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Polyrhachis femorata (Hymenoptera: Formicidae) habitat and colony defensive immobility strategy

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ABSTRACT

Many animal species 'play dead' or feign death (in some cases called tonic immobility) as a defence strategy against predators, including some ants, although triggers and durations are poorly understood. We repeatedly observed such death-feigning behaviour in *Polyrhachis femorata* ants that occupied pygmy-possum nest boxes deployed on Kangaroo Island following the 2019–2020 bushfires that burnt half of the island. Most of the 759 bat and pygmy-possum boxes (901 cavities) were on burnt ground. In 3312 box cavity checks on 13 diverse properties during monitoring visits, 28 of 40 *P. femorata* records (first for South Australia) occurred in unburnt Critically Endangered Narrow-Leaf Mallee Woodland community, seven in adjacent mallee community containing narrow-leaf mallee, three in cup gum unburnt habitat, and two in one box on burnt ground. Fire may have affected the abundance and re-establishment of the species. *Polyrhachis femorata* engages in a surprising defensive immobility strategy in boxes, since it is not only undertaken by individuals facing a potential predator, but also by entire colonies. The death-feigning behaviours were complemented by plugging box entrances. Nest boxes may be used to study this mysterious behaviour in this poorly known species, although frequent observation could lead to nest abandonment by the ant.

Keywords: ant defence, bushfire, catalepsy, *Eucalyptus cneorifolia*, playing dead, thanatosis, tonic immobility, tree cavity, tree hollow.

Introduction

Feigning death has been called thanatosis, tonic immobility, self-mimesis, freezing, and catalepsy in the literature (Pasteur 1982; Peters 2021; Sakai 2021), but all terms are not equivalent (Humphreys and Ruxton 2018; Sakai 2021). Here we use 'death feigning' to encompass freezing, curling up, and other death feigning (see Supplementary Text S1 for descriptions, and the indication that these behaviours could also demonstrate submissiveness or avoidance of detection). Many taxa feign death, including insects (Miyatake 2021 and references therein), and functions vary (most antipredatory), including survival from predators at the expense of more mobile conspecifics (Miyatake *et al.* 2009). Few studies mention this behaviour for ants, and even fewer examine it. Some ants feign death to survive attacks by aggressive conspecifics (Cassill *et al.* 2008) or during initial contact with conspecifics (Mbenoun Masse *et al.* 2011). They also feign death in defence against other species, particularly for slow foragers (Wilson and Brown 1984; Diniz and Brandão 1993; Dornhaus and Powell 2010), when nests are disturbed (Brandão *et al.* 1991; Rakotonirina and Fisher 2013), as specialist predators of spider eggs (Katayama 2013), and submissively to other species (Schumacher and Whitford 1974; Cardoso *et al.* 2016), including invasive ants (Peters 2021). Kannowski (1959) presented the interesting case of death feigning by nest intruder ants parasitising other ant species. Prey (Ayre 1959), predators, and parasites of ants (Parmentier *et al.* 2014) also feign death, which allows them to escape the attention of particular ant species. Death feigning among ants has received little specialised research attention considering the versatility and widespread use of the behaviour by many animal taxa.

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The deployment of 759 wooden boxes (some with dividers, for a total of 901 cavities) on 13 properties after the Kangaroo Island (South Australia) bushfires of 2019–2020 targeted pygmy-possum and insectivorous bat species. During the monitoring of pygmy-possum boxes on one Kangaroo Island property (summer 2021–2022), we discovered ants that feigned death in the boxes. Here we report death feigning in this ant species and suggest that it has the function of predator avoidance for both individuals and whole colonies. Because the species is a first record for South Australia and it is poorly known, we also describe its association with a Critically Endangered vegetation community and generally unburnt habitat. The ants' presence in nest boxes could facilitate the study of death feigning in this species.

Methods

Study sites

Kangaroo Island is the third largest island of Australia; it has a Mediterranean climate and is commonly windy. It was separated from the mainland 16 000 years ago (Bourman *et al.* 2016). After the bushfires of 2019–2020, which burnt the western half of the island, we installed 347 bat and 340 pygmy-possum nest boxes on 12 private properties between April 2020 and January 2021. Two of these properties (dominated by the stringybark, *Eucalyptus baxteri,* and sugar gum, *E. cladocalyx*) were unburnt, three had patches of unburnt vegetation, and the others were completely burnt. All these properties had a dominant overstorey of gum trees (*Eucalyptus* spp.) on a range of soil types. Some of the pygmy-possum boxes had double cavities, and the total number of cavities was 829. In the third week of December 2021, we added one unburnt property at Dudley West, on the eastern, unburnt side of the island, and placed 72 pygmy-possum boxes there (Text S2 gives additional information on box management). This study site had sand and loamy sand on limestone rocks, and the dominant overstorey consisted of multistemmed eucalypts (mallees): *E. cneorifolia* (narrow-leaf mallee), *E. diversifolia* (coastal mallee), and *E. rugosa* (Kingscote mallee). Each untreated pine box had a single chamber with internal dimensions 10 × 8 × 12 (depth) cm, with 18.5-mm thickness and a lid; every second box had a 20-mm entrance, and the others a 16-mm entrance. The holes of these boxes were located between 74 and 145 cm off the ground (mean = 107.9 cm; s.d. = 16.5 cm).

Monitoring and data collection

Monitoring involved checking the bat boxes with an inspection camera and slowly opening the pygmy-possum boxes. Monitoring started in August 2020, with each of the western properties monitored twice a year, for an average of 3.6 times each as of 3 November 2022. We monitored boxes on the Dudley West property (DW) for the first time on 28 January 2022, one month after installation, for a total of five times in 2022 (Table 1). Two nests were examined three additional times. By 3 November 2022, we had conducted 3312 artificial cavity checks. We recorded when nest boxes were occupied by ants, the total number of ants, whether they were feigning death, and classified the groups as 'nests' when eggs, larvae, or pupae were present. At the Dudley West property, we identified the trees that bore boxes and the surrounding eucalypt community by estimating the frequency of each of the dominant species of eucalypts around the box (visible trees at 360°) and recording the most common one (some had similar numbers; others had open environments without eucalypt upper canopy). We estimated numbers because of the difficulty of counting trees with several trunks (i.e. mallee). We used Fisher's exact test (IBM Corp. 2021) to determine whether the presence of ants was independent of the vegetation community at the Dudley West property (i.e. comparison of *E. cneorifolia* versus others).

Results and discussion

First record of *Polyrhachis femorata* for South Australia

Polyrhachis femorata Smith (Camponotini, Formicidae), identified at the Western Australian Museum, was discovered in six boxes in January 2022 at DW. It is the first record from South Australia for this species, which has now been recorded in all Australian states except the Northern Territory (antmaps.org, viewed 23 April 2022). *Polyrhachis* spp. are commonly nocturnal (Andersen 1991). In a eucalypt-dominated forest in Victoria, Andersen *et al.* (2009) collected most individuals in trees rather than on the ground, and most were in unburnt habitat. Heterick (2009) also observed *P. femorata* removing fresh sawdust from a jacaranda in south-western Australia, indicating that this species nests in tree cavities, which it may enlarge. The species' presence on a South Australian island suggests that it should be searched for on the State's mainland to determine its distribution and association with particular habitats there.

Association of *P. femorata* with vegetation communities

We found *P. femorata* in *E. cneorifolia* habitat at DW (12 boxes), three boxes in unburnt *E. cosmophylla* (cup gum) habitat at Middle River (MR1), and one box in the creek line of a burnt property at Middle River (MR2) in *Eucalyptus* sp. (non-mallee). All were pygmy-possum boxes, which represented 2016 cavity checks. The ant's apparent strong association with DW (mallee) may be due to the intense bushfires of 2019–2020, which completely or

Table 1. Number of *Polyrhachis femorata*, nests (with eggs, larvae, and/or pupae), and observations of death feigning at 72 pygmy-possum nest boxes on a Dudley West property, Kangaroo Island, South Australia.

Box no.	Tree host	Dominant tree	28 January 2022				5 February 2022				14 April 2022				24 April 2022 night			
			No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance
B13	ED	EC									11	n	y					
B17	ED	ER or ED									6	n	n	plugged				
B19	ED	ED									1	n	y					
B21	EC	EC																
B22	EC	EC	109	y	y	trace of plug					1	n	y					
B23	ED	EC	4	n	n													
B44	EC	EC	8	n	y	partial plug					6	n	y	hole plug down				
B49	ED	ED	1	n	y													
B54	EC	ER																
B60	ED	ED																
B61	EC	EC	105	y	y	(not recorded)	42	y	y	(not recorded)	113	y	y		8	n	y[A]	plug with hole
B68	EC	EC	191	y	y	partial plug	106	y	y	(not recorded)	106	y	y	all holes plugged	48	y	y[A]	plugged

Box no.	Tree host	Dominant tree	27 April 2022				17 June 2022				18 July 2022				19 September 2022			
			No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance	No. of ants	Nest	Feign death	Entrance
B13	ED	EC					5[w]	n	y		4[w]	n	y	partial plug				
B17	ED	ER or ED					2	n	n	partial plug	9	n	y	partial plug				
B19	ED	ED																
B21	EC	EC					1[Q]	n	y		1[Q]	n	y					
B22	EC	EC																
B23	ED	EC													1[QG]	n	y	
B44	EC	EC					10[c]	n	y		10	n	y	hole in plug				
B49	ED	ED																
B54	EC	ER													2[pp]	n	y	
B60	ED	ED					5[pp]	n	y									
B61	EC	EC	0	n		plug with hole	2	n	y	all holes plugged	12	y	y	all holes plugged	18	y	y	plugged
B68	EC	EC	37	n	y[A]	plugged	75	y	y	plug with hole	43	y	y	plugged	58	y	y	plug with hole

Numbers of ants were approximated using photographs when numbers were large. Entries under 'Entrance' refer to organic matter plugs ('all holes plugged' refers to the fact that even cracks along the lid were plugged); odd-numbered box entrances are 16 mm wide and even-numbered box entrances are 20 mm wide.
Dominant tree: EC, *Eucalyptus cneorifolia*; ED, *E. diversifolia*; ER, *E. rugosa*. Grey shading indicates boxes were not checked at that date. c, Small cockroach in box; G, marbled gecko *Christinus marmoratus*; Q, queen; pp, rotting pygmy-possum nest; w, water in box.
[A]see Text S2.

partially burnt 10 of 13 of our sites where this species could have occurred, and/or possibly to its affinity for *E. cneorifolia* (Fig. S1). This mallee is found mostly on Kangaroo Island, and the Narrow-Leaf Mallee Woodland is Critically Endangered (Australian Government 2014). All DW *P. femorata* nests were on *E. cneorifolia*; 6 of 12 boxes with ant records were on *E. cneorifolia*, and 28 of 35 DW box records (including repeat visits) were on *E. cneorifolia* or *E. diversifolia* trees in *E. cneorifolia*-dominated patches (Table 1) – others were dominated by *E. diversifolia* ($n = 3$), or *E. rugosa* ($n = 1$), or an even ratio of *E. diversifolia* and *E. rugosa* ($n = 3$). Considering that 19 *E. cneorifolia*, 25 *E. diversifolia*, and 28 other trees bore a box, and that only 23 boxes out of 72 were in *E. cneorifolia*-dominated or -co-dominated habitat, *P. femorata* on Kangaroo Island seems to favour *E. cneorifolia* and the Narrow-Leaf Mallee Woodland, as demonstrated by Fisher's exact test ($P_{\text{two-tailed}} = 0.044$). It took considerably longer for boxes in other communities to be colonised by *P. femorata*. One box installed in August 2020 in MR2 (*Eucalyptus* sp.) had a nest including uncounted workers and alates in February 2022, and in October 2022 had a nest with over 30 workers. The three boxes installed in November 2020, two of which contained *P. femorata* nests and another a single individual at MR1 (*E. cosmophylla*) in September 2022, were on *E. cosmophylla* ($n = 2$) and *Leptospermum continentale* ($n = 1$) associated with *Prostanthera spinosa*. Each nest was in a double-cavity box and one of them occupied both cavities (counted as one record). These records show that the Narrow-Leaf Mallee Woodland is not the only suitable community for this species, but considering the large number of cavities deployed on burnt habitat (551 cavities for 494 boxes, representing 61% of the cavities and 88% of the boxes), we would have expected to observe the ant in more boxes if it was not negatively affected by fires. It should be noted that we found no *P. femorata* on an unburnt stringybark-dominated property (*E. baxteri* and *E. obliqua*, with some *E. cosmophylla* and *E. fasciculosa*, pink gum). We had 263 bat boxes in burnt habitats and 84 in unburnt. None appeared occupied by *P. femorata*.

P. femorata feigns death alone and as a colony

Upon gently opening one of the boxes (Box 22) in January 2022, we were surprised to see dead-looking *P. femorata* with contorted bodies on the walls of the box. When the lid was fully open, it became apparent that some ants were moving, but most of the colony was already feigning death. Larvae and four alates were present in the box. Probing of an accumulation of ants in one corner of the box with a stick confirmed that all the ants were alive (the ones physically probed moved around), but many of the ants returned to death feigning. Some ants tending larvae attempted to move them (video A, Petit and Stonor 2022). The researcher was probably perceived as a predator and although some ants occasionally moved and movement increased towards the end of the 10-min observation, the whole colony was likely engaged in feigning death as a defensive strategy. Observations for this and following visits to DW are summarised in Text S3, Table 1, and Fig. S1; *P. femorata* at other sites behaved similarly.

These observations show that nests are dynamic, with contents changing frequently, and sites may be temporary. The impact of repeated visitation by researchers could cause stress to the colonies and was possibly the cause of nest abandonment in Boxes 22 and 61 (Table 1). The time taken to engage in death feigning varies, and whether individuals will engage in the behaviour may depend on context (Peters 2021 and references therein), such as previous experience and previous or current occupants, the submissiveness of individuals among local ant communities (*P. femorata* is monomorphic and likely subordinate), which include the aggressive *Camponotus terebrans* and *Iridomyrmex purpureus* at DW (Petit *et al.* 2020, 2022), and whether the cavity hosts a nest. A whole colony could achieve immobility, but often individuals moved and initiated movement in other individuals; the more numerous the ants were, the more difficult it seemed for the entire colony to achieve total immobility. This type of information could be collected with specialised equipment so that the role of individual ants, the changes in mobility of the colony, and the effects of light and other potential disturbances such as movement and contact with the box could be evaluated. The reasons and triggers for death feigning in ants are difficult to study (Peters 2021), making nest boxes an interesting tool for this purpose. Natural ant predators at our site potentially include echidnas (*Tachyglossus aculeatus*), goannas (*Varanus rosenbergi*), and some birds such as grey currawongs (*Strepera versicolor halmaturina*). Curiously, we found a queen *P. femorata* sharing a box with a marbled gecko (*Christinus marmoratus*). Ant colony defence was complemented by the plugging of box entrances and gaps with organic matter (Table 1; Fig. S1).

Conclusions

We cannot exclude the possibility that the apparent death feigning behaviour of *P. femorata* indicates submissiveness, defence (i.e. curling up with exposure of the spiny petiole), or avoidance of detection (see Text S1), but for us death mimicry is the most plausible explanation.

This death-feigning behaviour is used by both individuals and entire nests, but the variation in time (immediate to several minutes after opening the box) among individuals in achieving stillness (if at all) and the decision triggers are difficult to understand. The movement of a single or several individuals could affect the success of this likely antipredator strategy, implying that small nests may use it

more effectively than could large ones, simply because of the greater likelihood that all individuals would remain immobile at one time. Whether or not the behaviour is restricted to ants in confined locations is currently unknown. Artificial cavities with small openings may be a valuable way of studying arboreal ants engaging in death feigning, although nest abandonment could result from repeated observation. We recommend the use of boxes with smoothly opening lids and a floor plan that may be captured easily by a fixed video system. Experiment may be conducted with the use of a glass wall with a moveable opaque cover.

The association of *P. femorata* with a Critically Endangered community suggests that key habitat resources there maximise its fitness, and the study of ant community dynamics in this ecosystem deserves encouragement. Additionally, we recommend a search for this species on mainland South Australia, where it is likely to occur. In view of the paucity of information on the impacts of bushfires on invertebrates (Saunders *et al.* 2021), particularly for Kangaroo Island, more research should be supported to examine the effects of fires, including prescribed burns, which have increased over the island since the 2019–2020 bushfires. The rapid colonisation of boxes in unburnt mallee habitat indicates that *P. femorata* was actively searching for new nest sites. At other sites, populations may have been affected by direct or adjacent bushfire (MR2 and MR1, respectively), and this species may take a long time to re-establish itself in competition with aggressive ants that dominate burnt areas, considering the lack of cover and the destruction of tree hollows and cavities. Looking dead may protect nests from predators in these challenging environments.

Supplementary material

Supplementary material is available online.

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Data availability. Data are presented in the paper.

Conflicts of interest. The authors declare no conflicts of interest.

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