APPENDIX B

Recent introduction of an allodapine bee into Fiji: a new model system for understanding biological invasions by pollinators

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Abstract

Morphology-based studies have suggested a very depauperate bee fauna for islands in the South West Pacific, and recent genetic studies since have indicated an even smaller endemic fauna with many bee species in this region resulting from human-aided dispersal. These introduced species have the potential to both disrupt native pollinator suites as well as augment crop pollination, but for most species the timings of introduction are unknown. We examined the distribution and nesting biology of a long-tongued bee *Braunsapis puangensis* that was first recorded from Fiji in 2007. This bee has now become widespread in Fiji and both its local abundance and geographical range are likely to increase dramatically. The impacts of this invasion are potentially enormous for agriculture and native ecosystems, but they also provide opportunities for understanding how social insect species adapt to new environments. We outline the major issues associated with this recent invasion and argue that a long-term monitoring study is needed.

Keywords: Allodapini, Fiji, long distance dispersal, exotic species, pollinator competition

Introduction

Invasive species are generally regarded as having negative consequences for their new ecosystems because of their ability to disrupt relationships between endemic elements. However, invading species that are pollinators challenge this negative view of biological invasions as they are frequently associated with potentially beneficial effects, especially those that impact on crop pollination. For example, there is evidence that introduced honeybees, *Apis mellifera*, might disrupt native ecosystems (e.g. Paton 1996; Butz Huryn 1997; Hansen et al. 2002; Goulson 2003), yet their impact as exotic crop pollinators is often regarded as a positive influence (e.g. Morse and Calderone; Pejchar and Mooney 2009; Jaffe et al. 2010; Cock et al. 2012). Assessing and balancing these issues is important for managing the needs of both agriculture and conservation of indigenous ecosystems.

The introduction of exotic species to new environments also creates opportunities to examine how species adapt to novel environments. Such introductions may occur naturally as part of dispersal events involving both short and long distances. However, naturally occurring long-distance dispersals into very different ecosystems are often rare, and understanding the dynamics of adaptation to new environments can be difficult if the elapsed time since their arrival is long or unknown. Human mediated dispersals are becoming more frequent because of increased maritime trade. Whilst this elevates the risk of biological invasions that impact negatively on ecosystems, it also creates opportunities for understanding how species are able to adapt to novel environments, providing an opportunity to study adaptation in very recent timeframes.

Archipelagos in the South West Pacific have very depauperate endemic bee faunas (Groom and Schwarz 2011). For Fiji, the only bee taxa that are known to be endemic are the short-tongued halictine species belonging to the subgenus *Homalictus* (genus *Lasioglossum*) (Groom et al. 2013). Whilst a number of long-tongued leaf-cutter bees (family Megachilidae) are known from Fiji, they all appear to represent recent human-mediated arrivals (Davies et al. 2013). Four other long-tongued bee species are recorded from Fiji: the purposefully introduced honey bee, *Apis mellifera*, the small carpenter bee *Ceratina dentipes*, the anthophorine bee *Amegilla pulchra*, and the allodapine bee *Braunsapis puangensis* (Groom et al. 2014).

The bee tribe Allodapini (family Apidae, subfamily Xylocopinae) is widespread in Africa, Madagascar, southern Asia, the Indo-Papuan region and Australia (Michener 2007). The first published record of an allodapine bee from Fiji is an unidentified *Braunsapis* species reported by Evenhuis (2007), but attribution of this record was an unpublished personal communication with no locality data. However this is likely to be *B. puangensis*, recorded by Prasad & Hodge (2013) as now being common in the Suva region. Furthermore, this species has recently been recorded at various locations well removed from Suva (Groom et al. 2014), suggesting that it is rapidly spreading throughout Fiji. *B. puangensis* (Figure 1) was originally described from northern Thailand (Cockerell 1929), but has been recorded from across India and Nepal to southern China and Indonesia, reflecting an ability to inhabit a wide range of ecosystems (Reyes and Michener 1990; Reyes 1991). The expansion of this recently arrived species range in the tropical climate of Fiji is therefore not surprising, but raises concern for its impact on endemic Fijian species.

Allodapine bees are long-tongued and polylectic (Michener 2007), so their range of possible host plants is potentially much wider than the SWP endemic bee subgenus *Homalictus*, which is short-tongued. This suggests that *B. puangensis* may be able to exploit a wider range of angiosperm species than the endemic *Homalictus* species' because of their ability to extract nectar from flowers with longer corolla tube lengths. Two possible ecological consequences follow from this. Firstly, *B. puangensis* might be able to compete with endemic non-bee pollinators in Fiji, especially those that are adapted to plant species with long corolla tubes, such as Lepidoptera; and secondly, *B. puangensis* may be an effective pollinator of introduced weed species that are otherwise not effectively pollinated by endemic species. Interestingly, Prasad and Hodge (2010) have shown that *Apis mellifera* and *Braunsapis puangensis* are the two most common pollinating insects visiting the nuisance weed *Sphagneticola trilobata* (Asteraceae) in the Suva region. Furthermore allodapine bees nest in the stems of plants, and in India *B. puangensis* has been shown to benefit such host plants through pollination services (Shenoy and Borges 2008).

As an introduced pollinator, understanding the nesting biology of *B. puangensis* in a new environment is important for determining its invasive potential. Most allodapine bees show high rates of nest re-use because this allows them to increase colony size as a defense against predators and parasites (review in Schwarz et al.

2007), but the resulting philopatry will limit dispersal opportunities. If the Fijian population adapts to a lack of specialized enemies by evolving lower levels of nest re-use this would increase its ability to spread, and increase its invasiveness. It is, therefore, important to characterize the nesting and social biology of *B. puangensis* in Fiji at this time so that any subsequent changes in nesting biology can be documented and their effects gauged.

Here we present the most extensive list of locality records for *Braunsapis puangensis* in Fiji and outline nesting biology of this species in the Suva region. We then discuss possible impacts of this species for crop pollination and potential disruption of endemic ecosystems.

Materials and Methods

Flower-caught specimens. Bees were collected from flowers by sweep netting, with specimens preserved in ethanol for later DNA analyses. We collected from the four largest Fijian islands of Viti Levu, Vanua Levu, Taveuni and Kadavu, covering an altitudinal range of 0-906m above sea level (asl) between 16 July and 20 August during the dry season of 2010 (Fig. 1). The southern Lau islands of Fiji were sampled between 6 July and 8 August 2011, covering the islands of Ono-i-Lau, Vatoa, Ogea, Vulaga, Namuka, Kabara, Lakeba, Vanuavatu, Moala, Totoya, and Matuku.

Collection of bee nests. Bee nests were collected intact from the gardens of the Laucala Bay campus of the University of South Pacific, Suva on 10 - 13 July 2013 and 15 – 18 October 2013. Nest were collected in the late afternoon and early evening when extra-nidal bee activity had finished, so all adult nest occupants could be assumed to be present. Bee nests were recovered from dead stems of several herbaceous shrubs, including *Bambusa* sp., *Bougainvillea* sp., *Rosa* sp. Entrances were always at the exposed dead tips of branches resulting from pruning by gardeners. Nest tunnels never extended into living stem tissue.

All nest contents were preserved in 100% ethanol and for each colony the number of eggs, larvae, pupae and adults were recorded. All statistics were performed in SPSS 13.0 for Macintosh.

Results

Distribution of B. puangensis

Figure 2 shows all Fijian localities from which we collected bees, with *Braunapis puangensis* found at 16 sites, 14 of which were on Viti Levu, one in the Savusavu area of Vanua Levu and one on Tavenui. Collection sites are listed in detail in Table 1. Most *B. pungensis* sites were clustered in the regions of Viti Levu surrounding Tavua and Rakiraki in the north, the Sigatoka region in the south west, and the Suva region in the south east. Prasad and Hodge (2013) have also recorded *B. puangensis* from the island of Nukulau, east of Suva.

Colony characteristics

We collected a total of 32 nests from the July sample and 43 nests from the October collection. The number of adult females per nest is summarized in Figure 3 for each collection period, showing a modal colony size of one and a maximum of five. Mean colony size was larger in the October sample, but this may be due to recently eclosed females where callow pigmentation was no longer evident (see below).

The mean numbers of immature stages (eggs, larvae, pupae and callows) is summarised for the two sampling periods in Figure 4. All developmental stages were present in both samples, except for callows, which were only recognizable in the October sample. Figure 4 indicates a greater mean number of eggs in the July sample, but greater numbers of larvae, pupae and callows in the October sample.

The presence of both eggs and pupae in both samples indicates that brood rearing had commenced well before the July sample, and was likely to continue well after the October sample. However, the data also indicate seasonality in brood rearing traits, with both greater numbers of brood in October and a greater proportion of post-feeding brood.

A major selective factor in maintaining sociality in allodapines is increased efficiency in brood rearing with larger colony size, measured as the number of brood per adult female (i.e. per capita brood production, PCBP). We examined whether PCBP varied with the number of females per nest using Kruskal-Wallis non-parametric ANOVA. This indicated no effect of colony size for either July ($X^2_2 = 1.57$, $P = 0.456$) or October ($X^2_2 = 3.359$, $P = 0.339$). Because the number nests with more than two adult females were so few, we also compared single-female nests with two-female, using Mann-Whitney U tests. These also indicated no treatment effect for July ($Z = -0.759$, $P = 0.448$) or October ($Z = -1.647$, $P = 0.100$). Consequently, PCBP does not appear to vary with colony size for either of our sampling periods.

Lastly, we examined sex ratios in both samples, with colony sex ratio measured as the number of male pupae as a proportion of total number of pupae. The mean sex ratio in July was $r = 0.0833$ and a one-sample t-test indicated this was significantly different from equal sex ratios ($t_7 = -7.638$, $P < 0.001$). In contrast, the mean sex ratio for October was $r = 0.4184$ and this was not significantly different from parity

($t_{18} = -0.834$, $P = 0.415$). Consequently, sex ratios were significantly female biased in July and unbiased in October.

Discussion

Rapid spread of B. puanagensis in Fiji

The first record of *Braunsapis puangensis* from Fiji is Evenhuis (2007), but that record is from a checklist produced by the Bishop Museum and does not report locality data or species abundance. Earlier studies of Hymenoptera from Fiji by Turner (1919), Brues (1922) and Fullaway (1957) did not report this species. Michener's (1965) very extensive monograph of bees in Australasia and the South West Pacific did not list *Braunsapis* from Fiji, so it seems likely it was introduced sometime between 1965 and 2007. The recency of its introduction to Fiji is also suggested by a lack of any genetic variation from a 650 bp fragment of the mitochondrial DNA (COI) gene among Fiji samples and no haplotype difference to an Indian specimen collected from the Nilgiri Hills in Tamil Nadu (Groom et al. accepted). This contrasts strongly with extensive haplotype variation in the endemic halictine *Lasioglossum* (*Homalictus*) species (Groom et al. 2013).

Prasad and Hodge (2013) recorded *B. puangensis* from multiple locations in and surrounding Suva, but did not explore its distribution more distantly than approximately 20km from Suva. The outer limit of their collections reached Nukulau Island, approximately 10 km east of Suva, and the Rewa delta, approximately 20 km ENE from Suva. Our records greatly expand the known distribution of *B. puangensis* in Fiji and include records from the far north of Viti Levu, from Vanua

Levu and from Taveuni. We also recorded it from close to sea level in the Laucala region of Suva to an elevation of ca 800 m. asl in the Nadarivatu region in northern Viti Levu (see Fig. 1).

Our distributional records therefore indicate that *B. puangensis* has become widespread in Fiji and has managed to colonize both multiple islands as well as a wide range of elevations. It therefore does not appear that range expansion of *B. puangensis* will be impeded by moderate water barriers or moderately high elevations. We have collected *B. puangensis* from elevations greater than 950m in the Nilgiri Hills region adjacent to the Mudumalai Sanctuary in Tamil Nadu, India (Schwarz unpub. data), suggesting that if those altitudinal tolerances extend to the Fijian population, there will be few or no regions in Fiji where establishment of populations would be precluded by elevation.

A further aspect in the spread of *B. puangensis* in Fiji concerns the likelihood of diploid males and their effect in depressing population growth. Bees are haplodiploid and sex determination is via a complementary sex determination (csd) locus, whereby heterozygotes develop into females and haploid hemizygotes (or homozygous diploids) develop into males. However, most diploids that are homozygous at the csd locus develop into infertile diploid males (Zayed 2009). Populations that have been through a severe population bottleneck are likely to lose substantial variation at the csd locus, and the resulting frequency of sterile diploid males should depress population growth, or even lead to “extinction vortices” (Zayed and Packer 2005). If the recent presence of *B. puangensis* in Fiji arose from a small number of colonizing individuals, diploid males are likely to be a significant factor in limiting population growth. However, as mutations gradually arise at the csd locus they will be selected for (Zayed 2009) and intrinsic population growth should increase. In other words, it is possible that the current capacity of *B. puangensis* populations to expand will increase over time.

Sociality and seasonality of **B. puangensis** *in Fiji*

Analyses of our dataset comprising two sampling periods of *B. puangensis* nests from the Suva region reveals several key features. In both samples all life-history stages are represented and brood covered initial egg-laying phases, intermediate larval rearing phases, and pupal and early adult eclosion phases. This suggests that brood rearing occurs during both wet and dry seasons. However, mean brood numbers and the proportions of different brood developmental stages differed between the two samples suggesting a seasonal influence in brood rearing.

The modal number of adult females per nest was one in both samples, and although up to five females were found per nest in the October sample, some of these females are likely to represent newly emerged adults who will subsequently disperse (e.g. Joyce & Schwarz 2006; 2007). We found no evidence that the number of adult females per nest influences brood rearing efficiency, which is different from most other allodapines studied to date (Schwarz et al. 2007), but consistent with an escape into enemy-free space. Sex allocation was significantly female-biased in the October sample and although the bias was not significant in July, the smaller sample size for that collection entails lower power to detect bias. However the likelihood of diploid males resulting from a recent population bottleneck (Zayed 2009) may distort maternal sex allocation patterns.

Studies on allodapine bees in Africa, Madagascar, Asia, and Australia have indicated that multifemale nesting and female-biased sex allocation are adaptive responses to enemies-at-the-nest, including both predators and parasites (Schwarz et al. 2007). Fiji does not have any endemic stem-nesting bees (Groom et al. 2014), nor any endemic species in the family Apidae, so dispersal of *Braunsapis* to Fiji is likely to represent an escape into at least partially ‘enemy-free space’. We might therefore expect selection for lower levels of sociality and sex allocation bias. Monitoring responses of social and sex allocation traits to colonization of new habitats in the Seychelles Warbler (Komdeur 1992; Komdeur et al. 1997; Komdeur & Pen 2002) provided major insights into social evolution, and the responses of *B. puangensis* to its new Fijian habitats has the potential to provide similar insights for insect sociality. The studies by Komdeur and colleagues were based on detailed monitoring over decadal time-scales, and using *B. puangensis* to examine analogous responses in a social insect requires detailed studies at this early time after colonization, as well as subsequent studies.

Possible consequences and future research

Our data indicate that *Braunsapis puangensis* has rapidly spread to a wide variety of Fijian habitats as well as islands remote from Viti Levu. Just how rapid this expansion has been is not known, but the initial introduction is likely to have occurred after 1965 and prior to 2007. Given the likely recent introduction of *B. puangensis* to Fiji, this suggests that this species will continue to expand its range and abundance and does not seem to be bound by substantial water barriers or altitudinal differences. The continued spread of this species has four potentially broad and major implications: (i) Enhanced crop pollination, (ii) Enhanced pollination of weed species, (iii) Threats to endemic pollinator suites, and (iv) Tracking social adaptations to new habitats; discussed below.

(i) *Enhanced crop pollination*. Globally widespread declines in honeybee populations have raised major concerns for crop pollination because of the important roles that honeybees play in many managed crops (e.g. Allen-Wardell et al. 1998; Morse and Calderone 2000). There has been recent appreciation that native bee species may be as important as honeybees in providing crop pollination services (e.g. Winfree et al. 2007; Potts et al. 2010), and Asian species of *Braunsapis* have been identified as crop pollinators in Taiwan and India (Batra 1976; Batra et al. 1993). Fiji is unusual in that all endemic bees are short-tongued halictines (Groom et al. 2013) and their diversity is very low because they are recent elements in that region. *Braunsapis* is a long-tongued bee and able to extract nectar form a wider range of angiosperm species than *Homalictus*, and therefore has the potential to compensate for any losses of *Apis* in the SWP if honeybee diseases become prevalent. Consequently, the introduction of *Braunaspis* into Fiji may provide some buffer against any future declines of *Apis* in the region.

(ii) *Enhancement of weed species*. Prasad and Hodge (2013) recorded *B. puangensis* as a major visitor of the introduced weed *Spahgneticola trilobata* in the

Suva region. Allodapine bees are polylectic (Michener 2007) and also long-tongued, so are likely to pollinate a wider range of angiosperms than the endemic short-tongued *Homalictus* species. Consequently, it is possible that *Braunsapis* may facilitate pollination of introduced weeds more effectively than endemic bees. Where weedy plants are not palatable to grazing stock, or compete with crops, this may have potential to negatively impact on agriculture.

(iii) *Threats to endemic pollinator suites*. If nectar and or pollen are limited resources for endemic pollinators then *Braunsapis puangensis* may become negatively impact on these pollinators if it becomes *v*ery abundant. Importantly, two other introduced apid bees, *Ceratina dentipes* and *Amegilla pulchra*, have also become widespread in Fiji (Groom et al. 2014), so competition exerted by exotic bees has the potential to be significant. However, insect pollination dynamics in Fiji have not been explored, so the dimensions of possible competition remain speculative.

(iv) *Tracking social adaptations to new habitats*. Social living is an ancestral trait for allodapine bees, with no complete losses of this trait, and this has been linked to the need for cooperative defence of brood against enemies-at-the-nest, such as ants and specialised parasites (Chenoweth et al. 2007). Female-biased sex ratios are also linked to this need for cooperative defence, because of the importance of having replacement females in place if the reproductive female dies (Bull and Schwarz 2001). If dispersal of *B. puangensis* into Fiji represents an escape into enemy-free space, where specialized enemies are not present, then we might expect selection to favour non-social nesting and thereby decrease colony sizes and increase dispersal away from natal nests. Fiji represents an unequalled opportunity to explore whether such non-social adaptations arise and spread, with consequences for understanding the mechanisms that maintain social behavior.

Recommendations for future action

Given the above considerations there are very compelling reasons to establish long-term monitoring of *Braunsapis puangensis* in Fiji to assess the likely consequences of its continued expansion in the region. Because these consequences are likely to have impacts on both agriculture and native ecosystems, we recommend that monitoring and evaluation systems be set in place and guided by agencies that can represent this diversity in possible impacts. In particular, studies are needed to assess several key issues.

Baseline studies of natural history are severely lacking for the bees of the Pacific, while our understanding of species that have recently arrived is very limited. The case presented here indicates efforts should focus on coordinated monitoring of populations to assess the current distribution of *Braunsapis puangensis* in Fiji and changes to this distribution and local abundances over time.

The role of this recently arrived pollinator within ecosystems also needs to be assessed, with potential impacts likely to affect three main areas: endemic, non-endemic and agricultural interactions. Future studies must initially determine the floral host range of *B. puangensis* in Fiji, which may be broad as *Braunsapis* species are known to visit a wide range of angiosperm families (*e.g.* Proteaceae (Michener 1965). Amaranthaceae (Struck, 1994), Violaceae (Munzinger and Pauly, 2003), Solanaceae (Anderson and Symon,1988)). By determining the interactions of endemic pollinators with shared host plant species, we gain insight into the potential disruption of endemic plant-pollinator mutualisms. Likewise, identifying the role of the species in pollinating non-endemic flora is equally valuable. Where endemic pollinators are unable to effectively pollinate introduced plant species, the arrival of suitable pollinating species may enhance their invasive potential (Goulson 2003). *B. puangensis* has already been shown to be the primary floral visitor of the invasive *Sphagneticola trilobata* (Prasad & Hodge 2013), which is an agricultural pest throughout the Pacific (Meyer 2000). Evaluation is, therefore, required to determine whether enhanced pollination of those species will impact on primary industries. However, despite the potential to compete with endemic pollinators and enhance the invasive potential of non-endemic pants, it is possible that established *B. puangensis* populations might benefit agriculture (Batra 1977; Batra et al.1993). Studies are needed to assess the role of *B. puangensis* in Fijian agricultural landscapes, where long-tongued bees represent a recent novel pollination system (Davies et al. 2013; Groom et al. 2014).

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Disclosure

The authors declare no potential conflicts of interest

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Table 1. Collection localities for specimens *Braunapis puangensis* collected in Fiji. Sequence references are provided with BOLD-ID numbers. Sample ID corresponds to voucher specimen. Collection date, coordinates, and island collected from are provided.

BOLD-ID	**Sample ID**	**Date**	**Latitude**	**Longitude**	**Island**
MSAPB002-11	AAA002	28/07/2010	-18.15	178.443	Viti Levu
MSAPB005-11	AAA006	28/07/2010	-18.15	178.443	Viti Levu
MSAPB006-11	AAA007	28/07/2010	-18.15	178.443	Viti Levu
MSAPB007-11	AAA008	28/07/2010	-18.15	178.443	Viti Levu
MSAPB046-11	AAK009	29/07/2010	-18.149	178.424	Viti Levu
MSAPB047-11	AAK010	29/07/2010	-18.149	178.424	Viti Levu
MSAPB048-11	AAK011	29/07/2010	-18.149	178.424	Viti Levu
MSAPB049-11	AAK012	29/07/2010	-18.149	178.424	Viti Levu
MSAPB050-11	AAK013	29/07/2010	-18.149	178.424	Viti Levu
MSAPB051-11	AAK014	29/07/2010	-18.149	178.424	Viti Levu
MSAPB052-11	AAK015	29/07/2010	-18.149	178.424	Viti Levu
MSAPB053-11	AAK016	29/07/2010	-18.149	178.424	Viti Levu
MSAPB054-11	AAK017	29/07/2010	-18.149	178.424	Viti Levu
MSAPB057-11	AAL001	31/07/2010	-18.15	178.453	Viti Levu
MSAPB058-11	AAL002	31/07/2010	-18.15	178.453	Viti Levu
MSAPB059-11	AAL003	31/07/2010	-18.15	178.453	Viti Levu
MSAPB060-11	AAL004	31/07/2010	-18.15	178.453	Viti Levu
MSAPB182-11	AAL005	31/07/2010	-18.15	178.453	Viti Levu
MSAPB183-11	AAL006	31/07/2010	-18.15	178.453	Viti Levu
MSAPB184-11	AAL007	31/07/2010	-18.15	178.453	Viti Levu
MSAPB234-11	AAW001	3/08/2010	-17.382	178.158	Viti Levu
MSAPB237-11	AAX005	3/08/2010	-17.37	178.079	Viti Levu
MSAPB238-11	AAX006	3/08/2010	-17.37	178.079	Viti Levu
MSAPB254-11	AAZ002	3/08/2010	-17.422	177.996	Viti Levu
MSAPB252-11	AAZ003	3/08/2010	-17.422	177.996	Viti Levu
MSAPB253-11	AAZ004	3/08/2010	-17.422	177.996	Viti Levu
MSAPB261-11	ABA003	3/08/2010	-17.426	177.798	Viti Levu
MSAPB265-11	ABB010	3/08/2010	-17.404	177.782	Viti Levu
MSAPB264-11	ABB011	3/08/2010	-17.404	177.782	Viti Levu
MSAPB266-11	ABB022	3/08/2010	-17.404	177.782	Viti Levu
MSAPB267-11	ABB023	3/08/2010	-17.404	177.782	Viti Levu
MSAPB275-11	ABC003	3/08/2010	-17.401	177.765	Viti Levu
MSAPB276-11	ABC004	3/08/2010	-17.401	177.765	Viti Levu
MSAPB284-11	ABD004	3/08/2010	-17.592	177.755	Viti Levu
MSAPB291-11	ABE003	4/08/2010	-17.52	177.925	Viti Levu
MSAPB301-11	ABF002	4/08/2010	-17.549	177.943	Viti Levu
MSAPB302-11	ABF003	4/08/2010	-17.549	177.943	Viti Levu
MSAPB152-11	ACO003	18/08/2010	-18.165	177.48	Viti Levu
MSAPB153-11	ACO004	18/08/2010	-18.165	177.48	Viti Levu
MSAPB156-11	ACP001	18/08/2010	-18.139	177.508	Viti Levu
MSAPB155-11	ACP002	18/08/2010	-18.139	177.508	Viti Levu
MSAPB1160-12	AFI001	30/08/2011	-16.9349	179.901	Kadavu
MSAPB1161-12	AFL008	3/09/2011	-16.7728	179.33	Vanua Levu

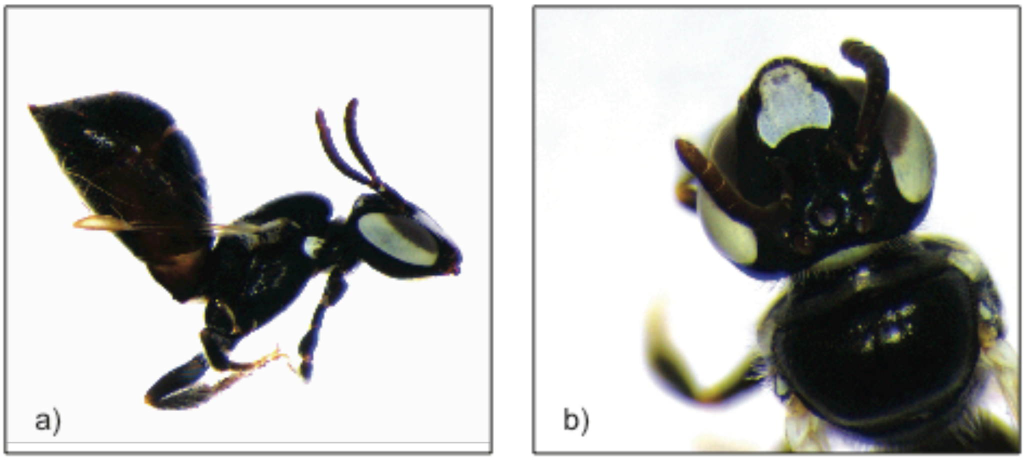

Figure 1: Lateral (a) and dorsal (b) images of *Braunsapis puangensis*

Figure 2: Localities where *Braunsapis punagensis* was collected. Stars indicate collection localities. Inset provides regional context with Fiji in bold border.

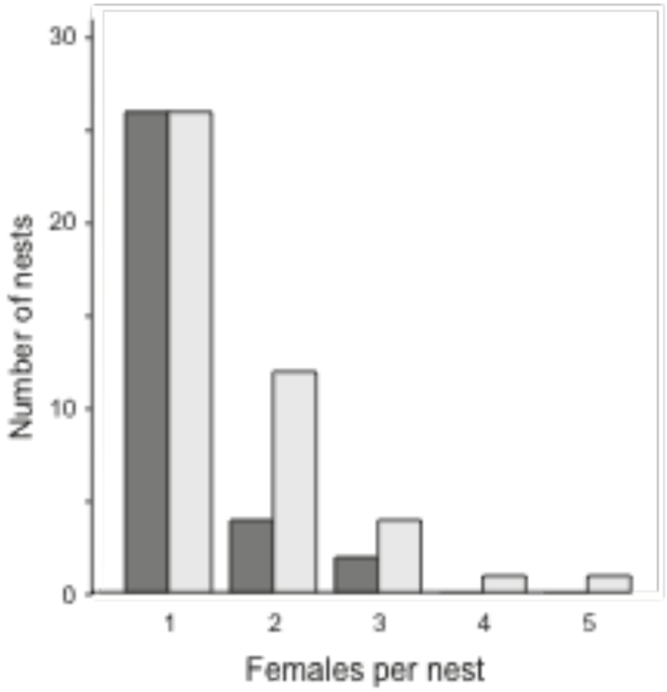

Figure 3: Number of adult females per nest for the July and October samples from the Laucala Bay campus of University of South Pacific.

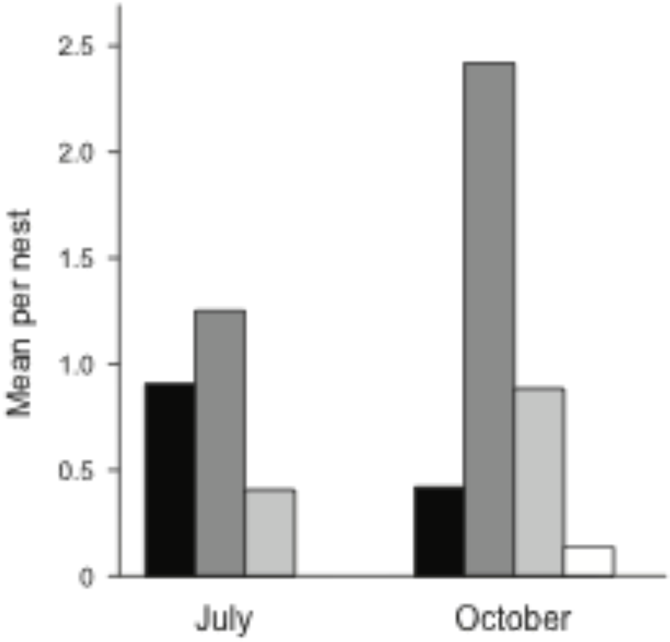

Figure 4: Mean number of eggs (black bar), larvae (dark grey bar), pupae (light grey bar) and callows (white bar) per nest for the July and October samples from the Laucala Bay campus of University of South Pacific.