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POPULATION ECOLOGY – ORIGINAL RESEARCH

Density dependence and the spread of invasive big-headed ants (*Pheidole megacephala*) in an East African savanna

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Abstract

Supercolonial ants are among the largest cooperative units in nature, attaining extremely high densities. How these densities feed back into their population growth rates and how abundance and extrinsic factors interact to affect their population dynamics remain open questions. We studied how local worker abundance and extrinsic factors (rain, tree density) affect population growth rate and spread in the invasive big-headed ant, which is disrupting a keystone mutualism between acacia trees and native ants in parts of East Africa. We measured temporal changes in big-headed ant (BHA) abundance and rates of spread over 20 months along eight transects, extending from areas behind the front with high BHA abundances to areas at the invasion front with low BHA abundances. We used models that account for negative density dependence and incorporated extrinsic factors to determine what variables best explain variation in local population growth rates. Population growth rates declined with abundance, however, the strength of density dependence decreased with abundance. We suggest that weaker density dependence at higher ant abundances may be due to the beneficial effect of cooperative behavior that partially counteracts resource limitation. Rainfall and tree density had minor effects on ant population dynamics. BHA spread near 50 m/year, more than previous studies reported and comparable to rates of spread of other supercolonial ants. Although we did not detect declines in abundance in areas invaded a long time ago (> 10 years), continued monitoring of abundance at invaded sites may help to better understand the widespread collapse of many invasive ants.

Keywords *Acacia drepanolobium* · Ant supercolonies · Extrinsic factors · Gompertz model · Population collapse

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Introduction

Relationships between population growth and abundance lie at the heart of many empirical and applied efforts in ecology, and our ability to detect such density dependence has often relied on long-term data (Brook and Bradshaw 2006). In animal populations, the functional form of density dependence can affect the likelihood of establishment (Leung et al. 2004; Drake and Lodge 2006; Tobin et al. 2011), the rate of population expansion (Lewis and Kareiva 1993; Hastings et al. 2005; Sullivan et al. 2017), and interact with environmental stressors (Hodgson et al. 2017). Biological invasions are particularly well suited for testing how abundance affects rates of population growth, since there is often strong spatial and temporal heterogeneity in an invader's abundance as it spreads: invaders tend to increase in density over time following establishment, and invasion fronts are characterized by lower densities relative to those behind it. Here, we exploit this temporal and spatial variation in invader abundance to assess how density dependence and environmental variability impact local population growth rates of big-headed ants (*Pheidole megacephala*), an invasive, unicolonial supercolony-forming ant species (Hoffmann et al. 1999) that is disrupting a keystone ant–plant mutualism in East Africa.

Ant supercolonies are among the largest cooperative units known in nature, capable of reaching densities of millions of individuals per hectare (Abbott 2005). In contrast to other ant species, supercolonial ants can establish territories that span large areas, within which ants cooperate to procure food, maintain defense, and reproduce (Holway et al. 2002). These traits make them extraordinary competitors, dominating native ant communities and often drastically reducing native biodiversity (Hoffmann et al. 1999; Holway et al. 2002; O'Dowd et al. 2003). Some of these supercolonial ants are among the most harmful invaders in the world and affected countries spend millions of dollars annually on their control and eradication (Hoffmann and Broadhurst 2016; Hoffmann et al. 2016).

Despite their strong competitive abilities, populations of invasive supercolonial ants can collapse, even in the absence of human intervention. This highlights the need to better understand the drivers of population growth, spread, and collapse, to efficiently control these populations. Over the course of 3 years, Cooling and Hoffmann (2015) reported declines of entire populations of invasive, supercolonial yellow crazy ants (*Anoplolepis gracilipes*) in northern Australia. In Europe, 10 out of 29 supercolonies of the invasive garden ant (*Lasius neglectus*) declined to extinction between the 1990s and 2015 (Tartally et al. 2016). Numerous mechanisms have been invoked to explain these declines, including pathogens, resource depletion, and the introduction of other invasive ants (Lester and Gruber 2016).

Ant population dynamics themselves can also contribute to such declines. For example, if populations are reduced by environmental stressors, positive density dependence (i.e., Allee effects), can lead to low densities, decreased competitive ability, and an increase in predation (Lester and Gruber 2016). The potential for Allee effects could be particularly high in supercolonial species, that require large population sizes for resource acquisition and defense (Luque et al. 2013). Negative density dependence, on the other hand, can set a limit to population growth and may help stabilize ant populations (Morris and Doak 2002), but supercolonial ant activities may deteriorate their habitats over time pushing carrying capacities to low densities where they are more likely to collapse (Clements et al. 2015; Zarada and Drake 2017).

The big-headed ant (*Pheidole megacephala*, hereafter "BHA") is a widespread, supercolonial species that is considered one of the most disruptive invasive species in the world (Lowe et al. 2000; Wetterer 2012). Like other supercolonial species, BHA form colonies with multiple queens and interconnected nests that spread generally through "budding", where a queen leaves its natal nest with a group of workers to found a new nest (Vanderwoude et al. 2000; Wilson 2003). Population collapses of BHA have been described on the islands of Culebrita, Puerto Rico (Torres and Snelling 1997) and Madeira, Portugal (Wetterer et al. 2006) where they were a plague by the end of the nineteenth century and are rare today. The impacts of BHA on native communities have been extensively studied in Australia, where they have extirpated native ants and strongly reduced the abundance and diversity of other native arthropods, particularly Coleoptera and Orthoptera (Hoffmann et al. 1999; Hoffmann and Parr 2008). Although the species was originally described from Mauritius (Fabricius 1793), its point of origin remains a mystery (Wetterer 2012). In Laikipia county, Kenya, the exact timing of the invasion is not well known but the species has established strongholds in many areas (Visitacao 2011).

On the Laikipia Plateau of central Kenya, tree cover of monodominant stands of the whistling-thorn tree, *Acacia drepanolobium*, is maintained by a mutualism between this tree and several species of native ants (Palmer et al. 2000). *Acacia drepanolobium* provide nest space (swollen spine domatia) and nectar to native ants, which in turn protect host trees against herbivory, including catastrophic herbivory by elephants (Goheen and Palmer 2010). Where BHA are present, they eliminate native *Acacia* ants but do not provide protection to the host plant, resulting in five- to sevenfold increases in catastrophic damage to these trees by elephants (Riginos et al. 2015). Over time, such sustained herbivory may reduce tree cover, potentially affecting species such as giraffes and black rhinos, which rely on *A. drepanolobium* as food. To manage such African savannas, it, therefore, is important to slow the spread of BHA and control populations where they have already established.

Our aim in this study was to evaluate the strength and shape of density dependence in BHA, and to assess potential environmental drivers of BHA population growth rates. To evaluate density dependence, we measured temporal changes in BHA abundance and rates of spread over 20 months along permanent transects running perpendicular to invasion fronts, extending from densely populated areas behind the front, to low abundance areas at the invasion front. We examined two potential extrinsic drivers of BHA local population growth: (1) spatial variation in the density of *A. drepanolobium* among transects, since extrafloral nectaries in *Acacia drepanolobium* may provide carbohydrate fuel to expanding colonies of BHA, and carbohydrate availability has been shown to drive invasive ant population dynamics in other systems (O'Dowd et al. 2003; Wilder et al. 2011; Wittman et al. 2018), and (2) temporal variation in rainfall across our 20-month sampling period, since bouts of high precipitation have been shown to be correlated with reductions in

BHA populations in both Hawaii (Beardsley et al. 1982) and monsoonal Australia (Hoffmann et al. 1999). Our approach allowed us to address three major questions: (1) are temporal changes in BHA abundance correlated with BHA density, and if so, what is the shape of that density dependence? (2) Are BHA local population growth rates associated with *A. drepanolobium* densities and/or rainfall? (3) How rapidly are BHA invasion fronts spreading and do these relate to rainfall and/or tree density?

Methods

Study area

We conducted our study at Ol Pejeta Conservancy (OPC) a privately owned 36,000-ha ranch in Laikipia county, central Kenya. Ol Pejeta Conservancy lies on the equator (0°N, 36°56′E), and receives a mean annual rainfall of 900 mm concentrated in the months of March, April, May, November, and December. The conservancy is comprised of four major habitats (wooded grassland dominated by *Acacia drepanolobium*, open grassland, shrub woodland dominated by *Euclea divinorum*, and riparian forest dominated by *Acacia xanthophloea*) and harbors important populations of megafauna including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*) and both white (*Ceratotherium simum*) and black rhino (*Diceros bicornis*) as well as a diverse assemblage of wild African ungulates. Ol Pejeta is also managed for cattle production at stocking rates compatible with wildlife conservation. We focused our work on the *Acacia drepanolobium* savanna. Each *A. drepanolobium* is occupied by a single species of one of four ant species that vary in their levels of aggressive defense of host plants, from the strongly mutualistic *Crematogaster mimosae* and *C. nigriceps*, to the non-defending exploiter *C. sjostedti* (Palmer and Brody 2007, Palmer et al. 2000, Tamashiro et al. 2019).

At Ol Pejeta, BHA have spread from human settlements to surrounding savannas, starting around 2000. By 2018, a significant part of the property was invaded, including an area of a 3-km radius surrounding the largest human settlement, and at least five other hubs of different size. The ants dwell primarily in the soil but also occupy acacia trees within invaded areas. BHA completely eliminate the three *Crematogaster* species on and behind their invasion fronts (Riginos et al. 2005), making it relatively easy to identify advancing fronts.

BHA are frequently seen feeding at extrafloral nectaries (hereafter "EFN") although the number of active nectaries falls abruptly after BHA invasion suggesting that, unlike native *Acacia* ants, BHA do not induce EFN production. BHA densities at trees are particularly high during the dry season while during rainy times fewer BHA are found on trees, probably because BHA rely more on arthropods found in the highly productive grasslands on the wet season. Possible benefits of the trees include EFNs and honeydew hemipteran associations. These have been found in other systems but at Ol Pejeta, we found no evidence of honeydew-producing hemipteran being tended by BHA after the invasion.

Data collection

In December 2016, we selected four active invasion hubs (North Control, NC; South Control, SC; Kamok, K; and the Tourism house, TH), and established two transects at each invasion hub, perpendicular to the invasion front and separated by 250 m. We identified the locations of invasion fronts in two ways, first by visual inspection of trees (presence or absence of *Crematogaster* and BHA ants), and then using tuna baits. All invasion fronts occurred ≥ 3.5 km from each other. Since the distance of BHA invasion fronts from the putative origin of the invasion was variable among sites, transect length varied from 300 m (K, TH) to 500 m (NC, SC). We placed baiting stations at 100-m intervals behind each invasion front, running towards invasion hubs. In addition, to estimate more accurately the rates of spread, we placed baiting stations at 20-m intervals beginning at the front and running 40 m inward towards invasion hubs, and at 20-m intervals outward from the front and running 40 m into uninvaded (at the time of the onset of monitoring) habitat (Fig. 1).

We performed six censuses at each baiting station between December 2016 and June 2018 (December 2016,

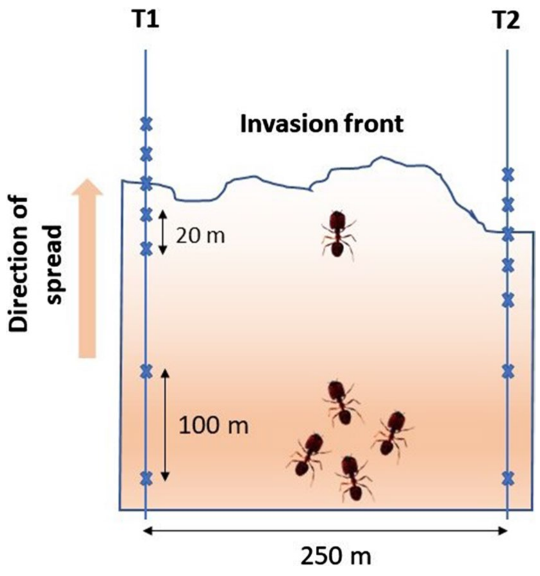

Fig. 1 Schematic disposition of two transects (T1 and T2) at a study site. Crosses represent baiting stations

February 2017, June 2017, October 2017, February 2018 and June 2018). Censuses were conducted from 8 to 10:30 (because BHA activity drops off sharply past 10:30 AM) on non-rainy days. For each census, at each baiting station, we chose a random direction (left or right) and a distance from the transect line (from 0 to 9 m) to place the first of three baits, which consisted of one tablespoon of tuna. The remaining two baits were placed at 10 and 20 m from the first bait, along the same perpendicular line running from the main transect. Two trained observers independently recorded the number of BHA workers (both castes were pooled) at each bait after 30 min and we averaged the two counts for each bait. We repeated ant counts the next day whenever possible, following the same protocols. Differences in count estimates between observers were minor (mean − 0.85; range − 20–30, $N=300$ baits), and the mean number of workers recorded was relatively small compared to other studies (mean 21; range 0–175, $N=3392$ baits) (Hoffmann et al. 1999). The use of lures has been used in the past to measure ant abundance (Holway 1998; Hoffmann et al. 1999; Gibb et al. 2017), and like other methods, it has its limitations. To verify how reliable our worker abundance estimates were, we ran a correlation between total abundance on surveys conducted on consecutive days. Correlation between the first and second survey was high (0.78) for all transects and censuses, suggesting baits consistently estimate worker abundance. Since invasion fronts often moved from one census to the next, new baiting stations were added and old baiting stations removed, to keep the number of baiting stations at the front (5) constant. The workers of some ant supercolonial species can move among nests at longer temporal scales, potentially biasing abundance estimates. There is very little literature on BHA territories and movement, however, analysis of movement for *P. megacephala* over 3 days in Malaysia showed short foraging distances (range 1.8–3.34 m) and relatively small foraging territories for individual nests (range 2.75–4.84 m^2) (Loke and Lee 2004). Our censuses were separated by 4 months, yet baits could be as far as 39 m from the transect. Thus, we believe that any short distance movement of workers among nests or even movement of nests will have little impact on abundance measures of our baiting stations.

To test the hypothesis that host tree density influences BHA local population growth rates and rates of spread, we counted the number of *A. drepanolobium* saplings (individuals < 1 m height) and trees (> 1 m) in strip transects 50 m long and 5 m wide, perpendicular to the transect and centered at each of the five baiting stations arrayed across the invasion front (Fig. 1). Correlation between numbers of saplings and trees was low ($r=0.23$) and BHA feed on EFN of both trees and saplings, so we kept both variables for our analyses. To examine the effects of rainfall on local population growth and spread of BHA we used daily rainfall data during inter-census period. Rainfall gauges were located at Kamok and Control (meaning records for NC and SC were the same). We used all local population growth rates to assess the influence of abundance and extrinsic factors, with the exception of data from the Tourism House. Since we lacked estimates of rainfall for the Tourism House, datapoints ($n=27$) from those transects were excluded from our analysis.

Data analysis

We estimated local population growth rates for each intercensus period at each baiting station within each transect. To do this, we first summed BHA counts at each baiting station and obtained an estimate for mean abundance by averaging counts from the 2-day replicates. We estimated 4-month growth rates as $\lambda = \left(\frac{N_{t+1}}{N_t}\right)^{1/i}$, where t is census number, N the mean abundance and i is the number of 4-month periods between censuses. Thus, we squared the lambdas of our first survey (2 months) to make them comparable to those of the following surveys (separated by 4 months).To test for density dependence, we calculated the correlation coefficient between the logarithm of the observed local population growth rates and abundance at time t (Morris and Doak 2002).

Visual inspection of population growth vs abundance plots helped us determine what population growth functions to fit. Since density may obscure the effects of extrinsic variables (and vice-versa), we fitted density-dependent models that included both extrinsic variables (acacia density, cumulative rainfall) and interactions of extrinsic variables with BHA counts. To take full advantage of the dataset, we ran mixed non-linear regressions with nested random effects of baiting station within transect to account for non-independence of the points. We later found that models including a random nested effect showed a singular fit and we chose to leave only the transect ID as a random effect. To incorporate uncertainty in the estimation of our population growth functions due to repeated sampling, we used a Monte Carlo simulation to generate 1000 datasets. First, we randomly drew abundance values from a normal distribution with mean equal to the mean abundance estimated at each baiting station and variance equal to the square of the standard deviation of the day replicates. Then, for each dataset, we fitted the selected population growth function, and stored the parameter estimates of the model. Last, we retrieved the 2.5 and 97.5% quantiles and the mean of the estimated parameters.

To estimate rates of BHA spread, we collected data on new ant detections within transects. We only recorded the detections that were farthest from the origin of the invasion, because location of the presumed invasion front may vary between day replicates. We used distance-regression methods to obtain an estimate of the rate of spread (Gilbert and Liebhold 2010). Distances from the point of origin to new detections were recorded and these were regressed against time. The slope of the regression line gives an estimate of the rate of spread. We compared these estimates with the average spatial offset between the first and last census for each transect. To explore synchrony in spread, we ran pairwise correlations among transects. Strong correlations among transects may indicate temporal and spatial covariates acting on the rates of spread. To examine the influence of extrinsic covariates on the rate of spread, we fitted four general linear models that each included only one predictor variable (because only points at the front were used for the analysis, $n=28$), and ranked them by $\mathrm{AIC_c}$ (Burnham and Anderson 2002).

Density-dependent models

Observed local population growth rates ($n=257$) were negatively correlated with abundance ($r=-0.43$) (Fig. 2). We fitted two stochastic population growth models that accounted for negative density dependence to our dataset, the Ricker model and a Gompertz model. Under the Ricker model, there is a constant linear decrease in r as population increases. This means that local population growth rates keep declining at a constant rate as population grow larger. We modeled the logarithm of the change in population size for the Ricker model as:

$$\ln\left(N_{t+1}/N_t\right) = r + b \times N_t \tag{1}$$

where N is the average number of ants counted at each baiting station at census t, the intercept r is the population growth rate at zero density and the slope b measures density dependence. We added linear terms to this model that included rain, tree cover, sapling cover, and the interaction of each of these extrinsic drivers with N_t.

In the Gompertz model, there is a linear decrease in the log population growth rate as the natural logarithm of population size increases. This means density dependence is stronger at small population sizes and weaker as population sizes grow larger. We used a stochastic version of the Gompertz model proposed by Dennis et al. (2006):

$$\ln\left(N_{t+1}/N_t\right) = r + b \times \ln\left(N_t\right) \tag{2}$$

Here, we also added a linear combination of the extrinsic drivers and the interaction of each with $\ln(N_t)$. We fitted models using the package lme4 (Bates et al. 2014) in R (R Development Core Team 2019). All covariates were standardized.

Results

We found great variation in abundance within our transects. A Gompertz model with the extrinsic drivers was much better ranked than the Ricker model with drivers ($\Delta\mathrm{AIC}=44$). Abundance had a strong and negative effect on local population growth rates (Fig. 2). In contrast, none of the extrinsic drivers clearly affected local population growth rates and all of their coefficients included zero within their confidence intervals (Fig. 3).

Invasion fronts moved at a maximum speed of almost 53 m/year (Table 1). Two of the other fronts showed

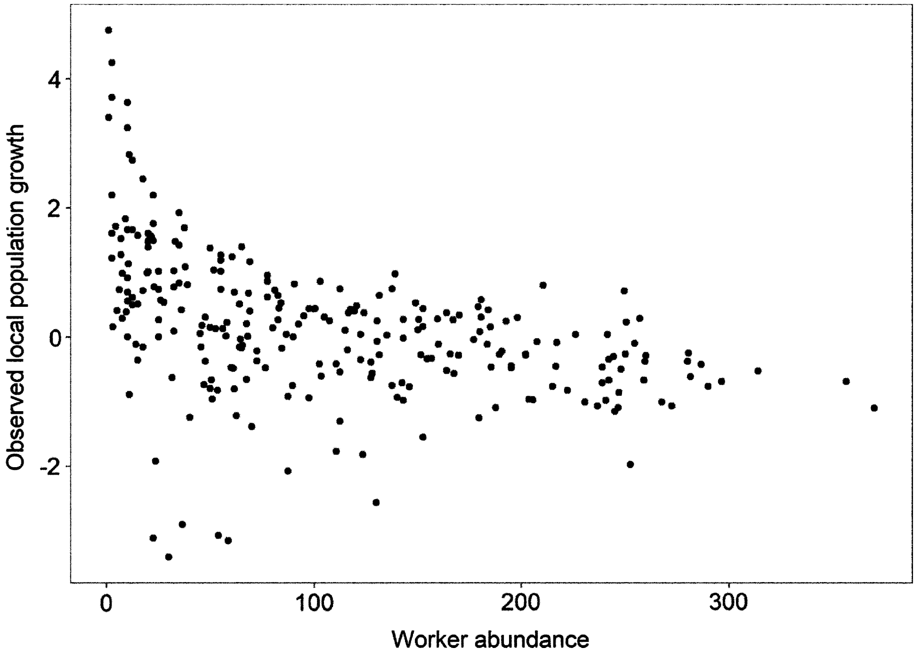

Fig. 2 Relation between the observed local population growth rates (estimated as the natural logarithm of λ, see "Methods") and worker abundance. Population growth rates tend to decrease at high density ($r=-0.43$)

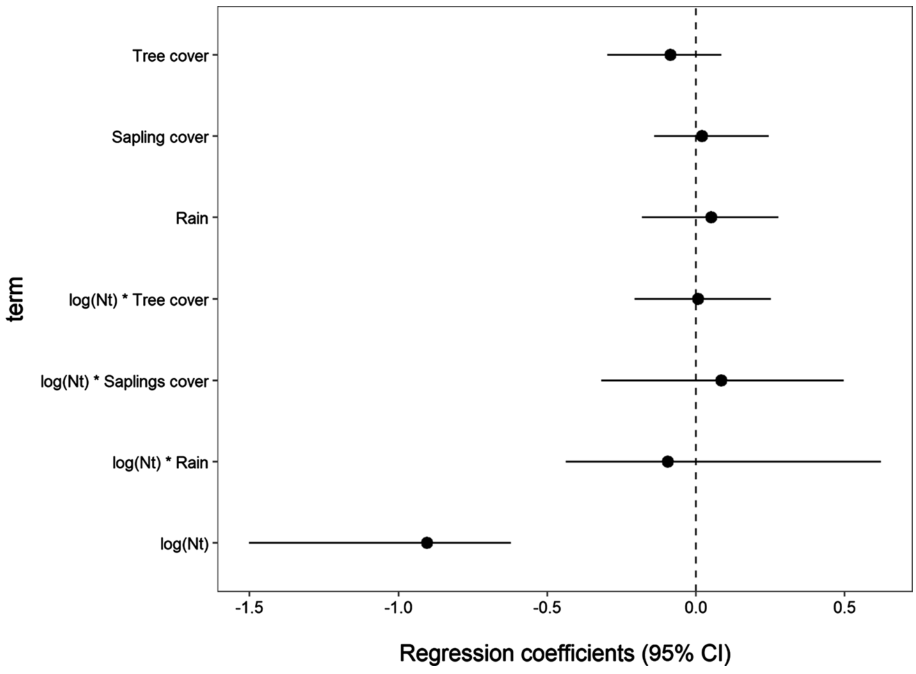

Fig. 3 Estimates of the regression coefficients for the best ranked model (Gompertz and extrinsic variables) predicting the natural log of local population growth rate of big-headed ants. The Natural logarithm of N_t (worker abundance) had a negative effect on population growth rate, whereas all other terms included zero within their confidence intervals

Table 1 Estimates of spread for different invasion fronts based on the distance-regression method

Active front	Slope	95% CI	Speed (m/year)	95% CI
North control	0.13	0.1–0.15	47.5	36.5–54
South control	0.14	0.12–0.16	52.6	43.8–61.3
Kamok	0.08	− 0.06–0.17	30.9	− 21.9–62.2
Tourism house	− 0.08	− 0.16–0.00	− 30.9	− 58.4–3.2

slightly slower rates of spread, and one (TH) retracted by 30.9 m. Estimates of invasion speed based on the spatial offset were similar to those based on the distance-regression method (NC = 54.9 ± 18.5 m/year, SC = 52.8 ± 0.6 m/year, *K* = 46.3 ± 0.5 m/year, TH = − 20.8 ± 29.5 m/year).

Transects within North Control (NC) and South Control (SC) fronts showed a high correlation in spread (Table 2), and correlation between transects at these two sites were also high suggesting synchrony in spread. In contrast, we found weak correlation among transects at Kamok (K) and the Tourism House (TH) and between these transects and NC and SC (Except for transect 7 in Kamok). When we modeled the effect of single covariates on the rate of spread (again excluding points from TH), a null model ranked best, followed by models that showed a positive association with rain ($\Delta AIC_c = 0.69$, slope = 0.03 ± 0.2), only trees ($\Delta AIC_c = 2.52$) and only saplings ($\Delta AIC_c = 2.51$).

Discussion

Although density dependence is a fundamental phenomenon of population dynamics, the role of density dependence in population growth and spread of invasive ants remains little explored. We exploited spatial variation in abundance of a spreading invasive ant to quantify the strength and direction

Table 2 Pairwise correlations to test synchrony in spread between transects

Site	NC		SC		K		TH	
Transect	1	2	3	4	5	6	7	8
1		0.93	0.78	0.91	0.81	0.47	− 0.68	0.09
2			0.89	0.92	0.91	0.6	− 0.82	0
3				0.89	0.88	0.58	− 0.58	0.58
4					0.98	0.58	− 0.88	0.09
5						0.44	− 0.94	0
6							− 0.38	0.63
7								0.33
8								

of density dependence. Our results demonstrate that abundance is the most important predictor of *Pheidole megacephala* local population growth rates at our study sites. BHA rates of spread at our sites on the other hand, were higher than other studies previously reported, and the effect of extrinsic variables on spread was weak.

In theory, there are reasons to expect positive or negative density dependence in supercolonial ants. For *Pheidole megacephala*, we found that local population growth rates declined with abundance (negative density dependence) and we did not find evidence of Allee effects at low densities. Instead, we found extremely high local population growth rates at near-zero abundances, best described by the Gompertz model. Allee effects have been reported for other invasions and researchers have suggested that positive density dependence is likely important for eusocial insects that cooperate for food and colony defense (Luque et al. 2013). However, Allee effects are probably less important for well-established supercolonies and more relevant at the initial establishment of BHA propagules into new areas or when populations fall to low abundance levels. Yet, Chang (1985) found that BHA ant colonies may thrive when starting from only a queen and ten minor workers. The higher population growth rates at low abundances we observed, compared to a simple Ricker model which would have shown comparatively lower growth rates at near-zero abundances, may explain the high rates of spread of BHA at our sites and other sites around the world. The absence of Allee effects may also facilitate establishment of BHA populations at low densities, making their invasions harder to control.

The relation of local population growth rates with abundance was not linear, and negative density dependence deaccelerated at higher abundances. Although it is difficult to identify a single mechanism that may give rise to this pattern, we suggest that the cooperative nature of supercolonial ants may weaken the disadvantages of density as density increases. For example, higher population abundance may facilitate more efficient foraging, patrolling and defense. At high abundance, invasive ants may display more aggressive behaviors or increase in body size, allowing them to overcome the resistance of native defenders (in this case, acacia ants), other prey and competitors (Sagata and Lester 2009; Wills et al. 2014). Likewise, large colonies may be better able to cope with environmental change. For instance, Kaspari and Vargo (1995) showed that queens of *Solenopsis invicta* stressed by the lack of food and water survived longer when they had more workers.

While few studies have looked at density dependence of supercolonial ants in the field, the large size of their colonies may increase the probability of negative density dependence for these species, consistent with suggestions that resource depletion may be more important for large colonies compared to small colonies (Kaspari and Byrne 1995). Large colonies are less susceptible to predation, and may be buffered more from environmental stochasticity, thus increasing the likelihood that they may deplete resources around their nests. Most evidence for negative density dependence in large colonies comes from studies of the red fire ant (*Solenopsis invicta*), another species that form supercolonies (Porter and Tschinkel 1985; Tschinkel 1988), while little support for negative density dependence was found in neotropical *Pheidole* ants that maintain small colonies (Kaspari and Byrne 1995). Luque et al. (2013), on the contrary, did not find negative density-dependent responses in Argentine ants reared in the lab. The methods we use here may help to quickly assess density dependence in other invasive ant species that show spatial variation in abundance.

The negative density dependence of *P. megacephala* observed in this study is inconsistent with observation of colony collapse reported from other systems (Cooling et al. 2011; Cooling and Hoffmann 2015; Lester and Gruber 2016). Both mathematical models we used assumed a fixed carrying capacity with ants tending to an equilibrium density. However, it is likely that carrying capacity will deteriorate over time because BHA may reduce food availability, pushing populations to lower densities, where they are more likely to collapse. Continued abundance monitoring over time, particularly at fixed points of the invasion, may help detect collapses, but if resources ahead of the invasion front are still abundant, BHA may continue to spread.

Extrinsic factors had negligible effects on local population growth rates of BHA. Our study design included only *A. drepanolobium* habitats, which constrains environmental variation. Nevertheless, at a finer scale, higher densities of trees and saplings (sources of extrafloral nectar) did not have an impact on local population growth rates, in contrast to studies of other supercolonial ants that emphasize the importance of carbohydrates in fueling the spread of ant invasions (Holway et al. 2002; Rowles and Silverman 2009; Wittman et al. 2018). In Australia, abundant carbohydrate supply from honeydew insects and extrafloral nectar has been shown to increase BHA abundance (Lach et al. 2009; Gaigher et al. 2011), but it is not well understood how these increased densities affect rates of spread. Unlike native *Acacia* ants, BHA do not induce extrafloral nectar production and nectaries dry up on trees behind the invasion front (Riginos et al 2015). This may explain the absence of any effects of tree and/or sapling density on BHA abundance. However, many of our datapoints were taken at the invasion front where BHA abundances are low and trees still offer abundant EFN, yet we still did not detect interactions between ant abundance and tree or sapling density. Thus, for supercolonial species that have multiple queens and show high densities, intrinsic factors such as density may play a more important role than climate or resources relative to other ant species, although we acknowledge that other extrinsic factors not considered in our study may be also important.

The apparent lack of importance of extrinsic factors, particularly carbohydrate-provisioning trees, suggests BHA are plastic and resilient to environmental change. Plasticity is a feature shared by many successful invaders (Forsman 2014; González-Suárez et al. 2015), and can be particularly important for eusocial insects (Manfredini et al. 2019). Argentine ants, for instance, have transitioned from a protein-rich diet to a sugar-rich diet in many parts of their invaded range (Shik and Silverman 2013; Hu et al. 2017). But *Pheidole* can also adjust their body size within castes or the caste ratio to adjust to changes in competition or resources (Passera et al. 1996; Wills et al. 2014), another strategy to potentially buffer their colonies from environmental variation.

The rates of BHA spread we observed on Ol Pejeta Conservancy were comparable to rates of spread recorded elsewhere for other invasive ants (Holway et al. 2002). We only found one study describing spread of BHA in monsoonal Australia, averaging 22 m in 17 months, considerably lower than the speed of the invasion reported here. In our study, spread was particularly synchronous between North and South Control, both of which we believe originated from the largest human settlement in the ranch. Distances from these two fronts and a third front not described here to the center of the human settlement are very similar (range 2.29–3.1 km, mean 2.76 km ± 0.3) suggesting isotropic spread, even though some of the areas behind the fronts were shrubland dominated by *Euclea divinorum* and open grassland, indicating that vegetation type may have little influence on rates of spread. At the regional scale, assisted dispersal by humans is likely a major factor affecting BHA expansion, as we found invasion fronts in Laikipia generally associated with human settlements.

In sum, our research shows that population dynamics of big-headed ants is best predicted by past abundance, with high local population growth rates at low abundance and low local population growth rates at high abundance. Despite the common expectation that eusocial animals experience Allee effects at low densities, we did not detect lower recruitment at low abundance, which may facilitate the establishment of BHA propagules in uninvaded areas. High local population growth rates may cause the rapid spread of big-headed ants, particularly given that queens and their workers move only a few meters from their natal nests to found new nests. We found little evidence for the effects of our measured extrinsic factors, particularly acacia trees, a major source of carbohydrates, on local population growth rates or spread. We believe that these expansive colonies may be more resilient to environmental factors, than other, smaller colonies. Further, the ability to cope with environmental variation is a feature common to many successful invaders that are hard to eradicate, suggesting that BHA pose a major threat to a key ant-acacia mutualism in East Africa.

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Author contribution statement AGP formulated the idea; AGP, TMP, JRG and CR developed the methodology; AGP and NJM conducted fieldwork; AGP analyzed the data; AGP, JRG, CR and TMP wrote the manuscript.

References

Abbott K (2005) Supercolonies of the invasive yellow crazy ant Anoplolepis gracilipes, on an oceanic island: forager activity patterns, density and biomass. Insectes soc 52:266–273

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7

Beardsley J Jr, Su T, McEwen F, Gerling D (1982) Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and pineapple mealybug wilt disease in Hawaii. Proc Hawaiian Entomol Soc 24:51–67

Brook BW, Bradshaw CJA (2006) Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87:1445–1451. https://doi.org/10.1890/0012-9658(2006)87[1445:Soefdd]2.0.Co;2

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Chang V (1985) Colony revival, and notes on rearing and life history of the big-headed ant. Proc Hawaiian Entomol Soc 25:53–58

Clements CF, Drake JM, Jason IG, Ozgul A (2015) Factors influencing the detectability of early warning signals of population collapse. Am Nat 186:50–58. https://doi.org/10.1086/681573

Cooling M, Hoffmann B (2015) Here today, gone tomorrow: declines and local extinctions of invasive ant populations in the absence of intervention. Biol Invasions 17:3351–3357

Cooling M, Hartley S, Sim DA, Lester PJ (2011) The widespread collapse of an invasive species: Argentine ants (*Linepithema humile*) in New Zealand. Biol Lett 8:430–433

Dennis B, Ponciano JM, Lele SR, Taper ML, Staples DF (2006) Estimating density dependence, process noise, and observation error. Ecol Monogr 76:323–341

Drake JM, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biol Invasions 8:365–375

Fabricius JC (1793) Entomologia systematica emendata et aucta. Secundum Classes, Ordines, Genera, Species, Adjectis Synonimis, Locis, Observationibus Descriptionibus. Copenhaguen, 519 pp

Forsman A (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. Proc Nat Acad Sci 111:302–307

Gaigher R, Samways MJ, Henwood J, Jolliffe K (2011) Impact of a mutualism between an invasive ant and honeydew-producing insects on a functionally important tree on a tropical island. Biol Invasions 13:1717–1721. https://doi.org/10.1007/s10530-010-9934-1

Gibb H et al (2017) A global database of ant species abundances. Ecology 98:883–884. https://doi.org/10.1002/ecy.1682

Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading populations. Ecography 33:809–817

Goheen JR, Palmer TM (2010) Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. Curr Biol 20:1768–1772

González-Suárez M, Bacher S, Jeschke JM (2015) Intraspecific trait variation is correlated with establishment success of alien mammals. Am Nat 185:737–746. https://doi.org/10.1086/681105

Hastings A et al (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101. https://doi.org/10.1111/j.1461-0248.2004.00687.x

Hodgson EE, Essington TE, Halpern BS (2017) Density dependence governs when population responses to multiple stressors are magnified or mitigated. Ecology 98:2673–2683

Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. NeoBiota 31:1

Hoffmann BD, Parr CL (2008) An invasion revisited: the African big-headed ant (*Pheidole megacephala*) in northern Australia. Biol Invasions 10:1171–1181

Hoffmann BD, Andersen AN, Hill GJ (1999) Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. Oecologia 120:595–604

Hoffmann BD, Luque GM, Bellard C, Holmes ND, Donlan CJ (2016) Improving invasive ant eradication as a conservation tool: a review. Biol Cons 198:37–49. https://doi.org/10.1016/j.biocon.2016.03.036

Holway AD (1998) Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206–212. https://doi.org/10.1007/s004420050509

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. Annu Rev Ecol Syst 33:181–233. https://doi.org/10.1146/annurev.ecolysis.33.010802.150444

Hu Y et al (2017) By their own devices: invasive Argentine ants have shifted diet without clear aid from symbiotic microbes. Mol Ecol 26:1608–1630. https://doi.org/10.1111/mec.13991

Kaspari M, Byrne MM (1995) Caste allocation in litter Pheidole: lessons from plant defense theory. Behav Ecol Sociobiol 37:255–263

Kaspari M, Vargo E (1995) Does colony size buffer environmental variation? Bergmann's rule and social insects. Am Nat 145:610–632

Lach L, Hobbs RJ, Majer JD (2009) Herbivory-induced extrafloral nectar increases native and invasive ant worker survival. Popul Ecol 51:237–243

Lester PJ, Gruber MA (2016) Booms, busts and population collapses in invasive ants. Biol invasions 18:3091–3101

Leung B, Drake JM, Lodge DM (2004) Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85:1651–1660

Lewis MA, Kareiva P (1993) Allee dynamics and the spread of invading organisms. Theor Popul Biol 43:141–158. https://doi.org/10.1006/tpbi.1993.1007

Loke PY, Lee C-Y (2004) Foraging behavior of field populations of the big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). Sociobiology 43:211–219

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database, vol 12. Invasive Species Specialist Group, Auckland

Luque GM, Giraud T, Courchamp F (2013) Allee effects in ants. J Anim Ecol 82:956–965. https://doi.org/10.1111/1365-2656.12091

Manfredini F, Arbetman M, Toth AL (2019) A potential role for phenotypic plasticity in invasions and declines of social insects. Front Ecol Evol. https://doi.org/10.3389/fevo.2019.00375

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Massachusetts

O'Dowd DJ, Green PT, Lake PS (2003) Invasional 'meltdown'on an oceanic island. Ecol Lett 6:812–817

Palmer TM, Young TP, Stanton ML, Wenk E (2000) Short-term dynamics of an acacia ant community in Laikipia. Kenya Oecologia 123:425–435

Palmer TM, Brody AK (2007) Mutualism as reciprocal exploitation: African plant-ants defend foliar but not reproductive structures. Ecology 88:3004–3011

Passera L, Roncin E, Kaufmann B, Keller L (1996) Increased soldier production in ant colonies exposed to intraspecific competition. Nature 379:630–631

Porter SD, Tschinkel WR (1985) Fire ant polymorphism: the ergonomics of brood production. Behav Ecol Sociobiol 16:323–336

R Development Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Riginos C, Karande MA, Rubenstein DI, Palmer TM (2015) Disruption of a protective ant–plant mutualism by an invasive ant increases elephant damage to savanna trees. Ecology 96:654–661. https://doi.org/10.1890/14-1348.1

Rowles AD, Silverman J (2009) Carbohydrate supply limits invasion of natural communities by Argentine ants. Oecologia 161:161–171

Sagata K, Lester PJ (2009) Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant Linepithema humile. J Appl Ecol 46:19–27

Shik JZ, Silverman J (2013) Towards a nutritional ecology of invasive establishment: aphid mutualists provide better fuel for incipient Argentine ant colonies than insect prey. Biol Invasions 15:829–836

Sullivan LL, Li B, Miller TEX, Neubert MG, Shaw AK (2017) Density dependence in demography and dispersal generates fluctuating invasion speeds. Proc Natl Acad Sci 114:5053–5058. https://doi.org/10.1073/pnas.1618744114

Tamashiro RA, Milligan PD, Palmer TM (2019) Left out in the cold: temperature-dependence of defense in an African ant–plant mutualism. Ecology 100:e02712. https://doi.org/10.1002/ecy.2712

Tartally A, Antonova V, Espadaler X, Csősz S, Czechowski W (2016) Collapse of the invasive garden ant *Lasius neglectus*, populations in four European countries. Biol Invasions 18:3127–3131

Tobin PC, Berec L, Liebhold AM (2011) Exploiting Allee effects for managing biological invasions. Ecol Lett 14:615–624

Torres JA, Snelling RR (1997) Biogeography of Puerto Rican ants: a non-equilibrium case? Biodivers Conserv 6:1103–1121

Tschinkel WR (1988) Colony growth and the ontogeny of worker polymorphism in the fire ant *Solenopsis invicta*. Behav Ecol Sociobiol 22:103–115

Vanderwoude C, Lobry De Bruyn LA, House APN (2000) Response of an open-forest ant community to invasion by the introduced ant *Pheidole megacephala*. Austral Ecol 25:253–259. https://doi.org/10.1046/j.1442-9993.2000.01021.x

Visitacao JM (2011) Multi-species interactions in African ant-acacias. Harvard University, Cambridge

Wetterer JK (2012) Worldwide spread of the African big-headed ant, Pheidole megacephala (Hymenoptera: Formicidae). Myrmecol News 17:51–62

Wetterer JK, Espadaler X, Wetterer AL, Aguin-Pombo D, Franquinho-Aguiar AM (2006) Long-term impact of exotic ants on the native ants of Madeira. Ecological Entomology 31:358–368

Wilder SM, Holway DA, Suarez AV, LeBrun EG, Eubanks MD (2011) Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. Proc Natl Acad Sci 108:20639–20644. https://doi.org/10.1073/pnas.1115263108

Wills BD, Moreau CS, Wray BD, Hoffmann BD, Suarez AV (2014) Body size variation and caste ratios in geographically distinct populations of the invasive big-headed ant, Pheidole megacephala (Hymenoptera: Formicidae). Biol J Linn Soc 113:423–438. https://doi.org/10.1111/bij.12386

Wilson EO (2003) Pheidole in the New World: a dominant, hyperdiverse ant genus, vol 1. Harvard University Press, Cambridge, Massachusetts, USA

Wittman SE, O'Dowd DJ, Green PT (2018) Carbohydrate supply drives colony size, aggression, and impacts of an invasive ant. Ecosphere 9:e02403. https://doi.org/10.1002/ecs2.2403

Zarada K, Drake JM (2017) Time to extinction in deteriorating environments. Theor Ecol 10:65–71