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# Drought-induced relocation of ant colonies and its consequences for the long-term spatial ecology of a population under stress

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## Abstract

1. Maintaining a central refuge such as a nest or burrow can offer protection against environmental stressors but comes at the expense of the capacity to disperse to new locations. This trade-off with mobility can be detrimental when environmental conditions become adverse for extended periods, necessitating animals to relocate in order to track shifting niche envelopes.

2. Long-lived ant colonies that invest in the construction of large nests are especially susceptible to changing environmental conditions. The Australian meat ant, *Iridomyrmex purpureus*, build large terrestrial nests at sites that balance shade and solar exposure.

3. Long-term study of a population of meat ants showed low nest turnover and a stable spatial distribution of nests across typical rainfall years. With the onset of drought, a dramatic surge in the production of new nests occurred through a process of budding that far exceeded historic trends. This appears to have allowed colonies to relocate nests into areas with more favourable microclimate conditions in a strategy reminiscent of the production of runners in stressed plants. The consequence has also been the packing of nests into a narrow habitable zone that has resulted in an apparent increase in competition among large rival colonies. Following the break in drought and the thinning of some nests through abandonment, competition has progressively eased in later years.

4. The surge in nest budding triggered by acute environmental stress in this population offers a possible strategy for long-lived colonies to effectively migrate across the landscape. With changes in environmental conditions becoming more frequent and severe with the climate crisis, any strategy available to central place foragers to track windows of preferred conditions is likely to become increasingly important.

**KEYWORDS**
annual rainfall, bet hedging, colony network, competitive exclusion, dispersal limitation, resilience

# 1 | INTRODUCTION

The spatial ecology of species manifests from a balance of abiotic and biotic requirements. This includes temperature and other environmental filters dictating where species can physiologically reside, through to the availability and level of competition for food and other resources needed to survive and reproduce. These factors are central to most theories of community assembly (Chase & Leibold, 2003; Gotelli & McCabe, 2002; Levine & HilleRisLambers, 2009; Soberon, 2007; Tilman, 2004), as is the ability of species to disperse to new areas in the first instance (Carvajal-Endara et al., 2017; Chisholm et al., 2016; Ord et al., 2017). In the case of animals, dispersal also allows individuals to shift locations to avoid adverse fluctuations in abiotic and biotic conditions (e.g. Gonçalves et al., 2016; Thompson & Gonzalez, 2017). This mobility becomes constrained, however, when animals invest heavily in the construction of burrows, nests or other centralised refuges (animals often categorised as 'central place foragers': e.g. Aarts et al., 2021; Elliott, 1988). These refuges can offer protection from environmental stressors in themselves, but at the expense of long-distance mobility. When environmental conditions become especially bad and long lasting, or competition increases following changes in community composition (e.g. the invasion of a new ecological competitor; Couper et al., 2021), the trade-off with mobility can be detrimental and facilitate local extinction (e.g. McCauley et al., 2014; Moore et al., 2008). To what extent animals can mitigate the benefits of creating a centralised refuge against the cost of potential future environmental adversity is unclear for most species.

Consider social insects that establish colonies in large centralised and long-lived nests, such as ants, which are exposed to similar ecological challenges from immobility as long-lived plants (sensu Andersen, 1995, 1997; reviewed by Gibb et al., 2022). First, the choice of nest location must balance key microclimate requirements to remain within a particular thermal and moisture window that will maximise a colony's activity and reproductive potential. This is contingent on various factors, from soil type to elevation (Gollan et al., 2013; Greenaway, 1981), but especially solar radiation (Gibb & Hochuli, 2004; Greenslade, 1975a). Just as plants struggle to survive under too much shade or too much sun, the temperature-dependent activity of ants and other ectotherms make some sites more suitable for nests than others (Batsleer et al., 2022; Gibb & Hochuli, 2003a; Heller & Gordon, 2006; Parr & Bishop, 2022). The distribution of food and other resources around the nest is also important (Heller & Gordon, 2006; McIver, 1991; van Wilgenburg & Elgar, 2007), and this can depend on competition from other neighbouring colonies (Boulay et al., 2010; Greenslade, 1975b; Sundaram et al., 2022). Second, once established, these permanent nests are exposed to any environmental change that impacts the microclimate of the nest or the distribution of resources around the nest. Both long-lived ant colonies and plants would therefore seem to share similar susceptibilities to environmental change because of a general constraint on the ability to track rapidly shifting niche envelopes.

There has been extensive modelling of the extent to which such dispersal limitation might slow species range shifts at regional scales under climate change (e.g. Block et al., 2022; Engler et al., 2009; Mammola et al., 2021; Svenning & Skov, 2004). Less clear is the degree to which limits on the mobility of individuals within a population might render species vulnerable to more localised changes in environmental conditions (Parr & Bishop, 2022). This is alarming given the magnification of both the frequency and severity of adverse conditions that are already being experienced by ecological communities at increasingly localised scales (e.g. Couper et al., 2021; Sundaram et al., 2022). In this local context, the strategies available to individuals that increase mobility likely matter for population survival as a whole. In the case of plants, some species can mitigate localised stressors by developing runners that allow a plant to effectively shift to sites where conditions are more favourable (reviewed by Song et al., 2013 and Guo et al., 2021). Ant colonies establish nests by a range of means, but an important mechanism includes budding satellite nests (reviewed by McGlynn, 2012) that are initially maintained through trail connections to the parent nest (Chapuisat et al., 1997; Heller & Gordon, 2006; Hölldobler & Carlin, 1985; Punttila, 1996). In theory, this should offer a method for colonies to effectively move location (McGlynn, 2012) and in a way similar to plants that produce stress-induced runners (e.g. Heller & Gordon, 2006). Indeed, workers of some ant species seem to evaluate alternative nest sites as part of their foraging excursions, which allows colonies to identify and relocate to new sites when conditions are found to be more favourable (Dornhaus et al., 2004).

Factors that impact colony survival in this way will have flow-on effects for ecosystem functioning (del Toro et al., 2012; Folgarait, 1998; Parr & Bishop, 2022). Ants are ubiquitous in all environments and make up a large amount of the biomass in many terrestrial environments (Gibb & Hochuli, 2004; Palfi et al., 2017; Parr & Bishop, 2022). An important functional group are those belonging to the Dolichoderinae, which tend to dominate many ant communities (Andersen, 2018; Andersen & Majer, 2004; Philpott et al., 2009) and have cascading effects on soil architecture and seed dispersal that can affect the composition of plant communities (Campbell & Clarke, 2006; Palfi et al., 2017). In Australia, the most ecological important species of the Dolichoderinae are arguably the meat ants *Iridomyrmex purpureus*. This species is distributed over nearly a third of the country (Cavill et al., 1984) and is typically locally abundant, making up the bulk of invertebrate biomass in many areas of eastern Australia (Gibb & Hochuli, 2004; Palfi et al., 2017; Stevens et al., 2002). Meat ants are generally superior ecological competitors in these communities as well (Andersen et al., 2009; Gibb & Hochuli, 2003b). Colonies construct large nests that can be decades old (Greenslade, 1973) and made up of hundreds of thousands of individuals (Greaves & Hughes, 1974). Meat ants are aggressive and territorial (Thomas et al., 1999), sending out large numbers of workers to forage for grains, dead arthropods or honeydew harvested from hemipteran insects aggregated in eucalypt trees (Gibb & Hochuli, 2003b; McIver, 1991; van Wilgenburg & Elgar, 2007). Colonies are often polydomous and can establish separate nests

connected by trails that exchange workers, food and other resources (Carew et al., 1997; Mobbs et al., 1978; van Wilgenburg & Elgar, 2007).

Every year for nearly a decade I have exhaustively surveyed a population of meat ants in the Central Tablelands of New South Wales, and informally monitored the population back to 2010. Meat ants dominate the invertebrate community at this location (Ord TJ, unpubli. data) and have a noticeable presence in the landscape, with large conspicuous nests scattered throughout the area. Serendipitously, this monitoring encompassed the onset of severe drought, which went on to devastate much of eastern Australia and magnified the catastrophic 2019–20 'black summer' bushfire season. In most years, the density of meat ant colonies was stable with the establishment of new nests and the abandonment of old nests being rare. The population underwent a surge in nest turnover in what appeared to coincide with the onset of drought. The dynamics of nest development differed from the typical background budding of nests and the establishment of colonies by newly mated queens following nuptial flights (swarms of which are associated with bouts of rain in the spring and summer months; Greaves & Hughes, 1974; Hölldobler & Carlin, 1985; Ord TJ, pers. obs.). The subsequent abandonment of nests was similarly unprecedented.

With the leverage provided by data collected over many years, I tested the hypothesis that the observed surge in nest turnover was stress induced and triggered by drought as colonies effectively engaged in a form of spatial bet hedging through nest budding. I also tested the additional hypothesis that the resulting migration of nests into an increasingly saturated (and seemingly contracting) habitable zone, in turn, coincided with increased competition among colonies for favourable nest positions (e.g. Boulay et al., 2010; Couper et al., 2021; Levings & Traniello, 1981; Sundaram et al., 2022). These hypotheses led to the following predictions. First, there would be a tight link between the dynamics of nest development and environmental stress, and particularly that induced by the onset of drought in 2017 to its break in early 2020. Second, new nests would be (at least initially) connected to parent nests via connection trails and connected nests would have improved chances of survival compared to isolated nests. Third, the mechanism of colony budding could have reflected drought-induced changes in localised food resources, in addition to shifts in vegetation cover dictating nest microclimate conditions. If colonies are limited by food resources, then nest survival and growth would be correlated to the number of foraging and tree trails (the latter reflecting harvesting of honeydew from hemipteran insects). Finally, the surge in new nests would lead to significant clustering within a narrow habitable zone in drought years. As this zone was progressively saturated with new nests, increased intra-colony competition would manifest in a spatial distribution of repulsion (evenness) as a function of nest size. Taken together, the objective of this study was to evaluate the prospect that the expansion of long-lived ant colonies via budding is a potential mechanism for ultimately shifting colony location to track moving microclimate niches, a strategy that would parallel the production of stress runners in plants.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

The population of meat ants, *I. purpureus*, was studied on a private property near the locality of Wollar in New South Wales, Australia. Research licences or permits were not required to undertake this work. The property consisted of large areas of cleared pasture previously used for low-density cattle farming up to 2007. This grassland transitioned abruptly to remnant dry sclerophyll eucalyptus woodland, along the boundary of which meat ant colonies often located their nests. The annual survey was conducted in late summer (February–March) and involved systematically walking the entire property from the property fence line butted against a public access road and into the woodland to approximately 50–150 m from the grassland–woodland boundary (this distance was dependent on the base of a rocky escarpment). No a priori assumption was made of where nests might be located in any year, and the manner of the survey walk ensured consistent visual overlap between adjacent path loops to reduce the likelihood of small nests being missed. The survey was considered exhaustive in each year.

Once a meat ant nest was located (Figure 1a), its coordinates were taken to a resolution of approximately ±2 m using a Garmin Oregon 600 GPS unit when at least 4 satellite links were registered on the unit. The number of entrance holes was counted to provide an estimate of nest size. For example, Greaves and Hughes (1974) fumigated and excavated 7 meat ant nests at a different location, first counting the number of entrance holes and then all ants within the nest. Using their data, a linear regression of entrance holes as a function of ant number recovered a positive relationship with an $r^2 = 0.95$. As a general guide, nests with 10, 50 and 100 entrance holes would be expected to have around 105,000, 680,000 and 1,400,000 ants, respectively. In this study, a count was also made of a nest's active trails (those observed to have ants moving along them). These were followed to identify whether they (i) lead to trees with honeydew secreting hemipteran (and subsequently categorised 'tree trails'); (ii) terminated at other food sources (usually dead arthropods) or otherwise petered out (both categorised 'foraging trails'); and (iii) or connected with another nest (categorised 'connection trails'). The nest was then permanently labelled with a metal tag, which was used in subsequent years to identify the nest (even if it was ultimately abandoned).

Annual rainfall data were collected from an onsite weather station. The 19-year average annual rainfall for this site is 646 mL. The drought began in 2017 with annual rainfall progressively decreasing to a record low of 314 mL in 2019 (Figure 1b). Nationally, the 2017–2019 drought coincided with unprecedented lows in annual rainfall across most of eastern Australia and is considered the country's worst drought on record because of its severity and duration (bom.gov.au). The drought broke in February 2020 and the site has since received unusually high annual rainfall (over 900 mL). Current monthly trends will likely see 2022 similarly near or above 900 mL.
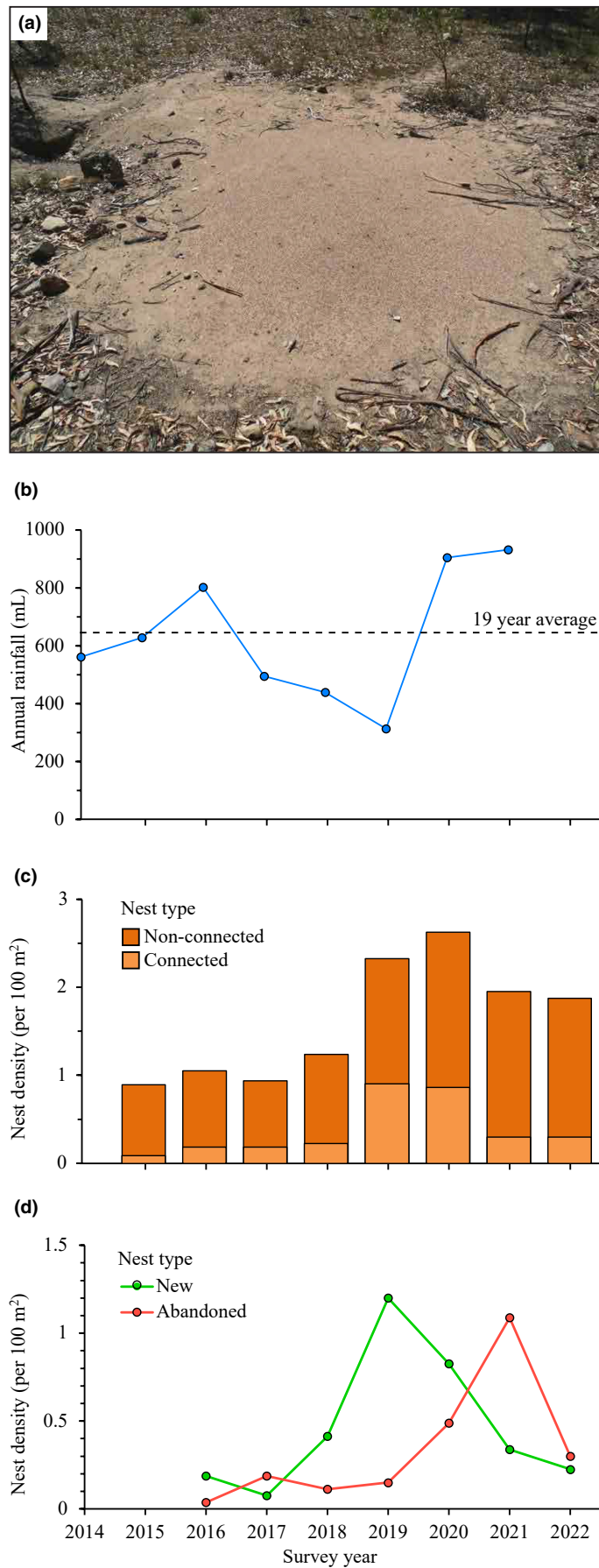
**FIGURE 1** Fluctuations in meat ant nests over 8 years of intensive study. Shown in the upper panel (a) is an example meat ant nest, while the central panel (b) presents data on the annual rainfall recorded onsite and (c) fluctuations in annual density of meat ant nests broken down by nests that were or were not observed to be connected to one or more nests. The bottom panel (d) shows the number of new nests established and nests abandoned each year, and highlights the unusual surge in nest turnover in years following the onset of drought.

## 2.2 | Statistical analysis

All analyses were conducted in R version 4.0.5 (R Core Team, 2018).

To test whether the formation of new nests and the persistence of nests were associated with annual rainfall, each nest was coded in two ways for each year between 2014 and 2022 depending on: (i) whether the nest emerged for the first time the following year (1), or whether it was already present (0); and (ii), once present, whether that nest remained active the following year (1) or was abandoned (0). Years in which a nest was yet to exist or continued to be abandoned following its initial year of abandonment were coded 'na'. A random effects logistic regression was implemented using the function 'glmer' applied with a binomial error distribution in the package LME4 version 1.1-28 (Bates et al., 2015). Models included a random intercept for nest and the predictor of annual rainfall mean-centred on the 19-year average and scaled to 100 mL units. Transforms of exponent parameter estimates to odds and odds ratios, as well as the calculation of associated 95% confidence intervals, were made using JTOOLS version 2.1.4 (Long, 2022).

To identify the nest characteristics associated with abandonment, each nest was coded for the total number of years it remained active, and whether it continued to remain active (0) or had been abandoned (1) prior to the last survey year of 2022. These data were entered into a Cox proportional hazards regression model using the package SURVIVAL version 3.3-1 (Therneau, 2022). A model selection approach was then used to test all possible combinations of the predictors nest size, number of forage trails, number of tree trails and number of connected nests. Values for each predictor were means computed across years in which a nest was recorded as being active and were log10 transformed. An intercept-only model was also applied as a null model, which effectively assumed nest abandonment was either stochastic or dependent on an as-yet unmeasured predictor variable. Models were compared using the sample-size-corrected Akaike information criterion, $AIC_c$. The model with the lowest $AIC_c$ was considered the best supported model, although any model within two units of this model ($\Delta AIC_c \leq 2.0$) was considered to be equally credible. Computed $z$ values for each predictor entered into a given model were used to distinguish among these supported models and to provide an indication of the magnitude and direction of effects. By convention, $z$ values greater than 1.96 were considered to be effects statistically distinguishable from zero. Kaplan–Meier curves were used to visualise the cumulative probability of nest abandonment over time using the SURVMINER package version 0.4.9 (Kassambara et al., 2020).

A second set of analyses were applied to identify the characteristics associated with nest growth more generally. In these analyses, nest size was the dependent variable (log10 transformed) and interaction terms between years active and all possible combinations of number of foraging trails, tree trails and connected nests (all log10 transformed) were predictors. These models were applied in addition to an intercept-only null model using the 'lmer' function of the package LME4 and used a random intercept and slope for nest and years active. $AIC_c$ was used to compare models and $t$ values of predictor interactions to identify the magnitude and direction of effects. Those $t$ values greater than 1.96 were considered statistically distinguishable from zero.

Finally, the position of most nests along the grassland–woodland boundary presumably spans the preferred microhabitat conditions for meat ant nests. In particular, the proximity of trees in the adjacent woodland would dictate the degree of shading at certain times of the day, and over the course of the year as the path of the sun shifted across the sky. Shading impacts the thermal and moisture conditions inside nests (Gibb & Hochuli, 2003a; Greaves & Hughes, 1974; Greenslade, 1975a), as well as the activity window available to workers for foraging outside of the nest (Andrew et al., 2013; Parr & Bishop, 2022). The impacts of drought were obvious on the surrounding vegetation, with thinning and canopy reduction tending to occur in the woodland and the loss of most ground vegetation in both the grassland and woodland habitats (e.g. compare images shown in Figure 3). The surge in new nests during drought further implies the conditions experienced at the original nest site had changed enough to prompt colonies to attempt establishing nests in new areas along the grassland–woodland boundary.

To confirm that nests were in fact clustered along the grassland–woodland boundary, and that this clustering has necessarily increased in drought years as habitable locations have become progressively settled by colonies, I used a linearised transform of Ridley's $K$ statistic, $L$, computed using the package SPATSTAT version 2.3-0 (Baddeley & Turner, 2005). This statistic is computed from the coordinates of mapped points (nests) over an expanding radius of distance (measured in metres). Values of $L$ converging on 0 are consistent with a distribution of complete spatial randomness, while values greater than 0 imply clustering of points in space and values less than 0 spatial evenness in point distributions (e.g. resulting from some form of repulsion among points, such as resource competition). The statistic was computed using an edge effect correction to control for points situated near survey edges necessarily having fewer neighbouring points because of an absence of information beyond the edge (Marcon et al., 2015). The survey edge coincided with the fence line along the eastern and southern portion of the property in the open grassland, the base of the rocky escarpment inside the forest on the western side of the survey area, and the northern limit of the survey area that corresponded with a break nest occurrence. The grassland–woodland boundary was situated roughly in the middle of this survey area. The edge effect correction was based on this border around the total area surveyed. To determine the statistical significance of empirically derived $L$ values of nest distribution for a given year, the package DBMSS version 2.7-7 (Marcon et al., 2015) was used to generate 95% confidence envelopes for a null distribution of complete spatial randomness using 1000 simulations. Values of empirical $L$ outside of this confidence envelope were considered statistically distinguishable from a random distribution.

The $L$ statistic was used to first verify that the distribution of nest locations in any given year was not random, and then to identify the distance over which clustering tends to manifest and the degree this distance has progressively shrunk as new nests have

become established in drought years. These analyses were restricted to unconnected nests and 'core' nests within a connected colony network (specifically the largest and likely most mature nest). This was because sets of connected nests within a colony are often adjacent to one another, which would subsequently bias any population wide spatial analysis to a greater preponderance of clustering. Nevertheless, analyses were also done on all active nests, regardless of their connections to other nests and results were qualitatively unchanged.

Finally, a second set of spatial analyses were applied that computed a version of the $L$ statistic, $L_{mm}$, that considers the impact of nest size on distribution pattern. This statistic was used to evaluate the consequences of the progressive saturation of nests along the grassland–woodland boundary and the extent to which larger nests have induced a distribution pattern consistent with competitive exclusion. This was based on the assumption that a larger nest requires more resources and subsequently a larger spatial area to sustain itself compared to a smaller nest. In addition, a larger nest has a larger force to aggressively defend resources and territory from other colonies compared to a smaller nest. Together, this should limit the proximity of nests to one another as a function of nest size. The same procedure was followed as described above for $L$, with the key difference being that nest size was included in the calculation to weigh nests by size. Values of $L_{mm}$ converging on 0 are consistent with a spatial distribution of nests independent of their size, values greater than 0 indicate a positive correlation with nest size, such that larger nests cluster more closely with one another than smaller nests (mutual clustering), while values less than 0 indicate a negative correlation with nest size in which larger nests locate themselves further away from each other than smaller nests (mutual repulsion; Penttinen et al., 1992). Empirically derived values of $L_{mm}$ were compared to a null distribution of $L_{mm}$ under complete spatial randomness using a 95% confidence envelope generated from 1000 simulations. Empirical $L_{mm}$ values outside of this envelope were considered statistically distinguishable from a random distribution.

# 3 | RESULTS

## 3.1 | Drought-induced nest budding and persistence

In an average rainfall year, there was a less than even odds of a new nest appearing the following year (odds = 0.39; Table 1a), confirming the budding of new nests was typically rare in the population. The odds further decreased as annual rainfall increased (odds ratio = 0.77; Table 1a). To place this into a clearer context with the surge in new nests in drought years (Figure 1c, Table S1), the odds of new nests appearing increased by 31% for every 100 mL decrease in annual rainfall the previous year (inverse odds ratio, OR = 1/OR = 1.31). At the peak of the drought, this would equate to a onefold increase (103%) in the odds of new nests appearing than would be expected following a typical rainfall year (i.e. the driest year was 332 mL below the 19-year annual rainfall average; Figure 1b).

The persistence of nests in the population was high, with a nearly 6 to 1 odds of a nest remaining active following an average rainfall year (odds = 5.94; Table 1b). That is, nests were rarely abandoned following typical rainfall years. Many nests were likely well over a decade old (Figure S1). However, the odds ratio of remaining active decreased by 20% with each 100 mL increase in annual rainfall the previous year (odds ratio = 0.80; Table 1b). For example, the incidence of nest abandonment increased following unusually high rainfall years, most notably in 2021 (following a year that was 260 mL above the 19-year average), but also to an extent in 2017 (following a year that was 157 mL above the 19-year average; Figure 1b,d). Nevertheless, the dynamics of nest abandonment in relation to rainfall was less straightforward than the budding of new nests. The acceleration of abandonment appears to have started in 2020 following the *driest* year on record (2019) and had begun to slow by 2022 following the *wettest* year on record (2021). Moreover, nest abandonment appeared to follow surges in new nest formation with a 2-year lag (e.g. the peak in nest abandonment occurred 2 years after the peak in new nest density).

**TABLE 1** The association between annual rainfall and the (a) appearance of new nests and (b) persistence of nests in the following year.

| Variable | Estimate (lower 95% CI, upper 95% CI) | z | p |
|---|---|---|---|
| (a) Appearance in the following year ($N_{nests, observations}$ = 111, 324) | | | |
| | Odds | | |
| Average rainfall year (intercept) | 0.39 (0.27, 0.57) | −4.91 | <0.001 |
| | Odds ratio | | |
| Increasing rainfall (per 100 mL) | 0.77 (0.68, 0.87) | −4.15 | <0.001 |
| (b) Remain active in the following year ($N_{nests, observations}$ = 111, 409) | | | |
| | Odds | | |
| Average rainfall year (intercept) | 5.94 (4.12, 8.54) | 9.62 | <0.001 |
| | Odds ratio | | |
| Increasing rainfall (per 100 mL) | 0.80 (0.70, 0.92) | −3.26 | 0.001 |

## 3.2 | Nest characteristics predicting survival and growth

The primary predictors of nest survival were the number of foraging and tree trails maintaining nests. The best supported model identified the average number of foraging trails leading from nests as the factor with the greatest effect on reducing the probability of abandonment ($z_{\text{forage trails}} = -4.0$), followed by the average number of tree trails ($z_{\text{tree trails}} = -2.3$; Table 2a). All other credible models similarly indicated the number of foraging trails and tree trails as the main factors reducing the probability of nest abandonment (Table 2a). For example, the probability of surviving a single year was greater than 85% for nests with at least 1 foraging trail, compared to 50% or less for nests with no foraging trails (Figure 2). Neither the size of the nest or the size of the connected colony network had tangible effects on survival ($z$ values from $-0.6$ to $-1.3$; Table 2a).

Focussing only on new nests that appeared in the population during the study, the predictors of nest survival continued to be the number of foraging trails, but also the number of connections new nests retained with others in the colony. All credible models showed the average number of foraging trails had the greatest effect on reducing the abandonment of new nests ($z_{\text{forage trails}} = -3.8$ to $-4.5$; Table 2b), followed by the average number of connected nests ($z_{\text{connected nests}} = -2.2$ to $-2.3$; Table 2b). For example, the surge in nest density in 2019 was disproportionately associated with increased numbers of connected nests (Figure 1c).

The best supported model for the annual growth of new nests that survived up to at least 2022 (Table 3a) estimated an on-average increase of 1 entrance hole every 4 years (e.g. Figure S1), with those nests maintaining at least one tree trail generally being larger in starting size (by about 12 entrance holes) than those without tree trails (Table S2). Yet, those nests with tree trails also had an on-average lower annual growth rate than nests without tree trails ($t_{\text{year*tree trail}} = -2.8$; Table 3a, Table S2), presumably because these nests were generally larger in size to begin with ($t_{\text{tree trail}} = 3.7$; Table 3a, Table S2). For new nests that were ultimately abandoned (e.g. Figure S1), the two most credible models (Table 3b) estimated an on-average annual decline of 1 entrance hole every 4 years, although those connected to at least one other nest within a colony network were typically larger at the outset compared to isolated new nests (Table S3). No predictor was computed to have a statistical effect on buffering (or accelerating) nest decline (i.e. the effect size of all interaction terms with year were indistinguishable from zero; Table 3b).

## 3.3 | Spatial dynamics of nest aggregations over time

The clustering of nests around the grassland–woodland boundary was clear in all years, irrespective of whether analyses (based on the $L$ statistic) were focussed on core and isolated nests (Figure S2) or all nests regardless of their network connection (Figure S3). The dynamics of this clustering has also progressively changed from year to year and in a manner consistent with surges in nest density in drought years (Figure 1c). For example, following a typical annual rainfall year (2015), nests were clustered over distances of 65 m and greater (defining the gross width of the habitable zone for meat ant colonies along the grassland–woodland boundary; Figure 3, 2016). The year following peak drought saw intensive clustering of nests over just a few meters (Figure 3, 2020). Two years after the drought broke, the distribution of nests had begun to thin out (through abandonment; Figure 1d) with clustering manifesting over distances of 20 m and greater (Figure 3, 2022).

In addition, there were signs of competitive exclusion in the intensive clustering of nests in drought years when analyses (using the $L_{\text{mm}}$ statistic) were focussed on core and isolated nests (Figure S3). There was a negative correlation in the spatial position of nests as a function of nest size during and following years of drought, whereas nest location was independent of nest size in typical rainfall years (Figure 3, 2016). This mutual inhibition of nests was most obvious in the year following peak drought (Figure 3, 2020), with larger nests tending to be more evenly distributed in the landscape compared to smaller nests. This is consistent with some form of repulsion, such as the competitive exclusion of large nests from adjacent locations. Post-drought, this repulsion has progressively relaxed (Figure 3, 2022). When analyses were inclusive of all nests, the distribution of nests was largely independent of nest size (Figure S4). The spacing of nests connected to colony networks effectively diluted the apparent size-dependent distribution of nests, and presumably because nests within a colony network are less likely to be in competition with one another. This is consistent with the notion that colonies have established new nests as a means of moving away from areas made unsuitable because of microhabitat changes caused by drought.

## 4 | DISCUSSION

Many ant species are capable of relocating colonies to new sites under a range of circumstances (reviewed by McGlynn, 2012). In some cases, this capacity has the potential to be quite labile, reflecting the continual evaluation of current site suitability relative to potential neighbouring alternatives (Dornhaus et al., 2004; McGlynn et al., 2004). In general, however, the investment in establishing a large nest and its associated site fidelity for long-lived ant colonies make these classic central place foragers susceptible to severe or abrupt changes in environmental conditions, and subsequently colony death (Couper et al., 2021; Sundaram et al., 2022). Andersen's (1995) notion that ant colonies are typically sedentary in a similar manner to plants continues to be broadly applicable (Gibb et al., 2022). This places a premium on the position of nests to ensure the balance of conditions favourable for survival and growth. In the case of ant species that establish nests in soil, the type of soil and its moisture are likely the immediate indicators used to determine site suitability (Ettershank, 1978; Greaves & Hughes, 1974; Greenslade, 1973; Heller & Gordon, 2006), with environmental filtering determining the persistence or abandonment of nests over

**TABLE 2** Support for alternative Cox proportional hazards regression models of nest survival for (a) all nests or (b) only new nests that appeared during the study.

| Model applied | $AIC_c$ | $\Delta AIC_c$ | $z_{nest size}$ | $z_{forage trails}$ | $z_{tree trails}$ | $z_{connected nests}$ |
|---|---|---|---|---|---|---|
| (a) All nests ($N_{nests}=111$) | | | | | | |
| Null | 508.5 | 75.7 | | | | |
| Connected nests | 508.0 | 75.1 | | | | |
| Forage trails | 438.0 | 5.1 | | | | |
| Tree trails | 458.4 | 25.5 | | | | |
| Forage trails+tree trails | 432.9 | 0.0 | | −3.98 | −2.32 | |
| Forage trails+connected nests | 438.7 | 5.8 | | | | |
| Tree trails+connected nests | 455.7 | 22.8 | | | | |
| Forage trails+tree trails+connected nests | 433.1 | 0.2 | | −3.75 | −2.40 | −1.34 |
| Nest size | 457.9 | 25.0 | | | | |
| Nest size+connected nests | 459.8 | 26.9 | | | | |
| Nest size+forage trails | 436.3 | 3.4 | | | | |
| Nest size+tree trails | 446.9 | 14.0 | | | | |
| Nest size+forage trails+tree trails | 433.9 | 1.1 | −1.04 | −3.27 | −1.93 | |
| Nest size+forage trails+connected nests | 437.9 | 5.0 | | | | |
| Nest size+tree trails+connected nests | 447.9 | 15.0 | | | | |
| Nest size+forage trails+tree trails+connected nests | 434.8 | 2.0 | −0.64 | −3.27 | −2.06 | −1.10 |
| (b) New nests ($N_{nests}=86$) | | | | | | |
| Null | 417.9 | 43.6 | | | | |
| Connected nests | 414.0 | 39.7 | | | | |
| Forage trails | 378.6 | 4.3 | | | | |
| Tree trails | 406.0 | 31.6 | | | | |
| Forage trails+tree trails | 379.5 | 5.2 | | | | |
| Forage trails+connected nests | 374.3 | 0.0 | | −4.53 | | −2.37 |
| Tree trails+connected nests | 401.0 | 26.7 | | | | |
| Forage trails+tree trails+connected nests | 375.7 | 1.4 | | −3.85 | −0.84 | −2.30 |
| Nest size | 397.2 | 22.9 | | | | |
| Nest size+connected nests | 396.6 | 22.3 | | | | |
| Nest size+forage trails | 379.4 | 5.1 | | | | |
| Nest size+tree trails | 394.6 | 20.3 | | | | |
| Nest size+forage trails+tree trails | 380.7 | 6.4 | | | | |
| Nest size+forage trails+connected nests | 376.2 | 1.9 | −0.54 | −3.84 | | −2.19 |
| Nest size+tree trails+connected nests | 393.3 | 19.0 | | | | |
| Nest size + forage trails+tree trails+connected nests | 377.8 | 3.5 | | | | |

longer timeframes based on a preferred thermal niche and the availability of resources for sustaining the nest. Meat ant nests tended to cluster within a habitable band along the grassland–woodland boundary (Figure 3 and Figure S3). Within this band, and in typical rainfall years, nests were generally randomly distributed (e.g. in

2016 and over distances less than 65 m). Nest turnover was also low in average rainfall years with nest development and abandonment being rare (Figure 1d; Table 1). Many nests were over a decade old and likely much older (Figure S1). Intuitively it would seem, then, that the location of meat ant nests were essentially fixed in place,

**FIGURE 2** The probability of nest survival in years as a function of the average number of foraging and tree trails recorded for a nest during the period it was active.
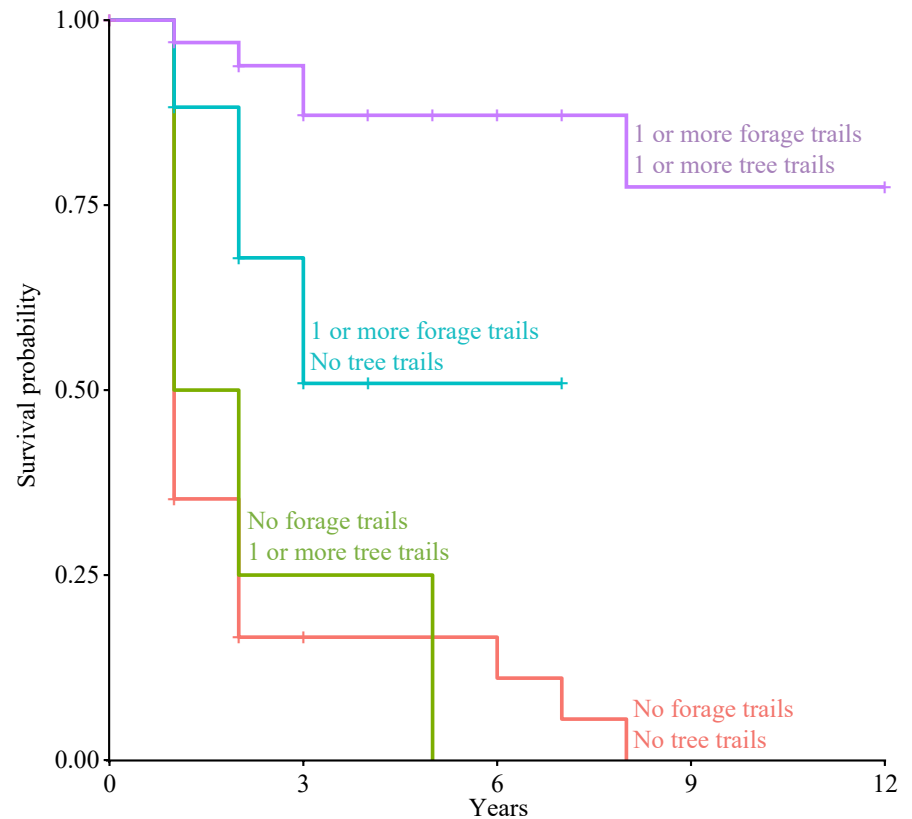


making colonies susceptible to any environmental change that might adversely impact microhabitat conditions at nest sites.

With the onset of drought, the vegetation surrounding nests changed noticeably and many nests became exposed to longer periods of direct sun. A reasonable prediction would have been a progressive reduction in population density as colonies died in areas made unfavourable through excessive solar exposure and the depletion of resources (Boulay et al., 2010; Sundaram et al., 2022; van Wilgenburg & Elgar, 2007; e.g. the number of foraging and tree trails sustaining a nest were key for its survival; Figure 2; Table 2). Instead, population density nearly doubled in drought years, fuelled by a dramatic increase in the development of new nests, many of which were from colonies budding nests closer to the grassland–woodland boundary or into the woodland itself (Figure 1 and Figure S2). Many of these new nests were abandoned if they were not initially connected to a colony network (Tables 2 and 3). There was also a progressive saturation of space around the grassland–woodland boundary to such an extent that the spatial ecology of nests appears to have tipped into a dynamic of competitive exclusion as a function of nest size (Figure 3).

Taken together, the current data are consistent with colonies having undergone budding as a form of spatial bet hedging. The mechanism of this budding of new nests is almost certainly the outcome of severe drought impacting both the vegetation structure surrounding nests (and the resulting balance of shade and solar radiation previously provided by that cover) and the potential distribution of localised food resources (e.g. the reduction in insect food and plant matter previously harvested in the grassland). The spatial

distribution of nests within the contracted habitable zone was also consistent with some form of repulsion occurring as a function of nest size, with the obvious mechanism being increasing competition with increasing nest density and neighbouring nest size. Anecdotally, ritualised fighting among workers from adjacent colonies has been observed in this population at distances as little as 10–15 m between nests (Ord TJ, pers. obs.), which roughly corresponds to the onset of repulsive spacing patterns computed in the year following the height of drought (2020 in Figure 3). Competition between large colonies presumably reflects the area around a colony required for workers to adequately harvest the necessary food resources to sustain nests (Boulay et al., 2010). The subsequent increased spacing between colonies would imply the availability of resources had progressively decreased with increasing drought (Sundaram et al., 2022). This type of expansion of spatial 'halos' reflecting the shifting area needed for resource harvesting is often a signature of central place foragers (e.g. Aarts et al., 2021; Weber et al., 2021). However, the extent to which the depletion of food resources specifically, rather than aggressive territoriality more generally (Chen et al., 2018; van Wilgenburd et al., 2005) or changes in abiotic conditions at nest sites (Dornhaus et al., 2004), prompts nest relocation in ants is unclear (e.g. Gordon, 1992; Smallwood, 1982; van Wilgenburg & Elgar, 2007). A companion study is currently being prepared on how the location of nests relative to the grassland–woodland boundary impacts worker behaviour and the thermal conditions experienced around and within nests. Future work is also being developed to experimentally induce stress on nests through artificial heating and shading to confirm the mechanistic basis of colony budding is not

**TABLE 3** Support for alternative random effect models of annual changes in nest size for new nests that (a) remained active or (b) were abandoned.

| Model applied | $AIC_c$ | $\Delta AIC_c$ | $t_{year}$ | $t_{forage\ trails}$ | $t_{tree\ trails}$ | $t_{connected\ nests}$ | $t_{year*forage\ trails}$ | $t_{year*tree\ trails}$ | $t_{year*connected\ nests}$ |
|---|---|---|---|---|---|---|---|---|---|
| (a) New nests that remain active ($N_{nests,\ observations}$ = 32, 106) | | | | | | | | | |
| Null | 78.5 | 3.8 | | | | | | | |
| Forage trails | 84.4 | 9.7 | | | | | | | |
| Tree trails | 74.8 | 0.0 | 3.30 | | 3.74 | | | −2.78 | |
| Connected nests | 91.2 | 16.4 | | | | | | | |
| Forage trails + tree trails | 83.5 | 8.7 | | | | | | | |
| Forage trails + connected nests | 98.3 | 23.5 | | | | | | | |
| Tree trails + connected nests | 88.4 | 13.7 | | | | | | | |
| Forage trails + tree trails + connected nests | 98.3 | 23.5 | | | | | | | |
| (b) New nests that become abandoned ($N_{nests,\ observations}$ = 52, 198) | | | | | | | | | |
| Null | 93.3 | 58.4 | | | | | | | |
| Forage trails | 64.9 | 30.0 | | | | | | | |
| Tree trails | 74.4 | 39.4 | | | | | | | |
| Connected nests | 61.1 | 26.2 | | | | | | | |
| Forage trails + tree trails | 57.3 | 22.4 | | | | | | | |
| Forage trails + connected nests | 35.0 | 0.0 | −6.75 | 1.90 | | 6.85 | 1.37 | | 0.48 |
| Tree trails + connected nests | 54.3 | 19.3 | | | | | | | |
| Forage trails + tree trails + connected nests | 36.6 | 1.7 | −6.89 | 1.87 | 1.87 | 6.18 | 1.00 | −0.48 | 0.01 |

exclusively contingent on the availability of food resources or competition among colonies.

To an extent, Andersen's (1995) plant analogy of ant spatial ecology can be extended to the phenomenon of stress runners (the production of stolons or rhizonmes; Guo et al., 2021). Strawberries will be a familiar example for any gardener who has witnessed stressed plants develop long runners in an attempt to take root in more favourable locations. Meat ant nests appear to be capable of something similar, with colonies attempting to establish new nests in more favourable microhabitats. The success of this strategy and the ability of colonies to effectively track shifting niche envelopes over local scales is contingent on budded nests being connected to the colony network and maintaining enough foraging activity to sustain the nest, and in the absence of competition from nearby rival colonies. This phenomenon has not been previously observed in meat ants, or possibly any other ant. Some super-colonial species annually migrate between winter and nearby summer nest locations (e.g. *Formica truncorum*; Elias et al., 2005), but this reflects a hibernation strategy in high-latitude environments in response to predictable summer resource pulses (and a harsh winter climate). While budding is a common mechanism for establishing new nests in many ant species (Gibb & Hochuli, 2003a; Gordon, 1992; Heller & Gordon, 2006; Hölldobler & Carlin, 1985; Punttila, 1996; Smallwood, 1982; Sundaram et al., 2022), the extent to which budding is instigated by non-seasonal environmental stress and allows long-lived colonies to effectively migrate to more favourable locations remains unclear (Boulay et al., 2010; Parr & Bishop, 2022; but see Dornhaus et al., 2004). This is probably because long-term studies of ant spatial ecology are rare and would need to coincide with a stress event. Sundaram et al. (2022) provide a rare example in which a population of North American red harvester ants have been tracked annually for several decades, inclusive of periods of severe drought. As with the meat ants of the current study, a key predictor of red ant harvester nest survival was the foraging area available to a nest, which was determined by competition from neighbouring colonies (see also Levings & Traniello, 1981).

**FIGURE 3** The spatial ecology of meat ant nests prior to (2016), during (2020), and post-drought (2022). The panels in the left column provide a satellite image of the study site overlaid with the GPS locations of each active nest recorded in that year. Upper panels in the right column report the $L$ and $L_{mm}$ values computed over an expanding radius of distance. The solid line in each plot represents the empirically derived values computed from the nest location data, while the grey area corresponds to the 95% confidence envelopes of complete spatial randomness. Values above and outside the grey area indicate significant clustering of nests, while values below and outside the grey area indicate significant spatial evenness in the distribution of nests. The $L$ statistic measures the spatial distribution of nests independently of nest size, whereas $L_{mm}$ measures spatial distribution as a function of nest size. To illustrate the impact of drought on surrounding vegetation, a photograph taken from the same location in all years with the camera facing towards the forest edge (where nests were found to be aggregated) are also shown for each represented year.
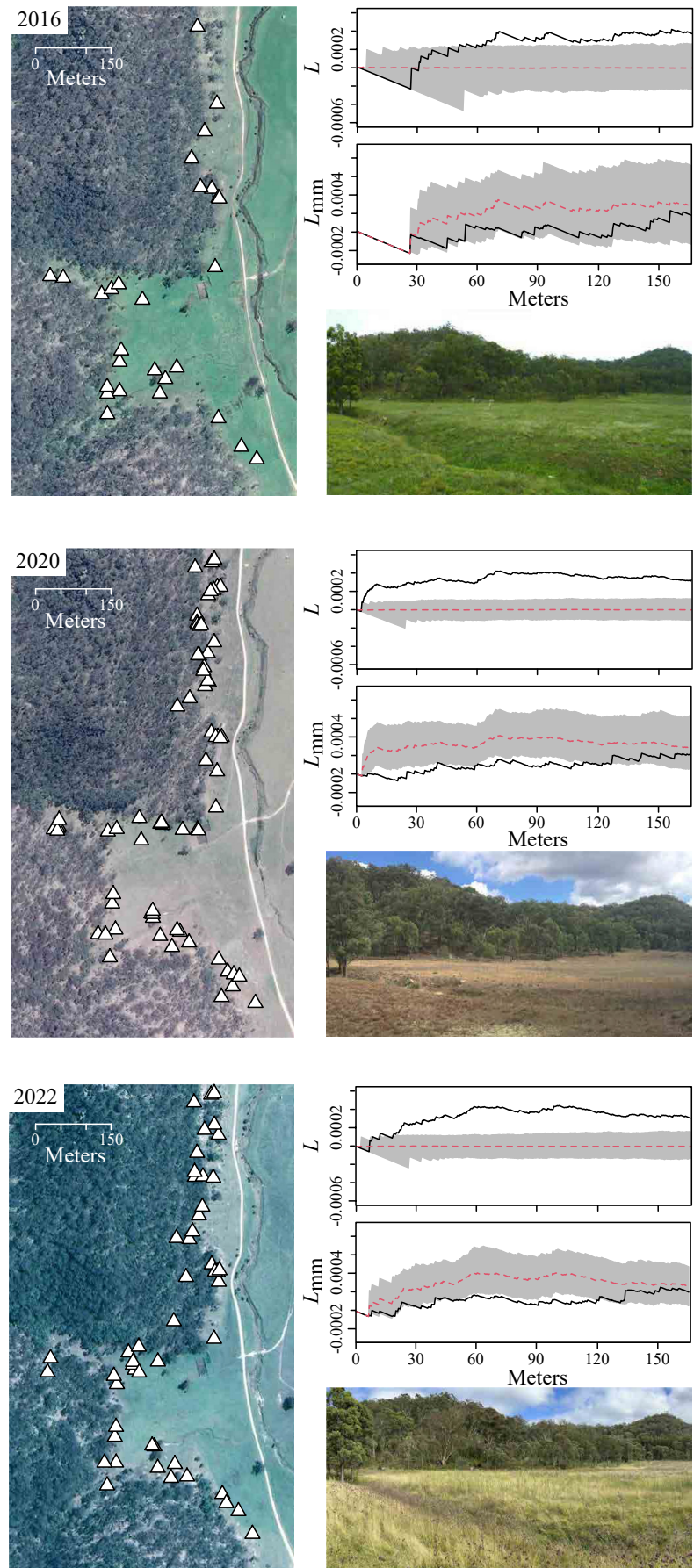
However, nest recruitment in red harvester ants decreased during periods of drought and presumably because of food shortages (Sundaram et al., 2022). A reduction in nest density in response to drought was reported in another long-term study focussed on the invasive Argentine ant (Couper et al., 2021). That is, there does not appear to have been the same strategy of spatial bet hedging under stress in these species as documented here for meat ants. The conspicuous networks of meat ant nests and how the spatial organisation of those nests relate to microhabitat choice was an early focus of research (e.g. Halliday, 1983; McIver, 1991). However, the longest monitoring program of nests in meat ants seems to have been 5 years (Greaves & Hughes, 1974; see also Greenslade, 1975a), during which time nest density was reported to be stable. Instances of nest abandonment were unusual and speculated to have been caused by human interference, with even fewer cases of colonies establishing new nests. This limited nest turnover was consistent with the population in the present study, up to 2018 (Figure 1c,d).

While the later surge in nest budding was almost certainly linked with drought (Table 1a), the abandonment of nests appeared to be associated with increases in annual rainfall (Table 1b). Both unusually low or high rainfall can be salient environmental stressors (e.g. Selwood et al., 2015; Thibault & Brown, 2008). In the instance of high rainfall, there has been a noticeable increase in ground vegetation around nests in the last 2 years (e.g. Figure 3, 2022) with previously exposed nests becoming shaded by tall weed. Excessive shading has been previously linked to the abandonment of nests by meat ants (Gibb & Hochuli, 2003b; Greaves & Hughes, 1974; Greenslade, 1975a). However, nest abandonment was probably dependent on other factors in addition to, or separate from, excessive rainfall. First, if nest abandonment was induced by environmental stress associated with rainfall, abandonment should have increased following any large deviation in annual rainfall, including those of drought years (e.g. Couper et al., 2021; Sundaram et al., 2022). Second, the dynamics of nest abandonment closely tracked the budding of new nests following a lag of 2 years (Figure 1d). If the strategy of budding nests was a mechanism for colonies to track a shifting niche envelope, then it would necessarily result in the subsequent abandonment of nests in areas made unfavourable by the changes in microhabitat conditions. Nonetheless, not all new nests would be expected to be placed in suitable areas because of (for example) continued shifts in microhabitat conditions as drought intensified or resource competition from nearby larger nests (Figure 3). This is consistent with the drop in nest density following the surge of budded nests in drought years (Figure 1c,d).

The implications of establishing a central refuge, such as a territory, burrow or nest, has typically been examined in the context of how that anchor point in an animal's spatial behaviour influences the defence of resources (Aarts et al., 2021; Kacelnik et al., 1992; Potts et al., 2012; Ydenberg et al., 1986) and foraging decisions (Elliott, 1988; Patenaude-Monette et al., 2014), as well as how central place foragers can, in turn, impact properties of the surrounding ecosystem (Chase, 1998; Fagan et al., 2007; Pringle et al., 2010;

Weber et al., 2021). Yet, a spatial ecology fixed on a central point has other important impacts on the capacity of animals to respond to acute environmental change through constrains on dispersal. This has rarely been the focus of investigation. While refuges have a direct benefit in providing shelter from environmental stress and other factors (e.g. predation), that benefit is contingent on mitigating short-term fluctuations in the environment. With the progressive impacts of the climate crisis being experienced by species over the long-term (years rather than days or weeks) and at increasingly local scales, any constraint on the ability of individual animals to track windows of preferred environmental conditions or shifting food bases becomes potentially critical for population persistence. Ants that establish long-lived colonies share the same types of challenges on the capacity for range shifts as long-lived plants. While meat ants have an extensive regional distribution in eastern Australia, colonies are nevertheless constrained in where nests can be placed because of the required balance of factors that influence nest temperature and resource availability, all of which are subject to short- and long-term fluctuation. It would seem long-lived colonies retain flexibility in their spatial distribution through the ability to quickly bud new nests and move to more favourable locations (see also Dornhaus et al., 2004). This should allow colonies to effectively migrate across the landscape to improve survival as local conditions shift over the long term.

## CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.n8pk0p31n (Ord, 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Proportion of nests connected to other nests across years and maximum recorded colony size in a given year.

**Table S2.** Parameter estimates from the best supported random effects model of annual changes in nest size for new nests that remained active (see Table 3a).

**Table S3.** Parameter estimates from the best supported random effects model of annual changes in nest size for new nests that were abandoned (see Table 3b).

**Figure S1.** The temporal dynamics of individually identified meat ant nests. A handful of large conspicuous nests had been observed from at least 2010 but not subject to systematic survey until 2015.

**Figure S2.** Two representative nests that appeared during the surge in nest density in 2019 and remained active (a) or was ultimately abandoned (b). Images have been rotated to a common viewing angle. Note the metal tag in the top left corner of each image was the permanent ID used to identify each nest. This ID number was written on a notepad to be visible in the photograph.

**Figure S3.** The *L* and *L*mm indices for core and isolated nests in each year surveyed.

**Figure S4.** The *L* and *L*mm indices for all nests (connected and unconnected) in each year surveyed.