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NATURAL HISTORY FIELD NOTE

Guests in nests: A parallel between social plants and animals?

Katrijn De Bock[1] | Ian Hutton[2] | Kevin C. Burns[1]

[1]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

[2]Lord Howe Island Museum, Lord Howe Island, New South Wales, Australia

Correspondence
Katrijn De Bock, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington 6012, New Zealand.
Email: katrijn.debock@vuw.ac.nz

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Abstract

This study explores the relationship observed between 'guests'—foreign inhabitants of social colonies—and the density and fecundity of eusocial-like staghorn ferns (*Platycerium bifurcatum*, Polypodiaceae). Our observations suggest that guests in staghorn colonies have a range of commensal and negative relationships, paralleling those seen in eusocial animal species.

KEYWORDS
coloniality, commensalism, eusociality, guests, parasitism, *Platycerium bifurcatum*

1 | INTRODUCTION

Many animals live in social groups that vary widely in structure and complexity. Eusociality is arguably the most complex form of social behavior (West et al., 2015), and is commonly characterized by overlapping generations, cooperative brood care and reproductive division of labour (Batra, 1966; Michener, 1969; Wilson, 1971). Although the strict definition of eusociality has been hotly debated (Clark et al., 2005; Costa & Fitzgerald, 1996, 2005; Gadagkar, 1994; Sherman et al., 1995), this study uses the core characteristics traditionally associated with the concept. Eusociality has evolved independently in numerous species, including several insect lineages (Aoki, 1977; Crespi, 1992; Wilson & Hölldobler, 2005), naked mole-rats (Jarvis, 1981), coral-reef shrimps (Duffy, 1973) and other species (Vollrath, 1986; Whyte, 2021). This diversity reflects the complexity of social structures across different life forms.

The 'common staghorn fern' (*Platycerium bifurcatum*) is an unusual epiphyte that grows in the tree canopies from Australasian forests. It has a colonial lifestyle by creating colonies of varying-aged individuals through asexual reproduction, known as ramets (Hoshizaki, 1972; Vail, 1984). Additionally, these colonies may also include unrelated, genetically diverse individuals that conjoin the colony (genets; Burns, 2021). In this context, an individual is defined as a unit with its own rhizome giving rise to roots and fronds, allowing independent growth and potential reproduction. Each individual also produces two types of fronds: 'strap' and 'nest' fronds (Hoshizaki, 1972; Kreier & Schneider, 2006). Strap fronds are long and narrow, remain photosynthetically active and are sometimes reproductively active. Nest fronds, which are always reproductively inactive, have a more circular shape and are short-lived, but remain functional after death. They articulate with nest fronds produced by other individuals in the colony to form a litter collecting 'nest'.

Fronds differ in size and shape according to their vertical position within the colony (Burns, 2021). Ongoing research indicates that individuals at the top of the colony possess erect, gutter-shaped strap fronds that collect rainwater, whereas individuals at the base of the colony have flattened, pendulous strap fronds (De Bock et al., in prep). Similarly, individuals at the top have large, fan-shaped nest fronds that collect water and falling leaf litter, whereas individuals at the base of the colony have clasping, spongy nest fronds that store water (Cronin et al., in prep). This variation suggests that individuals adapt morphologically to meet specific roles within the colony.

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According to research by Burns et al. (2021), approximately 40% of the colony's individuals, predominantly those at the top, reproduce through spore formation on strap fronds, whereas the strap fronds of the remaining 60% do not reproduce, indicating unequal reproduction rates among individuals. These observations in *P. bifurcatum* suggest eusocial-like life history attributes, potentially identifying it as the first documented plant species with such characteristics.

Foreign species regularly co-inhabit the colonies of eusocial insects, which in turn elevate the social dynamics of colonies (Parmentier, 2021). For instance, ant and termite nests can support thousands of 'guests', that influence eusocial colonies in a variety of ways. Some types of guests develop parasitic relationships with colony members (Parker & Grimaldi, 2014; Traynor et al., 2020). Conversely, other types of guests live as commensals within colonies, causing neither harm, nor benefit, to colony members (Messer, 1984; Phillips et al., 2017).

This study documents the occurrence of guests in staghorn colonies on Lord Howe Island and observes the relationship with colony density and fecundity. Results are used to address two research questions: (a) Are guests present in staghorn colonies, and if so, how frequent and diverse are they? (b) If guests are present, what patterns can be observed between guest presence and the density and fecundity of staghorn colonies? We hypothesize that variations in colony density and fecundity reflect differences in the nature of the relationship between colony and guest, which could be indicative of commensalism or parasitism.

2 | METHODS

The genus *Platycerium* comprises 18 epiphytic species with a pantropical distribution (Kreier & Schneider, 2006). The 'common staghorn fern' (*P. bifurcatum*) occurs on the Sunda Islands, Eastern Australia, Lord Howe Island and New Guinea (Hoshizaki, 1972; Kreier & Schneider, 2006). Our research focused on staghorn ferns occurring in Lord Howe Island, a volcanic island of <15 km^2 in area (31°33'S, 159°05'E), located app. 500 km east of Australia in the Tasman Sea. Although the island supports a diverse range of habitats (Harris et al., 2005), lowland areas are dominated by stunted tropical dry forest, where *P. bifurcatum* colonies are located within arm's reach (Dawes et al., 2020).

To investigate the frequency and diversity of 'guests' in staghorn colonies, we inspected all colonies located within a 5-m distance on either side of three narrow tracks winding through the island's tropical dry forest (total track length approximately 5 km; Figure S1). Morphological differences between guests and staghorn colonies, as well as among guests themselves, facilitated their identification. We recorded the relationship between guest presence and density and fecundity of staghorn colonies by measuring three variables for each colony: (1) colony density, (2) per capita fecundity and (3) colony-level fecundity. These traits reflect information about colony health and spatial dynamics. Colony density was determined by dividing the total number of individuals by the colony's volume (dm^3) calculated via the product of width, height, and depth measurements. To evaluate the fecundity-related parameters, we subdivided colonies into lower, middle, and upper sections, reflecting differential reproductive patterns (Burns et al., 2021). From each section, three mature individuals were randomly selected, and the number of reproductive fronds were counted per individual following Burns et al. (2021). Per capita fecundity was then calculated by dividing the total number reproductive fronds by the number of assessed individuals (mostly nine, unless insufficient mature individuals were present). Lastly, colony-level fecundity was calculated by multiplying per capita fecundity by colony density. To expand our sample size of guest-inhabited colonies for analyzing the relationship with their host, we also searched for colonies with guests off-track, in all accessible areas of dry forest. This approach allowed us to compile a dataset that likely encompasses most inhabited colonies on the island.

To assess differences in colony density, per capita fecundity, and colony-level fecundity among colonies inhabited by different guest species or not inhabited at all, we conducted three one-way ANOVAs using R v.4.0.4 with the 'car' package. Subsequently, we performed post hoc Tukey HSD tests to identify significant mean differences between inhabited and uninhabited colonies. To investigate colony density variations between on- and off-track locations, we employed a Mann–Whitney *U* test from the R base package. Similar tests were applied to fecundity metrics. As the outcomes of these tests were not significant for most colonies (Figure S2), both on- and off-track colonies were analyzed together to answer the second research question. All data were tested for normality and transformed where necessary.

3 | RESULTS

A total of 172 staghorn colonies were found on-track. Twenty-two (16%) were inhabited by five types of guests (Figure 1 & 2a): (1) the facultatively epiphytic but mainly terrestrial fern *Zealandia pustulata* subsp. *howensis* ($n = 10$, 7%), 2) the endemic, epiphytic fern

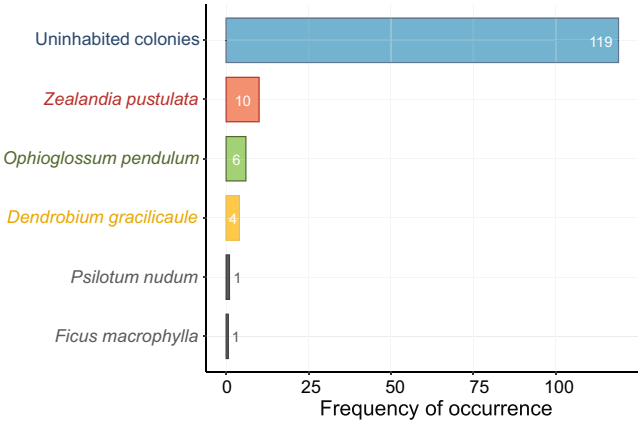


FIGURE 1 Visualization representing the frequency and diversity of guests that occurred in *Platycerium bifurcatum* colonies (within 5 m of the track).

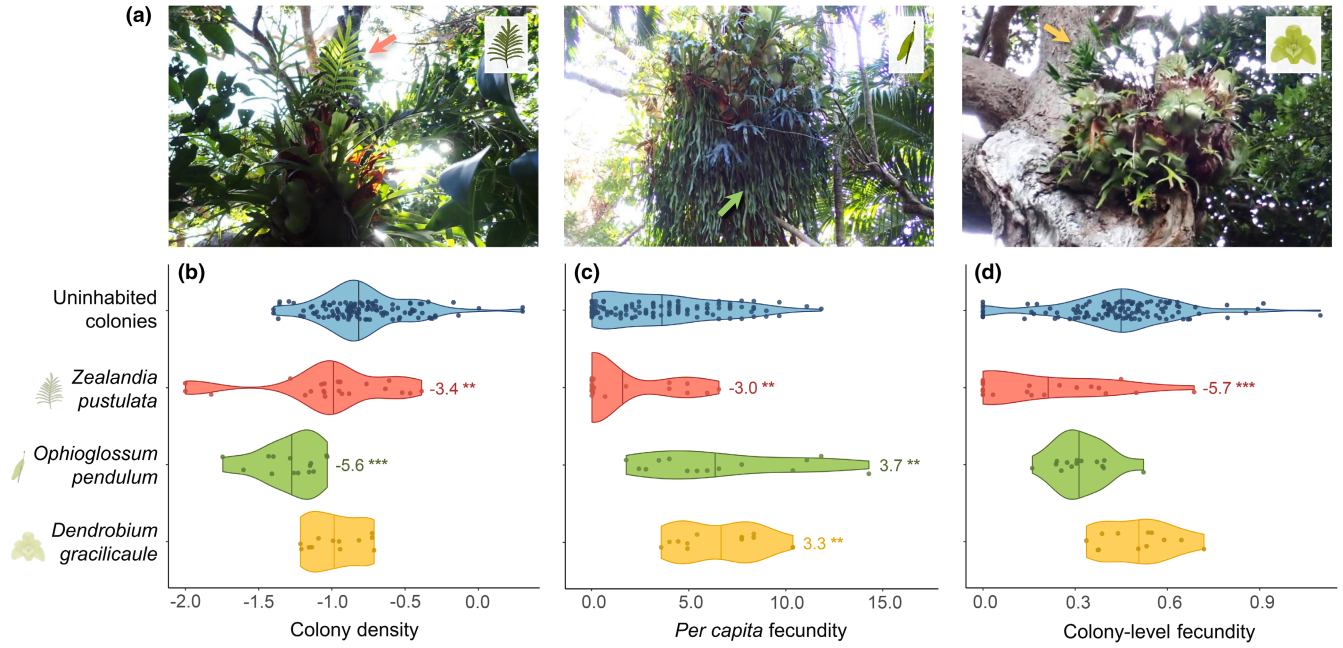


FIGURE 2 Representation of the investigated guests ($N = 48$) and the relationship between guest presence and colony density and fecundity. (a) Images from the guests (indicated by arrows) inhabiting a fern colony. From left to right: *Zealandia pustulata* (spread throughout the entire colony), *Ophioglossum pendulum* (hanging from the bottom) and *Dendrobium gracilicaule* (emerging from the top). (b) Violin plot displaying the relationship between guest-type and *Platycerium* colony density. (c) Violin plot displaying the relationship between guest-type and per capita fecundity. (d) Violin plot displaying the relationship between guest-type and colony-level fecundity. Numbers represent *t*-test results from post hoc comparisons. The data for (1) colony density were log-transformed, (2) per capita fecundity were squared, and (3) colony-level fecundity were square rooted. Asterisks indicate significance levels: $^{***}p \leq 0.001$; $^{**}p \leq 0.01$, respectively.

Ophioglossum pendulum ($n = 6$, 4%), (3) the endemic, epiphytic orchid *Dendrobium gracilicaule* var. *howeanum* ($n = 4$, 3%), (4) the skeleton fern *Psilotum nudum* ($n = 1$, 1%), and (5) the banyan tree *Ficus macrophylla* f. *columnaris* ($n = 1$, 1%).

An additional 31 inhabited colonies were found off-track (Table S1). Due to rarity, colonies with *P. nudum* and *F. macrophylla* (present in three and two colonies, respectively), were excluded. As a result, a total of 48 inhabited colonies and 119 uninhabited colonies were included in the second analysis.

Colony density differed significantly between colonies inhabited by different guest species ($F_{3,163} = 13.35$, $p < 0.001$; Figure 2b & Table S2). Staghorn colonies inhabited by *Z. pustulata* and by *O. pendulum* had fewer individuals per cubic meter compared to uninhabited colonies ($p = 0.004$ & $p < 0.001$, respectively). Staghorn colonies inhabited by *D. gracilicaule* showed no significant difference from uninhabited colonies ($p = 0.201$). Inhabited colonies were also significantly different in size ($F_{2,45} = 16.14$, $p < 0.001$). With an average volume of 328 dm^3, colonies inhabited by *Z. pustulata* were significantly smaller than colonies inhabited by *O. pendulum* (718 dm^3) and *D. gracilicaule* (636 dm^3; $p < 0.001$ & $p = 0.001$, respectively).

Per capita fecundity also varied significantly depending on whether colonies were inhabited ($F_{3,163} = 12.39$, $p < 0.001$; Figure 2c). Colonies inhabited by *Z. pustulata* showed lower ($p = 0.019$) per capita fecundity compared to uninhabited colonies, while those inhabited by *O. pendulum* and *D. gracilicaule* had higher per capita fecundity than uninhabited colonies ($p = 0.002$ & $p = 0.006$, respectively).

Differences in colony-level fecundity were also observed ($F_{3,163} = 12.69$, $p < 0.0001$; Figure 2d). Staghorn colonies inhabited by *Z. pustulata* had lower colony-level fecundity compared to uninhabited colonies ($p < 0.001$). However, no significant differences in colony-level fecundity were observed between colonies inhabited by *O. pendulum* and *D. gracilicaule* and uninhabited colonies ($p = 0.150$ & $p = 0.653$, respectively).

4 | DISCUSSION

Approximately one in six staghorn colonies was inhabited by other vascular plants (i.e., 'guests'). Three guest types were particularly common, each displaying different relationships with the staghorn colonies. *Zealandia pustulata* may have a negative relationship with the colony. In contrast, *O. pendulum* and *D. gracilicaule* exhibited varying patterns with respect to density and per capita fecundity, suggesting potential commensal relationships with the colony.

Colonies inhabited by *Z. pustulata* had both reduced density and per capita fecundity, which resulted in decreased colony-level fecundity. Unlike its terrestrial growth form, when *Zealandia pustulata* is rooted in staghorn colonies, its rhizome intricately weaves among the dead nest fronds of adjacent *Platycerium* members, suggesting an intertwined root system. This association suggests potential competition for water and nutrients that are captured and stored in the nest. Alternatively, they may compete chemically, via allelopathy

(Hierro & Callaway, 2021). However, the precise mechanisms responsible for this result, and determining whether the relationship is strictly parasitic (i.e., *P. bifurcatum* is harmed, which benefits *Z. pustulata*) or competitive (i.e., both harmed) await further study.

Conceptually similar patterns are observed in guests of eusocial insect colonies drawing a parallel between plants and animals. For example, the ant cricket *Myrmecophilus formosanus* inhabits various ant nests, consuming larvae, though its survival is not dependent on parasitising these colonies (Komatsu et al., 2009). Other examples of negative relationships include caterpillars of *Phengaris* butterflies (Witek et al., 2010) and the pselaphine rove beetle *Claviger testaceus* (Jałoszyński et al., 2020; Parmentier, 2021). Here, in both *Platycerium* and insect colonies, guests are not host specific, but the possible use of the host's resources seems to result in a negative relationship.

Colonies inhabited by *O. pendulum* had reduced density but increased per capita fecundity. These two patterns offset one another, resulting in no net change in fecundity at the scale of whole colonies. Unlike *Z. pustulata*, these results suggest that *O. pendulum* might have a more commensal relationship with staghorn colonies. *Ophioglossum pendulum* is typically located in the lower reaches of colonies, where spongy, water-storing nest fronds occur. Survival for these plants depends on such moist environments, as they occur exclusively in nests of staghorn ferns on Lord Howe Island (Green, 1988), demonstrating known drought sensitivity (Holttum, 1954; Mesler, 1974). This reliance might be a possible explanation for the observed reduction in colony density as they seem to take over this preferred space. Equally unclear are the mechanisms underpinning increased per capita fecundity. The absence of *O. pendulum* in smaller colonies might contribute to the observed increased fecundity rate suggesting a size-selective preference, though more data are needed to confirm this pattern.

Similar patterns are observed in eusocial insect colonies. For instance, ant crickets *M. kubotai* and *M. albicinctus* are host-specialist guests that cannot survive independently, relying instead on resources within their host environment (Komatsu et al., 2009; Parmentier, 2021). Similarly, the spider *Masoncus pogonophilus* lives exclusively in ant nests due to its high susceptibility to desiccation. The spider's feeding habit—consuming collembolans that help shield nests from fungal infections—potentially compromises ant colony fitness, but of negligible impact due to the spiders' limited population size (Cushing, 2012). Here, in both *Platycerium* and insect colonies, guests exhibit host-specificity and dependence on their host for survival, contributing to a nuanced relationship.

Colonies inhabited by *D. gracilicaule* had similar densities, but higher per capita fecundity. However, in this instance when considered jointly, they resulted in no statistically significant change in colony-level fecundity. Therefore, *D. gracilicaule* may maintain a commensal relationship with staghorn ferns. Orchids have a variety of specific adaptations against nutrient stress and desiccation (i.e., *velamen radicum*; Stern, 2014), which might explain their neutral relationship with staghorn colony density. Additionally, the orchid's independent lifestyle and their mycorrhizal associations might positively influence the nutrient availability, potentially explaining the observed increase in per capita and colony-level fecundity.

Similar results have been observed in eusocial insect colonies. Wallace's giant bee *Chalicodoma pluto* occurs exclusively in the nests of tree-dwelling termites (Messer, 1984) but lives communally without causing any harm to the colony. The bee *Centris segregate* lives as a commensal in termite nests, where it occupies space. However, once the bees depart, the vacant space is reutilised by the termites (Carrijo et al., 2012). Here, in both *Platycerium* and insect colonies, guests seem to live commensally with hosts possibly due to their self-reliant lifestyle.

Overall results from this study indicate that staghorn colonies often have 'guests', which interact with colonies in different ways. Although we have yet to establish how the concept of eusociality can be extended to include plants, the presence of guests with differing relationships with staghorn colonies parallels colony-guest interactions in eusocial animals. However, many interesting questions remain unanswered. How do host and guest roots, including fungal interactions, interact? Are colony-guest interactions similar throughout the range of *P. bifurcatum*? Are guests more fit when they coinhabit colonies compared to when they grow solitarily? Answers to these and other important and interesting questions await future research into 'guests' in plant 'nests'.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: 10.5061/dryad.3r2280gr4

ORCID

Katrijn De Bock https://orcid.org/0000-0002-6141-144X

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