leavitti	Kettle	restoration	f	1.33	2014
Heriades leavitti	Kettle	restoration	m	1.10	2014
Heriades leavitti	Kettle	restoration	m	1.22	2014
Heriades leavitti	McElroy	remnant	f	1.21	2014
Heriades leavitti	McElroy	remnant	m	1.15	2014
Heriades leavitti	McElroy	remnant	m	1.13	2014
Heriades leavitti	McElroy	remnant	m	1.11	2014
Megachile brevis	Coombs	restoration	f	2.57	2013
Megachile brevis	Coombs	restoration	m	2.27	2013
Megachile brevis	Coombs	restoration	f	1.84	2013
Megachile brevis	Coombs	restoration	f	1.71	2013
Megachile brevis	Coombs	restoration	f	2.08	2013
Megachile brevis	Coombs	restoration	f	1.97	2013
Megachile brevis	Coombs	restoration	f	2.21	2013
Megachile brevis	Coombs	restoration	f	2.30	2013
Megachile brevis	Coombs	restoration	f	2.17	2013
Megachile brevis	Coombs	restoration	m	2.16	2013
Megachile brevis	Coombs	restoration	f	2.56	2013
Megachile brevis	Coombs	restoration	f	2.53	2013
Megachile brevis	Coombs	restoration	f	2.33	2013
Megachile brevis	Coombs	restoration	f	2.49	2013
Megachile brevis	Coombs	restoration	f	2.80	2013
Megachile brevis	Coombs	restoration	f	2.30	2013
Megachile brevis	Coombs	restoration	f	2.44	2013

Megachile brevis	Kettle	restoration	m	2.62	2013
Megachile brevis	McElroy	remnant	f	2.67	2013
Megachile brevis	Reading	remnant	m	2.37	2013
Megachile brevis	Ross	remnant	m	2.36	2013
Megachile brevis	Ross	remnant	f	2.43	2013
Megachile brevis	Ross	remnant	m	2.41	2013
Megachile brevis	Ross	remnant	f	2.59	2013
Megachile brevis	Slaymaker	restoration	f	2.54	2013
Megachile brevis	Slaymaker	restoration	m	2.46	2013
Megachile brevis	Slaymaker	restoration	f	2.26	2013
Megachile brevis	Slaymaker	restoration	f	2.10	2013
Megachile brevis	Slaymaker	restoration	f	2.67	2013
Megachile brevis	Snyder	remnant	f	3.05	2013
Megachile brevis	Ross	remnant	f	2.57	2013
Megachile brevis	Ross	remnant	f	2.42	2013
Megachile brevis	Ross	remnant	f	2.51	2013
Megachile brevis	Ross	remnant	f	2.40	2013
Megachile brevis	Ross	remnant	f	2.60	2013
Megachile brevis	Ross	remnant	f	2.33	2013
Megachile brevis	Ross	remnant	f	2.42	2013
Megachile brevis	Baker	restoration	f	1.91	2013
Megachile brevis	Slaymaker	restoration	f	2.61	2013
Megachile brevis	Slaymaker	restoration	f	2.57	2013
Megachile brevis	Slaymaker	restoration	f	2.57	2013
Megachile brevis	Slaymaker	restoration	f	2.60	2013
Megachile brevis	McElroy	remnant	m	2.03	2013
Megachile brevis	McElroy	remnant	f	2.46	2013
Megachile brevis	McElroy	remnant	f	2.46	2013
Megachile brevis	McElroy	remnant	f	2.30	2013
Megachile brevis	McElroy	remnant	f	2.64	2013
Megachile brevis	McElroy	remnant	f	2.55	2013
Megachile brevis	Ross	remnant	f	2.46	2013
Megachile brevis	Ross	remnant	f	2.07	2013
Megachile brevis	Ross	remnant	f	2.06	2013
Megachile brevis	Ross	remnant	f	2.41	2013
Megachile brevis	Ross	remnant	f	2.39	2013
Megachile brevis	Ross	remnant	f	2.13	2013
Megachile brevis	Ross	remnant	m	2.80	2013
Megachile brevis	Anderson	remnant	m	2.34	2014
Megachile brevis	Anderson	remnant	f	2.61	2014

Megachile brevis	Coombs	restoration	f	2.67	2014
Megachile brevis	McElroy	remnant	f	2.64	2014
Megachile brevis	McElroy	remnant	f	2.64	2014
Megachile brevis	McElroy	remnant	m	2.24	2014
Megachile brevis	McElroy	remnant	m	2.44	2014
Megachile brevis	McElroy	remnant	m	2.40	2014
Megachile brevis	Pederson	restoration	f	2.57	2014
Megachile brevis	Pederson	restoration	f	2.50	2014
Megachile brevis	Pederson	restoration	f	2.40	2014
Megachile brevis	Pederson	restoration	f	2.59	2014
Megachile brevis	Pederson	restoration	f	2.51	2014
Megachile brevis	Pederson	restoration	m	2.40	2014
Megachile brevis	Pederson	restoration	f	2.73	2014
Megachile brevis	Pederson	restoration	f	2.56	2014
Megachile brevis	Pederson	restoration	f	2.33	2014
Megachile brevis	Pederson	restoration	m	2.23	2014
Megachile brevis	Pederson	restoration	m	2.43	2014
Megachile brevis	Pederson	restoration	m	2.33	2014
Megachile brevis	Pederson	restoration	m	2.17	2014
Megachile brevis	Pederson	restoration	f	2.72	2014
Megachile brevis	Pederson	restoration	f	2.51	2014
Megachile brevis	Pederson	restoration	f	2.61	2014
Megachile brevis	Pederson	restoration	f	2.56	2014
Megachile brevis	Pederson	restoration	f	2.50	2014
Megachile brevis	Pederson	restoration	m	2.57	2014
Megachile brevis	Pederson	restoration	m	2.44	2014
Megachile exilis	McKnight	remnant	f	2.30	2013
Megachile exilis	Anderson	remnant	m	1.98	2014
Megachile georgica	Busby	restoration	m	2.18	2013
Megachile georgica	Busby	restoration	m	2.13	2013
Megachile georgica	Busby	restoration	f	2.51	2013
Megachile policaris	Busby	restoration	m	2.54	2013
Megachile policaris	Busby	restoration	m	2.59	2013
Megachile policaris	Guess	remnant	m	3.05	2013
Megachile policaris	McKnight	remnant	f	3.06	2013
Megachile policaris	McKnight	remnant	m	2.79	2013
Megachile policaris	McKnight	remnant	m	2.77	2013
Megachile policaris	McKnight	remnant	m	2.26	2013
Megachile policaris	McKnight	remnant	f	3.42	2013
Megachile policaris	McKnight	remnant	f	3.24	2013

Megachile policaris	McKnight	remnant	m	3.02	2013
Megachile policaris	McKnight	remnant	f	3.10	2013
Megachile policaris	McKnight	remnant	f	2.84	2013
Megachile policaris	McKnight	remnant	m	3.03	2013
Megachile policaris	Ross	remnant	f	3.06	2013
Megachile policaris	Ross	remnant	f	2.49	2013
Megachile policaris	Ross	remnant	m	2.92	2013
Megachile policaris	Ross	remnant	f	3.09	2013
Megachile policaris	Ross	remnant	m	2.77	2013
Megachile policaris	Ross	remnant	m	3.19	2013
Megachile policaris	Ross	remnant	m	2.73	2013
Megachile policaris	Melvern (Indian Hills)	remnant	f	2.90	2013
Megachile policaris	Reading	remnant	f	3.51	2013
Megachile policaris	Slaymaker	restoration	f	2.87	2013
Megachile policaris	Slaymaker	restoration	f	3.30	2013
Megachile policaris	Melvern (Indian Hills)	remnant	f	2.63	2013
Megachile policaris	Melvern (Indian Hills)	remnant	m	2.83	2013
Megachile policaris	Reading	remnant	m	2.92	2013
Megachile policaris	Reading	remnant	f	3.09	2013
Megachile policaris	Slaymaker	restoration	f	3.10	2013
Megachile policaris	Slaymaker	restoration	f	2.86	2013
Megachile policaris	Slaymaker	restoration	m	2.70	2013
Megachile policaris	Coombs	restoration	m	3.38	2014
Megachile policaris	Coombs	restoration	m	3.16	2014
Megachile policaris	Coombs	restoration	m	3.20	2014
Megachile policaris	Coombs	restoration	f	3.08	2014
Megachile policaris	Guess	remnant	m	2.67	2014
Megachile policaris	Guess	remnant	m	2.84	2014
Megachile policaris	Guess	remnant	m	3.00	2014
Megachile policaris	Guess	remnant	f	3.32	2014
Megachile policaris	Guess	remnant	m	3.22	2014
Megachile policaris	Guess	remnant	m	2.82	2014
Megachile policaris	Guess	remnant	m	3.03	2014
Megachile policaris	Guess	remnant	m	3.21	2014
Megachile policaris	Guess	remnant	m	3.29	2014
Megachile policaris	Guess	remnant	m	3.28	2014
Megachile policaris	Guess	remnant	m	3.07	2014
Megachile policaris	Guess	remnant	m	3.00	2014

Megachile policaris	Guess	remnant	m	3.15	2014
Megachile policaris	Rockefeller	remnant	f	3.42	2014
Megachile policaris	Rockefeller	remnant	f	3.20	2014
Megachile policaris	Rockefeller	remnant	m	3.42	2014
Megachile policaris	Rockefeller	remnant	f	3.30	2014
Megachile policaris	Rockefeller	remnant	m	3.33	2014
Megachile policaris	Rockefeller	remnant	m	2.99	2014
Megachile policaris	Rockefeller	remnant	m	3.10	2014
Megachile policaris	Rockefeller	remnant	m	2.60	2014
Megachile policaris	Rockefeller	remnant	m	3.00	2014
Megachile policaris	Rockefeller	remnant	m	2.67	2014
Megachile policaris	Rockefeller	remnant	m	3.12	2014
Megachile policaris	Rockefeller	remnant	m	3.20	2014
Megachile policaris	Rockefeller	remnant	m	2.97	2014
Megachile policaris	Rockefeller	remnant	f	3.45	2014
Megachile policaris	Snyder	remnant	f	3.46	2014
Megachile policaris	Snyder	remnant	m	3.19	2014
Megachile rugifrons	Anderson	remnant	m	2.73	2014
Osmia albiventris	Busby	restoration	m	1.93	2014
Osmia albiventris	Busby	restoration	m	2.11	2014
Osmia albiventris	Busby	restoration	m	2.05	2014
Osmia albiventris	Busby	restoration	m	2.01	2014
Osmia caerulescens	Coombs	restoration	f	1.72	2013
Osmia caerulescens	Coombs	restoration	f	1.95	2013
Osmia caerulescens	Rockefeller	remnant	f	1.78	2013
Osmia caerulescens	Rockefeller	remnant	f	1.65	2013
Osmia caerulescens	Rockefeller	remnant	m	1.42	2013
Osmia caerulescens	Rockefeller	remnant	m	1.54	2013
Osmia caerulescens	Ross	remnant	f	1.97	2013
Osmia caerulescens	Ross	remnant	f	1.93	2013
Osmia caerulescens	Ross	remnant	m	1.68	2013
Osmia caerulescens	Ross	remnant	m	1.61	2013
Osmia caerulescens	Ross	remnant	m	1.55	2013
Osmia caerulescens	Ross	remnant	m	1.61	2013
Osmia caerulescens	Ross	remnant	m	1.65	2013
Osmia caerulescens	Ross	remnant	m	1.48	2013
Osmia caerulescens	Ross	remnant	f	1.74	2013
Osmia caerulescens	Ross	remnant	m	1.62	2013
Osmia caerulescens	Ross	remnant	m	1.48	2013
Osmia caerulescens	Ross	remnant	f	1.75	2013

Osmia caerulescens	Ross	remnant	m	1.42	2013
Osmia caerulescens	McElroy	remnant	f	1.90	2014
Osmia caerulescens	McElroy	remnant	f	1.78	2014
Osmia caerulescens	McElroy	remnant	f	1.93	2014
Osmia caerulescens	McElroy	remnant	m	1.78	2014
Osmia cordata	Kettle	restoration	f	2.43	2013
Osmia cordata	Kettle	restoration	f	2.47	2013
Osmia cordata	Kettle	restoration	f	2.34	2013
Osmia cordata	Kettle	restoration	m	2.14	2013
Osmia cordata	Kettle	restoration	m	2.07	2013
Osmia cordata	Kettle	restoration	m	2.01	2013
Osmia cordata	Kettle	restoration	m	2.07	2013
Osmia cordata	Kettle	restoration	m	2.17	2013
Osmia cordata	Kettle	restoration	m	1.94	2013
Osmia cordata	Kettle	restoration	f	2.43	2013
Osmia cordata	Kettle	restoration	f	2.37	2013
Osmia georgica	McKnight	remnant	f	1.67	2013
Osmia georgica	McKnight	remnant	f	1.95	2013
Osmia georgica	McKnight	remnant	f	2.18	2013
Osmia georgica	McKnight	remnant	f	1.65	2013
Osmia georgica	McKnight	remnant	f	1.67	2013
Osmia georgica	McKnight	remnant	f	1.91	2013
Osmia georgica	McKnight	remnant	f	1.89	2013
Osmia georgica	McKnight	remnant	m	1.82	2013
Osmia georgica	McKnight	remnant	m	1.68	2013
Osmia georgica	McKnight	remnant	m	1.65	2013
Osmia georgica	McKnight	remnant	m	1.55	2013
Osmia georgica	McKnight	remnant	f	2.00	2013
Osmia georgica	McKnight	remnant	f	2.15	2013
Osmia georgica	McKnight	remnant	m	1.44	2013
Osmia georgica	McKnight	remnant	m	1.45	2013
Osmia illinoensis	Anderson	remnant	f	2.17	2014
Osmia pumila	Guess	remnant	m	1.47	2013
Osmia pumila	Guess	remnant	m	1.59	2013
Osmia pumila	Guess	remnant	f	1.71	2013
Osmia pumila	Guess	remnant	f	1.74	2013
Osmia pumila	McKnight	remnant	m	1.48	2013
Osmia pumila	McKnight	remnant	m	1.38	2013
Osmia pumila	McKnight	remnant	m	1.54	2013
Osmia pumila	McKnight	remnant	m	1.49	2013

Osmia pumila	McKnight	remnant	m	1.49	2013
Osmia pumila	McKnight	remnant	m	1.32	2013
Osmia pumila	McKnight	remnant	m	1.39	2013
Osmia pumila	McKnight	remnant	m	1.44	2013
Osmia pumila	McKnight	remnant	m	1.57	2013
Osmia pumila	McKnight	remnant	m	1.48	2013
Osmia sp. 1	Kettle	restoration	m	2.04	2013
Osmia sp. 1	Kettle	restoration	m	1.90	2013
Osmia sp. 1	Kettle	restoration	m	1.93	2013
Osmia sp. 1	Kettle	restoration	m	2.00	2013
Osmia sp. 1	Kettle	restoration	m	1.81	2013
Osmia sp. 1	Kettle	restoration	m	2.03	2013
Osmia sp. 2	Anderson	remnant	f	1.47	2014
Osmia sp. 2	Anderson	remnant	m	1.54	2014

Table S1.3. Trap-nesting bee abundance table. Fixed effects are displayed from a generalized linear mixed model assessing the effects of site type, study year, and site type x study year interaction on bee abundance across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Site Type	1	21	0.483	0.494
Year	1	21	0.226	0.639
Site Type x Year	1	21	0.481	0.495

Table S1.4. Trap-nesting bee diversity table. Fixed effects are displayed from a generalized linear mixed model assessing the effects of site type, study year, and site type x study year interaction on bee diversity across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Site Type	1	13.89	3.740	0.073
Year	1	7.20	1.00	0.349
Site Type x Year	1	5.69	0.57	0.476

Table S1.5. Trap-nesting bee abundance table. Fixed effects are displayed from a general linear mixed model assessing the effects of local forb diversity, study year, and forb diversity x study year interaction on bee abundance across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Forb diversity	1	15	3.19	0.094
Year	1	15	0.554	0.468
Forb diversity x Year	1	14	0.117	0.738

Table S1.6. Trap-nesting bee diversity table. Fixed effects are displayed from a generalized linear mixed model assessing the effects of local forb diversity, study year, and forb diversity x study year interaction on bee diversity across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Forb diversity	1	13.26	6.689	0.022
Year	1	8.18	1.04	0.335
Forb diversity x Year	1	8.49	1.311	0.283

Table S1.7. Trap-nesting bee body size table. Fixed effects are displayed from a generalized linear mixed model assessing the effects of site type and study year on bee body size across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Site Type	1	20	0.0341	0.855
Year	1	20	0.0204	0.887

Table S1.8: Trap-nesting bee body size table. Fixed effects are displayed from a generalized linear mixed model assessing the effects of forb diversity and study year on bee body size across 17 Kansas tallgrass prairies.

Factor	Num d.f.	Den d.f.	*F*	*P*
Forb diversity	15	5.99	0.466	0.892
Year	1	5.92	0.078	0.788

Table S1.9. Percent land use at 1000 m radius surrounding tallgrass prairie study sites in eastern Kansas.

Site	Site type	Percent cropland	Percent grassland and CRP	Percent woodland
Baker	restoration	21.4	43.6	31.5
Busby	restoration	0	48.1	51.1
Coombs	restoration	0	71.5	26.8
Guess	remnant	5	54.2	39.5
Kettle	restoration	8.2	38	52.9
McElroy	remnant	12.8	55.2	31.7
McKnight	remnant	16.9	64.3	18.8
Melvern (Docking)	remnant	11.8	67.9	12
Melvern (Indian Hills)	remnant	3.5	73.6	12.7
Reading	remnant	0	62.7	17.4
Rockefeller	remnant	0	29.2	70.7
Ross	remnant	0	86.5	12.7
Slaymaker	restoration	37.2	33.2	18.4
Snyder	remnant	0	62.9	36.1
Scoggin	restoration	34.4	50.1	14.9

Table S1.10. Bee species and comparison of capture method in tallgrass prairie systems. Aerial net surveys were by Denning (2018).

Trap-nests and aerial netting	**Aerial net collections**	**Trap nest collections**
Coelioxys octodentata	*Anthidiellum notatum*	*Coelioxys texana*
Coelioxys sayi	*Coelioxys germana*	*Dianthidium simile*
Heriades carinata	*Hoplitis spoliata*	*Chelostoma sp.*
Heriades leavitti	*Hylaeus modestus group*	*Osmia caerulescens*
Megachile brevis	*Megachile addenda*	*Osmia illinoensis*
Megachile exilis	*Megachile frugalis*	*Osmia albiventris*
Megachile georgica	*Megachile mendica*	
Megachile inimica	*Megachile parallela*	
Megachile policaris	*Megachile petulans*	
Osmia georgica	*Osmia conjuncta*	
Osmia cordata	*Stelis lateralis*	
Osmia pumila		
Total cavity nesting species	29	
Total unique to aerial netting	11	
Total unique to trap-nesting	6	
Total shared	12	

Appendix 2: Supplemental Figures and Tables for Chapter 2

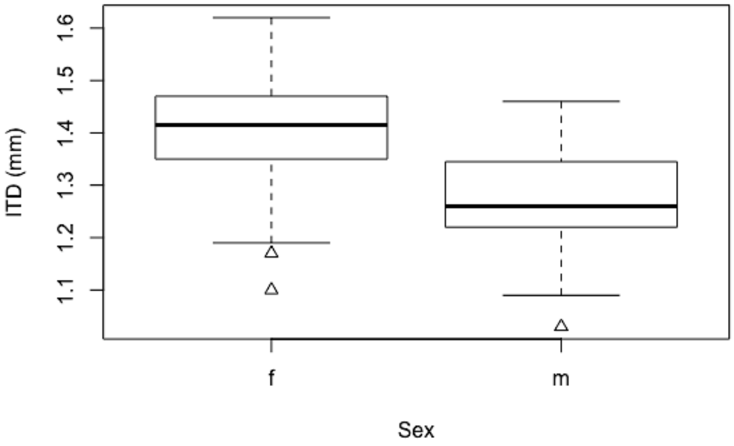

Figure S2.1. Boxplot of *Heriades carinata* body sizes for females and males collected within tallgrass prairie sites in 2013 and 2014.

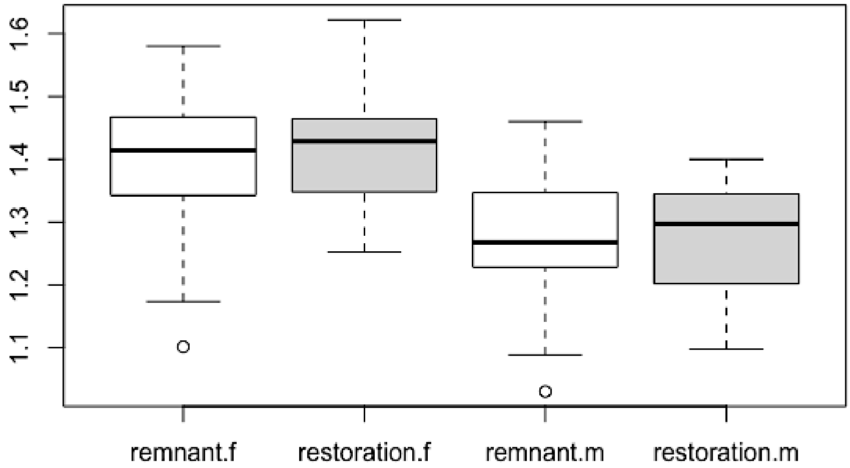

Figure S2.2. Boxplot of *Heriades carinata* body sizes of female and male bees collected within tallgrass prairie sites in 2013 and 2014.

Table S2.1. Characteristics of *Heriades carinata* collected in 2013 and 2014 within tallgrass prairie sites.

Site ID	**Site type**	**Date collected**	**Total offspring reared**	**Site sex ratio (females/total cells)**
BAK	restoration	2013	0	NA
BUS	restoration	2013	0	NA
COO	restoration	2013	0	NA
GUE	remnant	2013	6	0.16666667
KET	restoration	2013	0	NA
MCE	remnant	2013	44	0.5
MCK	remnant	2013	18	0.555555
MEL-D	remnant	2013	0	NA
MEL-IH	remnant	2013	6	1
REA	remnant	2013	9	0.8888888
ROC	remnant	2013	4	0.75
ROS	remnant	2013	0	NA
SCO	restoration	2013	0	NA
SLA	restoration	2013	0	NA
SNY	remnant	2013	44	0.6097561
AND	remnant	2014	27	0.7037037
BAK	restoration	2014	0	NA
BUS	restoration	2014	8	0.5
COO	restoration	2014	11	0.36363636
GUE	remnant	2014	9	0.55555556
KET	restoration	2014	0	NA
MCE	remnant	2014	8	0.625
PED	restoration	2014	10	1
ROC	remnant	2014	8	0.71428571
SNY	remnant	2014	2	0

Appendix 3: Supplemental Figures and Tables for Chapter 3

Figure S3.1. Stingless bee intertegular distance.

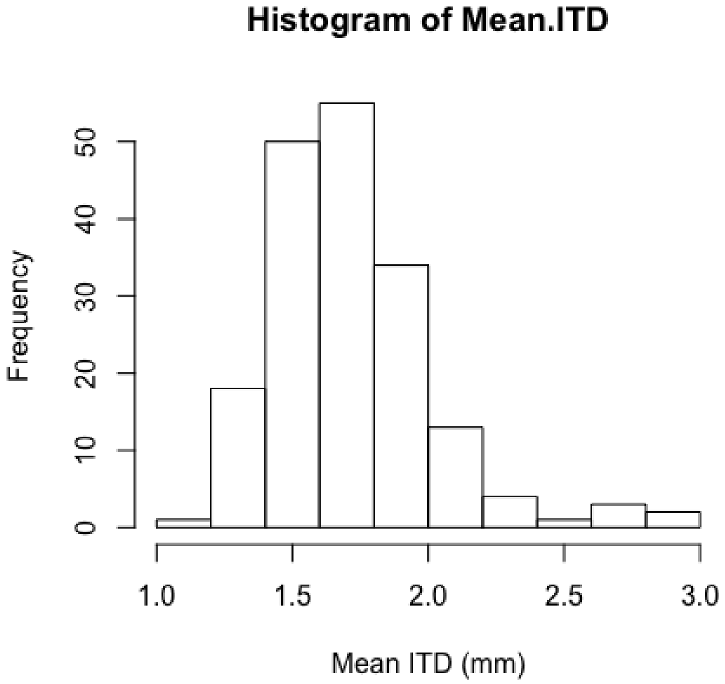

Figure S3.2. Frequency distribution of stingless bee body sizes collected in Rondônia, Brazil.

Table S3.1. Mean body size (mean ITD, mm) and standard deviation of stingless bee species collected in Rondônia, Brazil.

Species	n (#individuals measured)	Mean ITD (mm)	SD
Leurotrigona gracilis Pedro & Camargo, 2009	5	0.66	0.035
Trigonisca fraissei (Friese, 1901)	5	0.67	0.057
Dolichotrigona browni Camargo & Pedro, 2005	1	0.83	0.000
Dolichotrigona longitarsis (Friese, 1903)	4	0.85	0.041
Leurotrigona muelleri (Friese, 1900)	4	0.85	0.041
Frieseomelitta portoi (Friese, 1900)	4	0.85	0.085
Plebeia aff. *minima*	5	0.93	0.031
Celetrigona hirsuticornis Camargo & Pedro, 2009	5	0.94	0.069
Celetrigona longicornis (Moure, 1950)	5	0.98	0.045
Plebeia margaritae Moure, 1962	5	0.98	0.025
Scaura tenuis (Ducke, 1916)	4	0.98	0.043
Scaura latitarsis (Friese, 1900)	5	0.99	0.065
Tetragona handlirschii (Friese, 1900)	5	1.01	0.026
Frieseomelitta silvestrii (Friese, 1902)	5	1.01	0.077
Tetragonisca angustula (Latreille, 1811)	5	1.08	0.027
Schwarzula timida (Silvestri, 1902)	5	1.10	0.035
Paratrigona haeckeli (Friese, 1900)	5	1.11	0.032
Tetragonisca weyrauchi (Schwarz, 1943)	5	1.12	0.027
Paratrigona pacifica (Schwarz, 1943)	5	1.17	0.035
Paratrigona sp. n. aff. *lineata*	3	1.17	0.021
Nannotrigona schultzei (Friese, 1901)	4	1.21	0.013
Frieseomelitta flavicornis (Fabricius, 1798)	5	1.22	0.073
Scaura longula (Lepeletier, 1836)	5	1.24	0.123
Trigona permodica Almeida, 1995	5	1.24	0.022
Plebeia kerri Moure, 1950	5	1.24	0.055
Trigona recursa Smith, 1863	5	1.24	0.068
Plebeia variicolor (Ducke, 1916)	2	1.25	0.021
Nannotrigona melanocera (Schwarz, 1938)	5	1.26	0.068
Tetragona dorsalis (Smith, 1854)	5	1.26	0.065
Frieseomelitta trichocerata (Moure, 1990)	5	1.30	0.048
Trigona chanchamayoensis Schwarz, 1948	5	1.33	0.060
Trigona fulviventris Guerin, 1835	5	1.36	0.138
Tetragona goettei (Friese, 1900)	5	1.37	0.040
Trigona cilipes (Fabricius, 1804)	5	1.42	0.110
Tetragona clavipes (Fabricius, 1804)	5	1.42	0.034
Trigona hypogea Silvestri, 1902	5	1.44	0.021

Oxytrigona flaveola (Friese, 1900)	4	1.44	0.180
Oxytrigona obscura (Friese, 1900)	5	1.44	0.040
Lestrimelitta limao (Smith, 1863)	4	1.44	0.029
Geotrigona kwyrakai Camargo & Moure, 1996	4	1.45	0.033
Geotrigona mattogrossensis (Ducke, 1925)	5	1.48	0.042
Tetragona truncata Moure, 1971	3	1.50	0.000
Trigona pallens (Fabricus, 1798)	5	1.55	0.131
Trigona albipennis Almeida, 1995	5	1.58	0.058
Aparatrigona impunctata (Ducke, 1916)	5	1.60	0.064
Paratrigona prosopiformes (Gribodo, 1893)	3	1.60	0.173
Partamona testacea (Klug, 1807)	6	1.62	0.052
Ptilotrigona lurida (Smith, 1854)	5	1.63	0.060
Partamona vicina Camargo, 1980	5	1.67	0.023
Trigona branneri Cockerell, 1912	5	1.67	0.042
Partamona combinata Pedro & Camargo, 2003	5	1.67	0.081
Scaptotrigona depilis (Moure, 1952)	5	1.71	0.102
Trigona amazonensis (Ducke, 1916)	5	1.71	0.054
Trigona crassipes (Fabricius, 1793)	5	1.72	0.027
Trigona dallatorreana Friese, 1900	5	1.80	0.035
Partamona nhambiquara Pedro & Camargo, 2003	5	1.84	0.074
Trigona williana Friese, 1900	5	1.88	0.057
Scaptotrigona tricolorata Camargo, 1988	5	1.94	0.074
Scaptotrigona polysticta (Latreille, 1807)	5	1.96	0.022
Partamona ailyae Camargo, 1980	5	2.00	0.050
Duckeola ghilianii (Spinola, 1853)	5	2.00	0.141
Melipona illustris Schwarz, 1932	5	2.02	0.097
Trigona dimidiata Smith, 1854	5	2.07	0.029
Cephalotrigona femorata (Smith, 1854)	5	2.35	0.045
Trigona truculenta Almeida, 1984	5	2.56	0.081
Melipona brachychaeta Moure, 1950	5	2.65	0.221
Melipona schwarzi Moure, 1963	5	2.70	0.130
Melipona seminigra abunensis Cockerell, 1912	5	2.84	0.128
Melipona crinita Moure & Kerr, 1950	4	3.05	0.133
Melipona melanoventer Schwarz, 1932	5	3.12	0.203
Melipona grandis Guerin, 1834	5	3.21	0.141
Melipona fuliginosa Lepeletier, 1836	5	3.81	0.106