Phenology of a bee (Hymenoptera: Apoidea) community over a ten-year period in south-eastern Australia.

Running title: decade-long bee monitoring

Michael J. Neave¹, Julian Brown^{2*}, Michael Batley³, Sujaya Rao⁴, Saul A. Cunningham²

¹ CSIRO Ecosystem Sciences, Box 1700, Canberra, ACT 2601, Australia

² Australian National University, Fenner School of Environment and Society, 141 Linnaeus Way, Acton, ACT, 2601.

³ The Australian Museum, 1 William Street, Sydney, New South Wales 2010, Australia.

⁴ Department of Entomology, University of Minnesota, 1980 Folwell Avenue, St Paul, MN, 55108, USA.

*julian.macpherson.brown@gmail.com

Abstract

Bee responses to anthropogenic disturbances have received much recent attention in scientific literature. These studies typically involve one to three years of sampling along spatial gradients of disturbance, though occasionally greater temporal replication and/or longer time periods are used at the expense of spatial replication. We surveyed bees using a blue vane trap during spring, summer, and autumn from 2008 to 2017 at one location in Canberra, Australia. To the best of our knowledge, this is the longest near-continuous record of bee activity in the southern hemisphere. We use these data to describe the temporal dynamics of the bee community, which was characterised by high annual variability in overall abundance, richness, and composition, and a negative correlation between spring rainfall and bee activity. The phenologies of abundant species are also described. Our findings relate only to our study site, but are similar to findings from other long-term studies conducted in the northern hemisphere which collectively present a picture of high natural variability in bee communities that must be considered when interpreting findings of bee responses to anthropogenic disturbances.

Introduction

Population declines of wild pollinators have led to growing concern for these animals and the pollination services they provide (Potts et al., 2010; Garibaldi et al., 2011). To understand how best to conserve and manage populations of wild pollinators we need basic information about the biology of native species and their responses to anthropogenic disturbances.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/aen.12488

35 There is typically a trade-off between spatial and temporal sampling of ecological
36 communities, given limited funding and resources, and researchers investigating bee
37 communities have balanced this trade-off in different ways. Most field studies of bees are
38 short-term, typically focusing on spring-active bees over one to three years across multiple
39 sites. These studies often describe changes in bee communities along spatial gradients of
40 anthropogenic disturbance (e.g. agricultural land cover), and combine these descriptions with
41 knowledge of historical and projected anthropogenic disturbances to infer temporal trends in
42 bee communities (Winfrey et al., 2009, Kennedy et al., 2013). This kind of study may fail to
43 detect responses of bees to anthropogenic disturbances against the background of natural
44 spatial variability, including spatially asynchronous temporal dynamics of typically unknown
45 magnitude. Other studies have repeated historical surveys, or used museum collections and
46 data repositories spanning decades to infer responses of bee communities to anthropogenic
47 pressures over long time scales (Bartomeus et al., 2013, Scheper et al., 2014, Biesmeijer et
48 al., 2006, Burkle et al., 2013, Grixti and Packer, 2006). These studies are typically conducted
49 at coarse spatial and temporal resolutions, aggregating specimens collected across a large
50 area in different years, or collecting specimens decades apart without collection in the
51 intervening periods. They primarily provide insight into broad-scale changes in bee faunas
52 that can be interpreted in light of anthropogenic disturbances occurring over similar spatial
53 and temporal scales. A small number of studies have been longitudinal, repeatedly surveying
54 bees at one or few nearby locations over a decade or more of consecutive years (Iserbyt and
55 Rasmont, 2012, Onuferko et al., 2018, Roubik, 2001). In addition to describing long-term
56 trends, these longitudinal studies characterise the natural temporal variation of bee
57 communities against which the signal and biological significance of anthropogenic impacts
58 must be detected and assessed. The present study is a decade-long, near continuous
59 longitudinal study of an Australian bee community.

60 While short-term multi-site studies of bee communities have been conducted on all southern
61 continents except Antarctica (Kennedy et al., 2013), to the best of our knowledge there have
62 been no long-term studies in the southern hemisphere that characterise annual and seasonal
63 community dynamics. Australia has approximately 1600 species of native bees, and the
64 majority of these are solitary and nest in soil, hollow stems, or woody debris (Schwarz and
65 Hogendoorn, 1999). However, their population and community dynamics, as well as their
66 phenology remain poorly understood (Batley and Hogendoorn, 2009). Information about
67 emergence dates, development times, periods of activity, number of generations per year or
68 population variation from year-to-year is limited and obtaining such data can be protracted
69 and difficult.

70 The Australian bee fauna is dominated by the families Colletidae (53% of named species) and
71 Halictidae (23%), with Apidae, Megachilidae, and the endemic Stenotritidae comprising only
72 12, 10, and 1% respectively, and the otherwise widespread Andrenidae and Melittidae absent
73 (Batley and Hogendoorn, 2009). Life cycle studies do not reflect these relative proportions,
74 with most detailed studies focusing on Apidae. The most detailed account is of the life cycle
75 of *Amegilla (Zonamegilla) pulchra* (Apidae) in Brisbane (Cardale, 1968b, Cardale, 1968a,
76 Cardale, 1968c). This species overwinters as mature larvae (prepupae) and adults emerge in

summer. Females require a minimum of seven weeks for development and produce up to three generations per year. Allodapine bees (Schwarz et al., 2007) have also been studied extensively, largely because of interest in their primitively social status. Active throughout the warmer months, they overwinter as adults and most feed their larvae progressively. Egg laying, however, varies (Silberbauer, 1997) from a single burst, or two bursts (Tierney et al., 1997) to progressive laying throughout the active season (Hogendoorn et al., 2001). Reproductive females may have relatively long lives, reportedly as long as 18 months (Schwarz et al., 2007). The two *Xylocopa* (*Lestis*) species mass provision their brood cells and show a much lower level of cooperativity than the allodapines, but they also overwinter as adults (Steen and Schwarz, 2000). *Xylocopa aeratus* is predominantly univoltine, while *X. bombylans* is bivoltine.

With two exceptions, the life histories of Australian Halictidae are undocumented. In other parts of the World, inseminated females hibernate in winter, emerging in spring to forage and produce offspring. Most of the males are produced in late summer when they mate with young females that will hibernate and found the next generation (Michener, 2007). Long-lived queens have also been reported in social species of halictines, (Michener, 1990), but similar sociality is unknown in Australian representatives of the subfamily (Danforth and Shuqing, 2001). The Australian species *Lasioglossum* (*Chilalictus*) *hemichalceum* has been studied (Kukuk, 1996). Up to 20 females live in communal groups in which all individuals are reproductively active. In spring (November) females that have overwintered as mated adults rear brood consisting of males and females. After mating, these first-generation females go on to rear a second brood consisting of males and females (Kukuk et al., 2005). Second-generation females mate then overwinter (March-October in Victoria) to begin the cycle in the following year. A second Australian species, *Lipotriches* (*Austronomia*) *australica*, was studied by (Vogel and Kukuk, 1994). Colonies comprised two-three reproductive females, all of which foraged in spring. A general spring–early summer peak in Halictidae activity was reported from Hobart, Tasmania, though some species exhibited bimodal flight patterns peaking in spring and autumn (Hingston, 1998).

For families Colletidae, Stenotritidae or Megachilidae, inferences about emergence times and number of generations per annum have been drawn, with varying degrees of confidence, from collection data and field observations (Houston, 1987, Houston, 1991, Houston and Maynard, 2012). *Leioproctus plumosus* has been shown to be multivoltine (Batley and Brandley, 2014), while *Leioproctus fulvus*, whose nests are accompanied by conspicuous tumuli, is apparently univoltine (MB pers. obs.). Because adult activity of univoltine species lasts for no more than eight weeks, observation of activity over significantly longer periods is interpreted as evidence of multivoltinism (Houston, 1971, Houston, 1975a). While this assumption is reasonable in many cases, it should be used with care as *Amphylaeus morosus* (Colletidae) females have been reported as surviving for up to a year (Spessa et al., 2014). Similar inferences can be drawn from collection data found in taxonomic publications (Walker, 1995) or data repositories like Atlas of Living Australia. The information from such sources is averaged over many collection sites and different collection methods, which may provide a

distorted picture as demonstrated by the observation that the activity periods of the univoltine species *Amegilla dawsoni* at different localities were widely out of phase (Houston, 1991).

There is also a dearth of information regarding the range and drivers of inter-annual variation in Australian bee activity. Some anecdotal evidence exists, such as the observation that *L. hemichalceum* reproductive activity terminated early in a year with above average rainfall and below average temperature (Kukuk, 1996). Moisture and temperature are known to influence bee behavior and demography in other parts of the world (Stone and Willmer, 1989, Richards and Packer, 1995), and ground-nesting bees may be particularly susceptible to flooding and soil moisture which makes broods more susceptible to fungal attacks (Richards and Packer, 1995, Packer and Knerer, 1986). On the other hand, the emergence of *Leioproctus plumosus* was not strongly correlated with rainfall, but was affected by parasitism (Batley and Brandley, 2014).

The present study provides the first near-continuous, long-term (ten years) longitudinal study of bee activity in the southern hemisphere. Specifically, we describe: 1) seasonal and annual variation in overall bee abundance, species richness, and community composition; 2) overall bee abundance as it relates to rainfall; and 3) seasonal phenologies of abundant species. We also explore associations between species-specific emergence date and two bee traits: 1) total abundance, to test the hypothesis that more abundant bees are more likely to be detected earlier (as they reach detection levels at earlier stages of emergence), and 2) body size which may influence the range of temperatures over which bee species are active (Stone and Willmer 1989). Finally, we compared two trapping methods in terms of the bee species they detect as different trapping methods have been shown to detect different bee taxa (Hall, 2018).

Methods and Materials

Study site

We trapped bees at one location in the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Ginninderra Experimental station, Canberra ACT (35° 20' south, 149° 09' east) which is used as a mixed cropping/grazing farm of approximately 5.5km x 1.0km. Most of the land cover within 1 km of this site is urban, and some of this development occurred during the ten year study period. A single blue vane bee trap (SpringStar Inc., Woodinville, USA) was attached to a steel star picket using a right angled bracket at a height of 1.3 m as these have been effective in previous surveys of Australian bees (Lentini et al., 2012, Hall, 2018). No liquids, pheromones, or killing agents were used in this trap. A pan trap was also placed 150m away from the blue vane trap that consisted of a yellow plastic wash tub (37cm x 31cm x 14cm) with a 1cm hole drilled 2cm from the top of the tub and covered with fine gauze mesh to avoid overfilling during rain events, filled with water and detergent. In addition, we replaced all the blue coloured bee-attracting parts on an annual basis (the beginning of each season) to eliminate any possibility that the blue coloured parts would fade in sunlight and therefore become less attractive.

158

159 *Data collection*

160 Blue vane trapping started in early October 2008 and concluded at the end of November
161 2017. The trap was emptied of bees every 4 to 22 (mean = 7.69, SD = 2.7) days, and
162 operation of the trap ceased over winter (June, July, and August) except in 2011, 2013 and
163 2015, when colder temperatures from mid April onwards produced a zero catch for two or
164 more weeks in a row (excluding *Apis mellifera*). We also have no data for December 2008.
165 Single trapping events sometimes included days on either side of the change of month. When
166 summarising data by month we assigned samples to whichever month accounted for the most
167 days. Once collected the bees were sorted to species, sexed and then counted. Species were
168 named according to the Australian Faunal Directory, because this directory is used by other
169 Australian databases (e.g. the Atlas of Living Australia) as the definitive checklist of species
170 names. As a result, *Lasioglossum* (*Homalictus*) was treated as *Homalictus* (*Homalictus*).
171 Inter-tegular measurements (IT distance) were made from up to five male and five female
172 bees (depending on numbers caught) of each species as an indicator of bee size (Cane, 1987).

173 The yellow pan trap was opened for one week periods coinciding with a blue vane trap
174 weekly trapping event. These traps were open for one week for each of the months from
175 October 2015 to November 2016 (excluding winter).

176 Rainfall and temperature data were collected onsite from the Ginninderra farm
177 meteorological station situated 1.5 km from the trap.

178 *Data analysis*

179 Descriptive statistics are provided for 1) seasonal and annual variation in overall bee
180 abundance and species richness, 2) overall bee abundance as it relates to rainfall, and 3)
181 seasonal phenologies of abundant species averaged across years. Spearman correlation was
182 used when there was evidence of non-linearity (for relationships between bee abundance and
183 seasonal rainfall, see Figure 4), Pearson correlation was used when assumptions of linearity
184 were met.

185 Regression analyses were used to model species-specific emergence date as a function of
186 body size and total abundance of each species, with individual species (only those detected
187 during at least two sample periods) as replicates. Emergence data for each species was the
188 earliest date of detection across all years, measured as the number of days since the end of
189 July (the coldest month in Canberra). Response and predictor variables were log transformed
190 to normalise data (Poisson models were over-dispersed, and there were too few observations
191 to estimate the theta parameter of negative binomial models). Two models with different data
192 sets were used: 1) one data set containing all native bee species to explore overall
193 relationships, and 2) one data set containing only native Halictidae species to account for the
194 possibility of phylogenetic effects on seasonal activity (there were too few Apidae). Mixed
195 effects models with a random effect for year were used to account for the fact that different
196 bees emerged earliest in different years, using the glmmTMB package (Magnusson et al.,

2017) in the R statistical environment (R Core Team, 2013). Data transformation could not overcome the influence of one outlier species in each data set, so they were removed. *Hylaeus honestus*, the only Colletidae species, was removed from the data set containing all native species, while *Lipotriches sp.*, the only representative of the Nomiinae subfamily, was removed from the Halictidae data set leaving only species of the Halictinae subfamily.

Because the pan trap was open for a limited period, only results from the blue vane trap have been used for statistical analysis.

Results

We collected 3742 individuals comprising 31 species in the blue vane trap (Table 1a). All the species are native, except for *Apis mellifera*. Halictid bees accounted for 94% of all individuals caught. Four of the five most abundant Halictid species were in the genus *Lasioglossum*, *L. clelandi* (49.3%), *L. cognatum* (19.0%) and *L. lanarium* (16.5%). The fifth most abundant bee *Homalictus (Homalictus) sphecodoides* comprised 6.0% of the total bees caught.

Only 197 males, representing 5.5% of the total catch, were caught in the blue vane trap. Of these 132 (67%) were *L. lanarium*. This species had a relatively high male abundance of 132♂:450♀, as did *Amegilla asserta* 9♂:16♀ and *A. chlorocyanea* 1♂:3♀. All other species combined (excluding *A. mellifera*) had relatively low male ratios that changed throughout the year from 17♂:2261♀ in spring to 26♂:457♀ in summer and 12♂:188♀ in autumn. It is unclear why blue vane traps should be so inefficient at sampling males, which are expected to be more numerous than females (Fisher, 1958, Helms, 1994). The reason for the particularly high proportion of males of *L. lanarium*, which has been reported previously (Walker, 1995), is also unclear. Collection records from Atlas of Living Australia (ALA, 2018) show that, as for almost all Australian *Lasioglossum* species, variation in abundance with time is the same for both sexes of *L. lanarium* (unpub. results).

We collected 294 individuals from the pan trap, which included six species, all *Lasioglossum* and two individuals of *Apis mellifera* (Table 1b). No additional species were caught in the pan trap.

Seasonal variation

Total bee abundance (i.e. summed across all species) typically peaked in spring (September-November), with a secondary peak in summer (December-February) (Figure 2). Total bee abundance was highly correlated with the abundance of *Lasioglossum clelandi* (Pearson correlation = 0.92, p-value = <0.001), the most abundant species (Table 1a).

Species richness appeared to peak in summer during the first few observation years, but in spring thereafter, which might be explained by the loss of summer and autumn active species

in the second half of the sampling period (see below). Most of the halictids peaked in spring (Table 1; Figure 3), whereas larger-bodied Apidae and Megachilidae peaked or were not detected until after spring.

Several species of bees were caught in high enough numbers (22 minimum) that we were able to assess the phenology of these species individually over the multiple years of survey (Figure 3). All but two halictine species showed activity periods longer than eight weeks suggesting they are multivoltine. The exceptions were *L. clelandi* and *L. orbatum* which were active mostly in spring, though neither species was completely absent later in the year. *Amegilla asserta* did not appear until summer, but remained active until the colder months, which is consistent with the multigenerational behaviour reported for *A. pulchra* (Cardale, 1968b).

Phenology, abundance, and body size

Whether all bee species or only halictid species were analysed there was a significant negative relationship ($\alpha = 0.05$) between bee abundance and earliest detection date, such that more abundant species tended to be detected earlier in the season (Table 2). Using all bee species there was a marginally significant ($0.1 < p\text{-value} < 0.05$) positive relationship between earliest date of detection and inter-tetragonal distance, but a non-significant negative relationship when only Halictidae bees were included (Table 2).

Annual variation

Year-to-year variation in total bee abundance was high, species richness was less variable (Figure 2). The ratio of bee abundance per day (i.e. total number of bees trapped divided by total number of sample days in each year) in one year relative to the previous year ranged from 0.16 to 5.70 (Table 3), while the ratio of species richness per day in each year compared to the previous year ranged from 0.49 to 1.95.

Similarity in bee community composition, calculated as the Bray-Curtis (using abundance data) and Jaccard (using presence-absence data) similarity indices between consecutive years averaged 45% and 38% respectively (Table 3). Of the 31 species detected across the entire ten-year sampling period, five were detected in all years, *L. clelandi*, *L. cognatum*, *L. lanarium*, *L. orbatum*, and *Apis mellifera*. These five species collectively comprised >74% of specimens in every year. *Lasioglossum clelandi* was the most abundant species in nine out of ten years, *L. cognatum* was dominant in the remaining year. Fourteen species were detected in only one year. The mean number of years in which a given species was detected was 3.4. Species that were more abundant tended to be detected more frequently (Pearson correlation between number of years each species was present and the average abundance of each species = 0.66, $p\text{-value} = < 0.001$, across all species).

There was a large decline in bee abundance and richness following the first year of sampling (Figure 2). Of the 14 species observed in only one year, eight were observed only in the first year of sampling (spring 2008–autumn 2009), three of which were spring and/or summer active Halictids and five were summer or autumn active Colletids. Four species were

observed only in the 2010–2011 sampling period (one Halictidae, two Megachilidae, one Colletidae), another only in 2011–2012 (Halictidae), and another only in 2012–2013 (Colletidae). Thus, the decline in bee species across the first half of the ten-year sample period may have partly arisen from the loss of rare, predominantly Colletidae species (all but one colletid species disappeared in this period).

Seasonal rainfall appeared to play a role in determining overall bee abundances from year-to-year (Figure 4). The greatest numbers of bees were detected in springs with low rainfall (Spearman correlation between total bee abundance in spring and total rainfall in spring = -0.72, p-value = 0.02). Spring rainfall was almost identical (and below average) in the first two sampling years, making lack of rain an unlikely candidate for causing the initial decline in bee numbers (data not shown). There were no statistically significant correlations between autumn bee abundance and autumn rainfall (Spearman correlation = -0.18, p-value = 0.64), or summer bee abundance and summer rainfall (Spearman correlation = -0.30, p-value = 0.44).

Discussion

We used a near-continuous bee monitoring program of a single site over ten years to gain a better understanding of the basic biology of native Australian bees and long-term community dynamics at this site. To the best of our knowledge, this is the longest such monitoring period published in the southern hemisphere. While our results cannot be generalised to other sites, when considered in the context of existing literature they contribute to our understanding of Australian bee biology and the nature of temporal variation in bee communities.

Bee biology

There were clear patterns of taxonomic variation in phenology over the ten year sample period at our study site. Most Apidae and Megachilidae species were detected in summer and/or autumn, whereas most Halictidae species were spring and/or to a lesser extent summer active. The colletid bees sampled were also collected later in the year, but these numbers were very small and this pattern is not typical of colletids (Maynard, 2014, Houston, 1975b). Other Australian studies (Cardale, 1968b, Cardale, 1968a) also observed the Apidae genus we detected (*Amegilla*) emerging late in the year, though other Apidae genera are known to be active in spring (Schwarz *et al.*, 2007) highlighting the limits to generalisations that can be made from studying a single location. Most of the larger-bodied species were Apidae and Megachilidae, such that spring was dominated by small halictid bees and large bees were active mostly after spring.

There was also variation in the shape of activity patterns. Some species were unimodal while others appeared to be bimodal. *Lasioglossum hemichalceum* is one of the few species of bee whose phenology has been studied in Australia, and appeared to be bimodal in western Victoria, except in an unusually wet and cold year where it was unimodal (Kukuk, 1996). In the present study *L. hemichalceum* appeared to be multivoltine.

Lasioglossum species are likely to be important crop pollinators in the study area and surrounding regions. *Lasioglossum* was the most speciose and abundant genus at our study site, and four of five species detected in all ten sample years were *Lasioglossum* (the fifth was *Apis mellifera*). These and other species of this genus were also the most abundant in blue vane traps in agricultural regions of inland New South Wales (Lentini *et al.*, 2012), north-east Victoria (Hall *et al.*, 2019), and south-east Victoria (Brown *et al.*, 2020), where in the latter study they were also relatively frequent visitors to apple, pear, plum, cherry, raspberry, blueberry, and blackberry flowers. *Lasioglossum* species may thus be temporally reliable at sites other than ours (i.e. because they are abundant) and may also provide spatially reliable pollination services (i.e. are present in most years at most sites). Most Australian *Lasioglossum* species are generalist in their foraging habits (Walker, 1995, Batley, 2019) so are likely to visit a range of crops.

Homalictus sphecodoides was detected in nine of ten years and was the fourth most abundant species. Similarly, *H. urbanus* was the most abundant species in agricultural landscapes of south-east Queensland (Cunningham *et al.*, 2013). Given the very small size of these species, they are likely to be pollinators of Asteraceae and other flowers in which the pollen is readily accessible, and have been observed to visit these flowers more frequently than others in agricultural landscapes of south-east Victoria (Brown *et al.*, 2020).

Amegilla asserta was detected in six of ten years, at a relatively low abundance. For some flowers, bee body size is important to pollination function (Hoehn *et al.*, 2008) such that the large-bodied *A. asserta* may play an important role in the pollinator community.

Trapping

The pan trap detected a nested subset of the species detected with the blue vane trap. This suggests these alternative methods do not detect different sections of the bee assemblage, and is in agreement with previous research from the northern hemisphere (Joshi *et al.*, 2015, Buchanan *et al.*, 2017).

Annual variation

One important advantage of long-term longitudinal studies such as ours over coarser long-term studies, or studies with high spatial replication but not temporal replication, is they provide insight into annual variation in bee communities. We observed that total bee abundance more than halved between some consecutive years, and more than quadrupled between other years. Species richness halved between some consecutive years and doubled between others. While our results are not generalizable beyond our study site, similarly high annual variation in bee communities has been reported from long-term studies in the northern hemisphere, even in undisturbed nature preserves (Roubik, 2001). Caution should therefore be taken in inferring trends in bee abundance and richness from a small number of points in time. Further, multi-site short-term studies may be subject to large amounts of unexplained spatial variation when bee communities at different sites fluctuate asynchronously through time in response to a range of spatio-temporally variable factors such as rainfall (a potential contributor to annual variation at our site).

We also found that bee community composition was highly variable between years, being on average 45% (based on abundance data) and 38% (based on presence-absence data) similar between consecutive years. Fourteen of 31 species (45%) were detected in only one year, spread across the first five years of sampling, and these tended to be the less abundant species. However, community composition was more stable in terms of the dominant species, with >74% of all specimens in every year consisting of the same five species, one of which (*L. clelandi*) was the most abundant species in all but one year. Again our results are not generalizable beyond our study site, but some long-term studies of bee communities from the northern hemisphere also found that less abundant species were detected in one sample period only, while highly abundant species persisted across decades (Cane et al., 2005). Multi-site, short-term studies might thus be subject to inflated compositional differences as a result of missing rarer species, while capturing the dominant species across sites.

There was a large decline in bee abundance and richness following the first year of sampling. Interestingly, long-term longitudinal studies of bee communities in the northern hemisphere have also reported declines in abundance and/or diversity through time, which the authors attributed to long-term weather patterns or landscape change (Onuferko et al., 2018, Iserbyt and Rasmont, 2012). Landscape change could have been important at our study site as a large urban development (the suburb of Crace) commenced within 1 km in the second year of sampling. Long-term decline could also be due to any number of unmeasured environmental factors, or possibly an effect of trapping, but without spatial replication at the appropriate scale it is only possible to speculate.

Regardless of whether studies of bee responses to anthropogenic disturbances favour spatial or temporal replication, they often provide some evidence of decline (Scheper et al., 2014, Biesmeijer et al., 2006, Bartomeus et al., 2013, Burkle et al., 2013). These declines would tend to represent declines in average abundance, richness, and or composition, but to fully appreciate extinction risk the natural variation around this average must be ascertained because more variable populations are more likely to go extinct (Vucetich et al., 2000). The considerable natural annual variability reported here and in other studies of bee communities (Roubik, 2001, Iserbyt and Rasmont, 2012) suggests that bees in decline could be closer to extinction than trends of average abundance suggest.

Acknowledgements

We would like to acknowledge several technicians who helped clear the bee trap over the years. These include Kim Pullen, Melissa Piper and Patrick Gleeson. An OECD Fellowship to S. Rao enabled her to travel to Australia and initiate the study in 2008.

References

- BARTOMEUS, I., ASCHER, J. S., GIBBS, J., DANFORTH, B. N., WAGNER, D. L., HEDTKE, S. M. & WINFREE, R. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, 110, 4656-4660.
- BATLEY, M. 2019. Flower-visiting records for Australian native bees. *Collections*. figshare: <https://doi.org/10.6084/m9.figshare.c.3521328.v4>.
- BATLEY, M. & BRANDLEY, B. 2014. Phenology of the Australian solitary bee species' *Leioproctus plumosus*'(Smith)(Hymenoptera: Colletidae). *Australian Entomologist, The*, 41, 7.
- BATLEY, M. & HOGENDOORN, K. 2009. Diversity and conservation status of native Australian bees. *Apidologie*, 40, 347-354.
- BIESMEIJER, J. C., ROBERTS, S. P., REEMER, M., OHLEMÜLLER, R., EDWARDS, M., PEETERS, T., SCHAFFERS, A., POTTS, S. G., KLEUKERS, R. & THOMAS, C. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313, 351-354.
- BROWN, J., BARTON, P. S. & CUNNINGHAM, S. A. 2020. Flower visitation and land cover associations of above ground- and below ground-nesting native bees in an agricultural region of south-east Australia. *Agriculture, Ecosystems and Environment*, 295.
- BUCHANAN, A. L., GIBBS, J., KOMONDY, L. & SZENDREI, Z. 2017. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. *Insects*, 8, 30.
- BURKLE, L. A., MARLIN, J. C. & KNIGHT, T. M. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 339, 1611-1615.
- CANE, J. H. 1987. Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society*, 145-147.
- CANE, J. H., MINCKLEY, R., KERVIN, L. & ROULSTON, T. A. 2005. Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: the bees of *Larrea tridentata*. *Biological Journal of the Linnean Society*, 85, 319-329.
- CARDALE, J. 1968a. Immature stages of Australian Anthophorinae (Hymenoptera: Apoidea). *Australian Journal of Entomology*, 7, 35-41.
- CARDALE, J. 1968b. Nest and nesting behaviour of *Amegilla* (*Amegilla*) *pulchra* (Smith)(Hymenoptera: Apoidea: Anthophorinae). *Australian Journal of Zoology*, 16, 689-707.
- CARDALE, J. 1968c. Observations on nest and nesting behaviour of *Amegilla* (*Asaropoda*) sp.(Hymenoptera: Apoidea: Anthophorinae). *Australian Journal of Zoology*, 16, 709-713.
- CUNNINGHAM, S. A., SCHELLHORN, N. A., MARCORA, A. & BATLEY, M. 2013. Movement and phenology of bees in a subtropical Australian agricultural landscape. *Austral Ecology*, 38, 456-464.
- DANFORTH, B. N. & SHUQING, J. 2001. Australian *Lasioglossum*+ *Homalictus* form a monophyletic group: resolving the "Australian enigma". *Systematic Biology*, 50, 268-283.
- FISHER, R. A. 1958. *The genetical theory of natural selection*, Рипол Классик.
- GARIBALDI, L. A., AIZEN, M. A., KLEIN, A. M., CUNNINGHAM, S. A. & HARDER, L. D. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences*, 108, 5909-5914.
- GRIXTI, J. C. & PACKER, L. 2006. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist*, 138, 147-164.
- HALL, M. 2018. Blue and yellow vane traps differ in their sampling effectiveness for wild bees in both open and wooded habitats. *Agricultural and Forest Entomology*.
- HALL, M. A., NIMMO, D. G., CUNNINGHAM, S. A., WALKER, K. & BENNETT, A. F. 2019. The response of wild bees to tree cover and rural land use is mediated by species' traits. *Biological Conservation*, 231, 1-12.
- HELMS, K. R. 1994. Sexual size dimorphism and sex ratios in bees and wasps. *The American Naturalist*, 143, 418-434.

- HINGSTON, A. B. 1998. Temporal and spatial variation in abundances of native bee species on an altitudinal gradient in southern Tasmania. *Australian Journal of Zoology*, 46, 497-507.
- HOEHN, P., TSCHARNTKE, T., TYLIANAKIS, J. M. & STEFFAN-DEWENTER, I. 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B. Biological Sciences*, 275, 2283-2291.
- HOGENDOORN, K., WATINIASIH, N. & SCHWARZ, M. P. 2001. Extended alloparental care in the almost solitary bee *Exoneurella eremophila* (Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology*, 50, 275-282.
- HOUSTON, T. F. 1971. Notes on the biology of a lithurgine bee (Hymenoptera: Megachilidae) in Queensland. *Australian Journal of Entomology*, 10, 31-36.
- HOUSTON, T. F. 1975a. Nests, behaviour and larvae of the bee *Stenotritus pubescens* (Smith) and behaviour of some related species (Hymenoptera: Apoidea: Stenotritinae). *Australian Journal of Entomology*, 14, 145-154.
- HOUSTON, T. F. 1975b. A revision of the Australian hylaeine bees (Hymenoptera: Colletidae). I. Introductory material and the genera *Heterapoides* Sandhouse, *Gephyrohylaeus* Michener, *Huleoides* Smith, *Pharohylaeus* Michener, *Hemirhiza* Michener, *Amphylaeus* Michener and *Meroglossa* Smith. *Australian Journal of Zoology Supplementary Series*, 23, 1-135.
- HOUSTON, T. F. 1987. A second contribution to the biology of *Ctenocolletes* bees (Hymenoptera: Apoidea: Stenotritidae). *Records of the Western Australian Museum*, 13, 189-201.
- HOUSTON, T. F. 1991. Ecology and behaviour of the bee *Amegilla* (Asaropoda) *dawsoni* (Rayment) with notes on a related species (Hymenoptera: Anthophoridae). *Records of the Western Australian Museum*, 15, 591-609.
- HOUSTON, T. F. & MAYNARD, G. V. 2012. An unusual new paracolletine bee, *Leioproctus* (*Ottocolletes*) *muelleri* subgen. & sp. nov. (Hymenoptera: Colletidae): with notes on nesting biology and in-burrow nest guarding by macrocephalic males. *Australian Journal of Entomology*, 51, 248-257.
- ISERBYT, S. & RASMONT, P. The effect of climatic variation on abundance and diversity of bumblebees: a ten years survey in a mountain hotspot. *Annales de la Société entomologique de France*, 2012. Taylor & Francis, 261-273.
- JOSHI, N. K., LESLIE, T., RAJOTTE, E. G., KAMMERER, M. A., OTIENO, M. & BIDDINGER, D. J. 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Annals of the Entomological Society of America*, 108, 785-799.
- KENNEDY, C. M., LONSDORF, E., NEEL, M. C., WILLIAMS, N. M., RICKETTS, T. H., WINFREE, R., BOMMARCO, R., BRITAIN, C., BURLEY, A. L. & CARIVEAU, D. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16, 584-599.
- KUKUK, P. F. 1996. Male dimorphism in *Lasioglossum* (*Chilalictus*) *hemichalceum*: the role of larval nutrition. *Journal of the Kansas Entomological Society*, 147-157.
- KUKUK, P. F., BITNEY, C. & FORBES, S. H. 2005. Maintaining low intragroup relatedness: evolutionary stability of nonkin social groups. *Animal Behaviour*, 70, 1305-1311.
- LENTINI, P. E., MARTIN, T. G., GIBBONS, P., FISCHER, J. & CUNNINGHAM, S. A. 2012. Supporting wild pollinators in a temperate agricultural landscape: Maintaining mosaics of natural features and production. *Biological Conservation*, 149, 84-92.
- MAGNUSSON, A., SKAUG, H., NIELSEN, A., BERG, C., KRISTENSEN, K., MAECHLER, M., VAN BENTHAM, K., BOLKER, B. & BROOKS, M. 2017. glmmTMB: Generalized linear mixed models using a template model builder, R package version 0.1.3.
- MAYNARD, G. V. 2014. Revision of *Goniocolletes* and seven Australian subgenera of *Leioproctus* (Hymenoptera: Apoidea: Colletidae), and description of new taxa. *Zootaxa*, 3715, 1-114.
- MICHENER, C. D. 1990. Reproduction and castes in social halictine bees. *Social insects*. Springer.
- MICHENER, C. D. 2007. The Bees of the World. 2nd. Ed. *Johns Hopkins, Baltimore*.

- 489 ONUFERKO, T. M., SKANDALIS, D. A., LEÓN CORDERO, R. & RICHARDS, M. H. 2018. Rapid initial
490 recovery and long-term persistence of a bee community in a former landfill. *Insect*
491 *Conservation and Diversity*, 11, 88-99.
- 492 PACKER, L. & KNERER, G. 1986. An analysis of variation in the nest architecture of *Halictus ligatus* in
493 Ontario. *Insectes Sociaux*, 33, 190-205.
- 494 POTTS, S. G., BIESMEIJER, J. C., KREMEN, C., NEUMANN, P., SCHWEIGER, O. & KUNIN, W. E. 2010.
495 Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, 25,
496 345-353.
- 497 R CORE TEAM 2013. R: A language and environment for statistical computing.
- 498 RICHARDS, M. H. & PACKER, L. 1995. Annual variation in survival and reproduction of the primitively
499 eusocial sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). *Canadian Journal of Zoology*,
500 73, 933-941.
- 501 ROUBIK, D. W. 2001. Ups and downs in pollinator populations: when is there a decline? *Conservation*
502 *ecology*, 5.
- 503 SCHEPER, J., REEMER, M., VAN KATS, R., OZINGA, W. A., VAN DER LINDEN, G. T., SCHAMINÉE, J. H.,
504 SIEPEL, H. & KLEIJN, D. 2014. Museum specimens reveal loss of pollen host plants as key
505 factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of*
506 *Sciences*, 111, 17552-17557.
- 507 SCHWARZ, M. P. & HOGENDOORN, K. 1999. *Biodiversity and conservation of Australian native bees*,
508 Royal Zoological Society of NSW.
- 509 SCHWARZ, M. P., RICHARDS, M. H. & DANFORTH, B. N. 2007. Changing paradigms in insect social
510 evolution: insights from halictine and allodapine bees. *Annu. Rev. Entomol.*, 52, 127-150.
- 511 SILBERBAUER, L. 1997. The effect of non—synchronous dispersal on brood production in an
512 allodapine bee, *Exoneura bicolor* Smith (Apidae, Allodapini). *Insectes sociaux*, 44, 95-107.
- 513 SPESSA, A., SCHWARZ, M. P. & ADAMS, M. 2014. Sociality in *Amphylaeus morosus* (Hymenoptera:
514 Colletidae: Hylaeinae). *Annals of the Entomological Society of America*, 93, 684-692.
- 515 STEEN, Z. & SCHWARZ, M. P. 2000. Nesting and life cycle of the Australian green carpenter bees
516 *Xylocopa* (Lestis) *aeratus* Smith and *Xylocopa* (Lestis) *bombylans* (Fabricius) (Hymenoptera:
517 Apidae: Xylocopinae). *Australian Journal of Entomology*, 39, 291-300.
- 518 STONE, G. & WILLMER, P. 1989. Warm-up rates and body temperatures in bees: the importance of
519 body size, thermal regime and phylogeny. *Journal of Experimental Biology*, 147, 303-328.
- 520 TIERNEY, S. M., SCHWARZ, M. P. & ADAMS, M. 1997. Social behaviour in an Australian allodapine
521 bee *Exoneura* (Brevineura) *xanthoclypeata* (Hymenoptera: Apidae). *Australian Journal of*
522 *Zoology*, 45, 385-398.
- 523 VOGEL, M. E. & KUKUK, P. F. 1994. Individual foraging effort in the facultatively social halictid bee,
524 *Nomia* (Austronomia) *australica* (Smith). *Journal of the Kansas Entomological Society*, 225-
525 235.
- 526 VUCETICH, J. A., WAITE, T. A., QVARNEMARK, L. & IBARGÜEN, S. 2000. Population variability and
527 extinction risk. *Conservation Biology*, 14, 1704-1714.
- 528 WALKER, K. 1995. Revision of the Australian Native Bee Subgenus *Lasioglossum*
529 (*Chilalictus*) (Hymenoptera: Halictidae). *Memoirs of the Museum of Victoria*, 55, 1-423.
- 530 WINFREE, R., AGUILAR, R., VÁZQUEZ, D. P., LEBUHN, G. & AIZEN, M. A. 2009. A meta-analysis of
531 bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068-2076.

Tables

Table 1a. Abundance of each bee species collected, organised by family. Counts are assigned to three different periods: Spring (September, October, November) Summer (December, January, February) and Autumn (March, April, May). IT span records the inter-tegular distance (mm), as a guide to body size (Cane 1987). We have measured the mean IT distance for both males and females.

Species	Spring Early		Summer Peak		Autumn Late		Total	IT span	
	Females	Males	Females	Males	Females	Males		♀	♂
Blue Trap									
Apidae									
<i>Amegilla</i> (<i>Notomegilla</i>) <i>chlorocyanea</i> (Cockerell, 1914)			1	1	2		4	3.40	3.04
<i>Amegilla</i> (<i>Zonamegilla</i>) <i>asserta</i> (Cockerell, 1926)			8	6	8	3	25	3.55	3.31
<i>Apis mellifera</i> L.	19		53		98		170	3.14	
Megachilidae									
<i>Megachile erythropyga</i> Smith, 1853			2		1		3	3.20	
<i>Megachile</i> (<i>Hackeripis</i>) <i>oblonga</i> Smith, 1879					4		4	2.40	
<i>Megachile</i> sp. Latreille, 1802					1		1	2.96	
Colletidae									
<i>Leioproctus</i> (<i>Leioproctus</i>) <i>spatulatus</i> (Cockerell, 1905)					1		1	1.44	
<i>Leioproctus</i> (<i>Leioproctus</i>) <i>maculatus</i> (Rayment, 1930)					1		1	2.24	
<i>Leioproctus</i> (<i>Minycolletes</i>) <i>wahlenbergiae</i> Michener, 1965					1		1	1.84	
<i>Euryglossina</i> (<i>Euryglossina</i>) <i>hypochroma</i> Cockerell, 1916					1		1	0.80	
<i>Euhesma</i> (<i>Euhesma</i>) <i>wahlenbergiae</i> (Michener, 1965)			1				1	1.12	
<i>Hylaeus</i> (<i>Euprosopis</i>) <i>honestus</i> (Smith, 1879)	2						2	2.96	
<i>Hylaeus</i> (<i>Gnathoprosopis</i>) <i>euxanthus</i> (Cockerell, 1910)			1				1	1.36	
Halictidae									

<i>Homalictus (Homalictus) sphecodoides</i> (Smith, 1853)	129	1	53	8	20	1	212	1.06	0.80
<i>Homalictus (Homalictus) urbanus</i> (Smith, 1879)			3				3	1.12	
<i>Homalictus (Homalictus) sphecodopsis</i> (Cockerell, 1905)					1		1	1.12	
<i>Lasioglossum (Chilalictus) mundulum</i> (Cockerell, 1916)	2				1		3	1.12	
<i>Lasioglossum (Chilalictus) clelandi</i> (Cockerell, 1910)	1671	3	52	2	9	1	1738	1.71	1.57
<i>Lasioglossum (Chilalictus) cognatum</i> (Smith, 1853)	321	4	247	11	81	8	672	1.36	1.18
<i>Lasioglossum (Chilalictus) expansifrons</i> (Cockerell, 1914)	10		9		3		22		
<i>Lasioglossum (Chilalictus) hemichalceum</i> (Cockerell, 1923)	21		70	4	56	1	152	1.12	0.82
<i>Lasioglossum (Chilalictus) lanarium</i> (Smith, 1853)	329	68	98	38	23	26	582	2.08	1.74
<i>Lasioglossum (Chilalictus) orbatum</i> (Smith, 1853)	91	8	6		2		107	1.76	1.50
<i>Lasioglossum (Chilalictus) mediopolitum</i> (Cockerell, 1914)			5				5	1.26	
<i>Lasioglossum (Chilalictus) imitans</i> (Cockerell, 1914)	8		2			1	11	1.52	
<i>Lasioglossum (Chilalictus) biceps</i> Walker, 1995					1		1	1.12	
<i>Lasioglossum (Chilalictus) globosum</i> (Smith, 1853)	2	1					3	1.28	1.04
<i>Lasioglossum (Chilalictus) greavsi</i> (Rayment, 1930)	4						4	1.16	
<i>Lasioglossum (Chilalictus) willsi</i> (Cockerell, 1906)					1		1	1.52	
<i>Lasioglossum (Parasphecodes) imitator</i> Michener, 1965				1			1		2.00
<i>Lipotriches</i> sp. Gerstaecker, 1858			6		3		9	1.97	
Total species =31	2609	85	617	71	319	41	3742		

Table 1b. Abundance of each bee species collected in the pan trap only. Note the trap was only open from October 2015 to November 2016.

Species	Spring Early		Summer Peak		Autumn Late		Total
Pan Trap (Oct 2015 to Nov 2016 only)							
Apidae	♀	♂	♀	♂	♀	♂	
<i>Apis mellifera</i> L.	1			1			2
Halictidae							
<i>Lasioglossum (Chilalictus) lanarium</i> (Smith, 1853)	3	4	3	5			15
<i>Lasioglossum (Chilalictus) cognatum</i> (Smith, 1853)	3		4		1		8
<i>Lasioglossum (Chilalictus) clelandi</i> (Cockerell, 1910)	121	2	3		1		127
<i>Lasioglossum (Chilalictus) orbatum</i> (Smith, 1853)	32	4			2		38
<i>Homalictus (Homalictus) sphecodoides</i> (Smith, 1853)	76	2	21		4		103
<i>Lasioglossum (Chilalictus) expansifrons</i> (Cockerell, 1914)	1						1
Total species =6	237	12	31	6	8	0	294

Table 2: Parameter estimates and p-values from linear mixed effects models with (log transformed) earliest date of detection (number of days since July) for either all bee species ($n = 17$) or Halictidae bee species ($n = 12$) as the response variable, and both (log transformed) inter-tegular distance (IT) and (log transformed) total number of individuals detected for each species as predictor variables. (DF is residual degrees of freedom).

Data set	Parameters	DF	Estimate	p-value
All bees	log(IT)	13	0.75	0.078
	log(abundance)	13	-0.24	<0.001
Halictidae	log(IT)	8	-1.34	0.192
	log(abundance)	8	-0.26	<0.001

Table 3: comparisons of total bee abundance, species richness, and compositional similarity between consecutive years. Abundance and richness ratios were calculated as the total number of bee individuals or species caught per day in one year (i.e. total number of individuals or species trapped divided by the total number of trapping days) divided by the total number of individuals or species caught per day in the previous year. Similarity was calculated as the Bray-Curtis (using abundance data) and Jaccard (using presence-absence data) similarity indices between consecutive years.

	Abundance ratio	Richness ratio	Bray-Curtis similarity	Jaccard similarity
2009 vs 2008	0.32	0.49	48%	33%

2010 vs 2009	0.24	0.92	35%	62%
2011 vs 2010	1.92	0.66	33%	47%
2012 vs 2011	2.46	1.10	54%	33%
2013 vs 2012	0.52	0.92	47%	39%
2014 vs 2013	0.89	0.74	82%	36%
2015 vs 2014	2.84	1.32	48%	30%
2016 vs 2015	0.16	0.77	27%	30%
2017 vs 2016	5.70	1.95	27%	29%
Average	1.67	0.99	45%	38%

Figure legends

Fig 1. Ginninderra Farm surrounded on three sides by Canberra Australia. Black star indicates position of trap.

Figure 2. Number of bees caught divided by the number of trapping days, and total number of species caught, for each month across the entire sampling period (trapping did not occur in December 2008 and most winter months). Grey bars highlight spring months.

Figure 3: Phenology of the eight most abundant bees caught. White bars = total number of female specimens, black bars = total number of male specimens.

Figure 4: Total number of bees caught per day as a function of rainfall for Autumn, Spring, and Summer.

Figures

Figure 1.

Figure 2.

Figure 3

Figure 4

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Neave, MJ;Brown, J;Batley, M;Rao, S;Cunningham, SA

Title:

Phenology of a bee (Hymenoptera: Apoidea) community over a 10 year period in south-eastern Australia

Date:

2020-07-13

Citation:

Neave, M. J., Brown, J., Batley, M., Rao, S. & Cunningham, S. A. (2020). Phenology of a bee (Hymenoptera: Apoidea) community over a 10 year period in south-eastern Australia. AUSTRAL ENTOMOLOGY, 59 (3), pp.602-611. <https://doi.org/10.1111/aen.12488>.

Persistent Link:

<http://hdl.handle.net/11343/298007>