Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2013 doi: 10.1111/1365-2656.12036

Colony life history and lifetime reproductive success of red harvester ant colonies

Krista K. Ingram[1], Anna Pilko[2], Jeffrey Heer[3] and Deborah M. Gordon[2]*

[1]*Department of Biology, Colgate University, Hamilton, NY 13346, USA;* [2]*Department of Biology, Stanford University, Stanford, CA 94305-5020, USA; and* [3]*Department of Computer Science, Stanford University, Stanford, CA 94305-5020, USA*

Summary

1. We estimate colony reproductive success, in numbers of offspring colonies arising from a colony's daughter queens, of colonies of the red harvester ant, *Pogonomyrmex barbatus*.

2. A measure of lifetime reproductive success is essential to understand the relation of ecological factors, phenotype and fitness in a natural population. This was possible for the first time in a natural population of ant colonies using data from long-term study of a population of colonies in south-eastern Arizona, for which ages of all colonies are known from census data collected since 1985.

3. Parentage analyses of microsatellite data from 5 highly polymorphic loci were used to assign offspring colonies to maternal parent colonies in a population of about 265 colonies, ages 1–28 years, sampled in 2010.

4. The estimated population growth rate R_o was 1·69 and generation time was 7·8 years. There was considerable variation among colonies in reproductive success: of 199 possible parent colonies, only 49 (˜ 25%) had offspring colonies on the site. The mean number of offspring colonies per maternal parent colony was 2·94 and ranged from 1 to 8. A parent was identified for the queen of 146 of 247 offspring colonies. There was no evidence for reproductive senescence; fecundity was about the same throughout the 25–30 year lifespan of a colony.

5. There were no trends in the distance or direction of the dispersal of an offspring relative to its maternal parent colony. There was no relationship between the number of gynes produced by a colony in 1 year and the number of offspring colonies subsequently founded by its daughter reproductive females.

6. The results provide the first estimate of a life table for a population of ant colonies and the first estimate of the female component of colony lifetime reproductive success. The results suggest that commonly used measures of reproductive output may not be correlated with realized reproductive success. This is the starting point for future investigation asking whether variation in reproductive success is related to phenotypic variation among colonies in behavioural and ecological traits.

Key-words: ant colony population, demography, parentage analysis, microsatellites

Introduction

The demography and spatial ecology of a population depend on the basic parameters of life history: when individuals reproduce, how many offspring they have and how offspring disperse. Measures of these parameters are needed to estimate individual fitness. Ecological factors act on phenotypic variation to produce variation in fitness; to investigate this requires a measure of individual reproductive success (Kingsolver *et al.* 2001; Metcalf & Pavard 2007). For long-lived animals, such measures must be based on long-term data tracking known individuals through their lifetimes. Long-term studies in a few vertebrate animal populations have been able to link phenotypic variation and reproductive success (e.g. Altmann 1991; Stopher *et al.* 2008; Frere *et al.* 2010).

For clonal organisms (Damman & Cain 1998; Albright *et al.* 2010; Takahashi *et al.* 2011) or colonial organisms such as social insects, measures of individual fitness must

*Correspondence author. E–mail: dmgordon@stanford.edu

take into account reproduction at more than one level. Here we investigate the life history of ant colonies, organisms that reproduce as a colony of closely related individuals. Ants are extremely abundant, diverse and crucial to terrestrial communities everywhere on Earth. Yet we know little about colony fecundity and population demography in this ubiquitous taxon, and even less about colony lifetime reproductive success. Empirical investigation of the evolution of ant colony behaviour and ecology in natural populations has been limited by a lack of basic knowledge about the population biology and life history of colonies. Measures of colony reproductive success are needed to link phenotypic variation with variation in colony reproductive success. Such studies will make it possible to learn how natural selection is shaping colony organization across the enormous ecological diversity of ant species.

In populations of ants, the colony can be considered a reproductive individual. In harvester ants, mated reproductive females, called 'queens', produce new male reproductives and female reproductives, called 'gynes', as well as the sterile workers that help to raise the reproductives. Males and gynes mate with the reproductives of other colonies in the population. A newly mated gyne then becomes the founding queen of a new colony. The colonies that produced that founding queen and her mates can thus be considered the parents of the offspring colony she produces. To date it has been very difficult to determine, for any ant species, at what age a colony produces offspring colonies, how far from the parent colony an offspring colony is founded, and the lifetime reproductive success of a single colony. Long-term data are needed to determine colony age. In addition, offspring colonies are not easily identified in those ant species in which males and gynes mate in a population-wide aggregation, from which the newly mated queens disperse to found new colonies.

The quantitative study of ant population genetics has tackled these questions, beginning with the pioneering work of Pamilo and others on red wood ants (*Formica rufa* group) (Pamilo 1981; Goropahnaya, Seppa & Pamilo 2001; Sundström, Seppä & Pamilo 2005). The technological innovations of the past 15 years have led to an explosion of empirical work on social insect evolution (Crozier & Pamilo 1996; Ross 2001). Measures of relatedness and genetic variation have been used to examine mating systems (e.g. Hammond, Bourke & Bruford 2001; Fournier, Aron & Milinkovitch 2002; Trontti *et al.* 2007; Pearcy, Goodisman & Keller 2011; Thurin *et al.* 2011), inbreeding and population structure (e.g. Sundström 1993; Chapuisat & Keller 1999; Bargum, Helantera & Sundstrom 2007), and queen number (e.g. Ross *et al.* 1997; Chapuisat, Bocherens & Rosset 2004; Qian *et al.* 2011).

Studies of population genetic structure have made it possible to infer dispersal distances in many species (e.g. Pamilo, Chautems & Cherix 1992; Chapuisat, Goudet & Keller 1997; Pedersen & Boomsma 1999; Ingram & Gordon 2003; Sundström, Keller & Chapuisat 2003; Hardy, Pearcy & Aron 2008). For ants and other social insects, it has been possible to measure queen longevity and the age at which queens begin to produce reproductives (Jervis *et al.* 2001; Thorne, Breisch & Haverty 2002; Leibig & Poethke 2004; Schrempf *et al.* 2005). However, these measures do not provide all the information needed to produce a life table, such as the ages at which particular colonies produce offspring colonies, and they do not elucidate the variation among colonies in realized reproductive success, in numbers of offspring colonies.

To date there have been no measures of the lifetime reproductive success of ant colonies. For species that reproduce through the dispersal of winged reproductives, rather than budding, the best measure so far is reproductive output, in numbers of winged reproductives that a colony produces (e.g. MacKay 1985; Tschinkel 1987; Keller & Passera 1990) or that it sends out to a mating flight (e.g. Gordon & Wagner 1997; Wagner & Gordon 1999; Helms Cahan & Julian 2010). As theory predicts (e.g. Nonacs 1993; Tsuji & Tsuji 1996), reproductive output in ants depends on colony age and size (e.g. Brian, Clarke & Jones 1981; Tschinkel 1993; Beshers & Traniello 1994; Schmidt *et al.* 2011) and on ecological conditions such as intra- or interspecific density (e.g. Foitzik, Strätz & Heinze 2003; Molet, Van Baalen & Peeters 2008; Foitzik, Achenbach & Brandt 2009; Boulay *et al.* 2010) or nest site availability (Frederickson 2006). But as Keller (1993) points out, reproductive output, in numbers of reproductives, is not a measure of realized reproductive success, since not all reproductives mate and not all mated queens survive to found new colonies. Some studies have used some measure of colony size or numbers of sterile workers produced as a proxy for reproductive success, but to test the validity of such proxy measures, an independent estimate of reproductive success is needed.

Here we estimate the reproductive success, in numbers of offspring colonies arising from a colony's daughter queens, of colonies of known age of the red harvester ant (*Pogonomyrmex barbatus*). We use the data from our long-term study at a 10 hectare site, located in the midst of a large, contiguous area of suitable habitat for this species, near Rodeo, New Mexico, USA. The long-term study has monitored about 300 individual colonies each year since 1985, so that the ages of all colonies are known. A single queen mates many times and, if successful, founds a new colony that survives for about 25 years (Gordon & Kulig 1998). A colony begins to produce other colonies when it is 4–5 years old (Gordon 1995), by sending reproductives each year to a single, annual mating aggregation.

This population of *P. barbatus*, like many in this genus in the south-western US, has a dependent-lineage genetic system (Volny & Gordon 2002a; Helms Cahan & Keller 2003). There are two interbreeding but genetically independent lineages. Matings between a queen and a male of the same lineage lead to reproductive female offspring;

matings between a queen and a male of the alternate lineage lead to sterile worker offspring, and males are produced from haploid, unfertilized eggs laid by the queen. Thus, a queen must mate with at least two males, one of each lineage, to found a viable colony with both workers and reproductives. Here we measure reproductive success as the number of a queen's daughter reproductives that successfully founded new colonies, without evaluating the contributions of males to daughter colonies. We used our results, which identified mother-daughter pairs of colonies, to consider how a colony's fecundity depends on its age. We examined the spatial dispersion of colonies, and whether or not there are year-to-year differences in dispersal distance and direction. For some of the parent colonies, we were able to compare the results on numbers of offspring, a measure of realized reproductive success, with previous results on numbers of winged reproductives, a measure of reproductive output, for the same colonies.

Materials and methods

COLLECTION OF SAMPLES

A sample of 20 workers was collected in August 2010 from each of 265 colonies at a long-term study site near Rodeo, New Mexico (31 °52′16·36″N 109 ° 2′22·34″W). Ants were collected as they entered or left the nest entrance, so that colony identity was certain. Ages of the colonies were known from a census conducted each year since 1985, including some colonies that were censused since 1981. Colonies ranged in age from 1 to 28 years old. Details of census methods are given in Gordon & Kulig (1996). Each year all new colonies, founded the previous year and thus 1 year-old, are added to the census, and all deaths of colonies are noted. The total number of colonies on the site each year is around 300. The site is an arbitrarily selected rectangular area of about 10 hectares, 250 × 375 metres, surrounded by similar desert chapparal habitat that extends for tens of kilometres on all sides, with some roads and a few buildings. On the day of the mating aggregation, there is always at least one aggregation on the 10 hectare site; it appears that aggregations form every 200–400 metres. Newly mated gynes do not enter existing colonies, and after dispersing from the mating flight, while searching for a new nest site, they are frequently attacked by the workers of conspecific colonies.

GENETIC ANALYSIS

Sampled workers were frozen in liquid nitrogen and then stored in −80 °C. DNA was extracted from individual ants that were pulverized and boiled in 200 µl of 10% Chelex®100 (Bio-Rad) solution for 15 min. Samples were centrifuged for 1 min and the supernatant was stored at −20 °C for later use as a template for PCR amplification.

We genotyped 20 workers per nest from a total of 265 colonies at 5 microsatellite loci: Pb5, Pb6, Pb7, Pb8, Pb9 (Volny & Gordon 2002b).The primer sequences were redesigned to match the targeted flanking regions and modified with an M13 tag on the 5′ end of the forward primers and a 7bp pigtail sequence (GTGTCTT) on the 5′ end of the reverse primers (Table S1).

PCR amplifications were performed in a 2 µl final volume containing 5 ng of genomic DNA, 0·3 pmol/µl of M13-tailed forward primer and 'pig-tailed 'reverse primer, 0·2 µl 10 × buffer, 0·1 µl 50 mm $MgCl_2$, 0·1 µl 2 mm dNTP, 0·04 µl DMSO 100%, 0·02 µl 0·5 U *Taq* DNA polymerase (Qiagen) and 1·54 µl water. Reactions were performed via a 'touchdown' PCR, with an initial 5 min of denaturation at 95 °C; 14 cycles at 94 °C for 20 s, annealing at 65 °C for 20 s (0·5 °C decrease in each cycle) and extension at 72 °C for 45 s; 35 cycles at 94 °C for 20 s, 58 °C for 20 s and 72 °C for 45 s; and final extension of 10 min at 72 °C. Amplified fragments were analysed on an ABI 3730 Genetic Analyzer (Applied Biosystems, Foster City, CA) and sized using GeneMapper 4·1 and GeneScan 400 HD ROX Size Standard (Applied Biosystems, Foster City, CA). All allele calls were manually verified. No multiplexing was attempted.

Parentage exclusion probabilities for each locus were calculated in COANCESTRY (Wang 2010) to evaluate the suitability of the locus for relatedness estimation.

Genetic diversity (F_{st}, F_{is}, F_{it}) was estimated from allele frequencies as in Weir and Cockerham (1984) using GENEPOP [vs. 4·1·0; (Rousset 2008)] with colonies entered as populations. G_{0st} (Hedrick 2005) and D_{est} (Jost 2008) were also estimated to evaluate population genetic differentiation using SMOGD: Software for the Measurement of Genetic Diversity online vs. 1·2·5 (Crawford 2010).

In the dependent-lineage system in *P.barbatus*, the mating of a male and female from the same lineage produces female reproductives, or gynes, so a daughter queen is of the same lineage as her mother. Thus, we were able to increase the specificity of our analysis by testing for parent-offspring pairs separately within each lineage. We determined lineage as mitochondrial haplotypes using one worker from each nest. Universal insect *cox*1 primers modified for *P.barbatus* (forward C1-j-1751 (Pb) C1-N-2191 (Pb) 5′) were used to amplify the 433bp portion of mitochondrial gene *cox*1 as in Helms Cahan & Keller (2003). All reactions were run in 25 µl volume with the following PCR conditions: 94 °C for 4 min followed by 35 cycles of 94 °C for 30 s, 48 °C for 30 s, and 72 °C for 90 s paused and completed by 72 °C for 6 min. PCR products were purified and run on an ABI 3100 automated DNA sequencer (Applied Biosystems). Both forward and reverse strands were sequenced using fluorescent dyes. The DNA haplotypes were classified to one of the two lineages (J1 and J2) using the phylogenetically informative positions of unique *cox*1 sequence variants that were compared with previously defined J1 or J2 clades (Helms Cahan & Keller 2003; Anderson *et al.* 2011) using a neighbour joining topology in MEGA 5·0 software (Tamura *et al.* 2011).

ASSIGNMENT POWER AND FALSE EXCLUSION FACTORS

For each microsatellite locus, we calculated for each lineage the exclusion probabilities (Table S1) that an individual taken at random from the population is excluded as a parent of an offspring in three scenarios: P_{E1} when one parent is known, P_{E2} when no parents are known and P_{E3} when a pair of individuals chosen at random from the population are excluded as both parents of an offspring individual (Wang 2010). These probabilities are calculated as follows

$$P_{E1} = 1 - 2a_2 - 2a_2^2 + a3 + 2a_4 - 3a_5 + 3a_2a_3 \qquad \text{eqn 1}$$

one parent known;

$$P_{E2} = 1 - 4a_2 + 2a_2^2 + 4a_3 - 3a_4, \quad \text{eqn 2}$$

no parents known;

$$p_{E3} = 1 - 8a_2^2 + 8a_2a_3 + 2a_3^2 + 4a_4 - 4a_5 - 3a_5, \quad \text{eqn 3}$$

pair of individuals chosen at random.

The average probability that a random individual unrelated to the true parents is excluded as a parent of the offspring is $a_n = \sum_{i-1}^{k} p_i^n$ for a number of offspring (n) and number of alleles (k) and frequency p_i of allele i at a locus (Wang 2007).

IDENTIFICATION OF PARENT-OFFSPRING COLONY PAIRS

To identify parent-offspring colony pairs within each lineage, we first used the worker genotypes within a colony to infer the genotype of that colony's queen. Individual workers for which fewer than three of five loci amplified were not included in the analysis. We reconstructed putative queen genotypes based on observed worker genotypes (mean $n = 18$ workers from each colony) in COLONY2 using the full likelihood method with estimated allele frequencies (Wang 2004; Wang & Santure 2009). When inferring the genotype of the queen that produced a group of workers, COLONY2 provides an estimate of the probability that all the workers have the same parent and thus come from the same colony. There were three colonies for which the probability that some workers came from a different colony was greater than 0·05; these were excluded from further analysis. In 20 of the remaining 262 colonies, two plausible queen genotypes could be inferred, and the genotype with the highest posterior probability greater than 95% was chosen. We used MATESOFT (Moilanen, Sundström & Pedersen 2004) to calculate that the power of our data set to correctly infer queen genotypes from worker genotypes was 0·999.

We then used the inferred queen's genotype to determine which offspring queens were daughters of which parent queens. We tested for parent-offspring pairs within each lineage, because in the dependent-lineage system in *P.barbatus*, a daughter queen is of the same lineage as her mother. As in other dependent-lineage populations of harvester ants (Anderson *et al.* 2011), J1 is the rare lineage (90 colonies) and J2 the more common lineage (172 colonies) (Gordon *et al.* in review); there were 69 J1 and 130 J2 colonies considered as possible parents. Colonies usually begin to send winged reproductives to the annual mating flight at age 5 years and occasionally at age 4 years (Gordon 1995), so we chose as possible parents for each year those colonies 4 years and older, old enough to be parents. Within each lineage, we considered as possible parent colonies for the 1 year-old offspring colonies in a given year, all colonies that were at least 4 years old the previous year when the offspring colonies' founding queens mated. Within each lineage, all colonies were grouped by age in intervals of 4 years, overlapping each interval by 1 year, so as to avoid excluding any possible parent colony; the oldest possible parent colonies in one interval were also included as the youngest possible parent colonies of the next. There were 7 such 4 year groupings for the J1 colonies, and 10 for the J2 colonies; the number of groupings was larger for J2 because all the oldest colonies were of the J2 lineage.

Parentage analysis was performed using a maximum-likelihood approach implemented in the program COLONY2. We considered parentages assigned at the 95% confidence level based on the allele frequencies within each lineage. For each time interval we ran 3 analyses using different random seeds. The results from the COLONY2 program list all relationships that were not excluded as true relationships with a 95% confidence level. We then applied a more stringent criterion by accepting only the relationships assigned a posterior probability of 0·8 or higher that were identified in all three runs (as in Walling *et al.* 2010). This may underestimate number of offspring per colony, but allows us to minimize false positive parentage assessments.

ESTIMATION OF LIFE-HISTORY AND DISPERSAL VALUES

To determine the distance between parent and offspring colonies, we found the Euclidean distance between the locations of the parent and offspring colony. As some colonies move their nests (Gordon 1992), we used the parent's location in the year of the mating flight in which the offspring colony was founded, and the offspring location the earliest year it was mapped. To test whether dispersal distance differed among years, we used a one-way ANOVA to test whether or not there was an effect of year on the distance between parent and offspring colonies. To test whether some colonies were likely to produce daughter queens that disperse farther than those of other colonies, we used a one-way ANOVA to test for an effect of the parent colony's identity on dispersal distance.

To evaluate whether or not the direction of dispersal is random, we compared the observed distribution to a statistical model that assumes random dispersal. Our model calculated the probability of finding an offspring colony in a given angular sector given the location of its parent colony. To construct the model, we first calculated the convex hull, or minimal enclosing convex polygon, for all colonies observed on the site. Then for each offspring colony we found its parent, and subdivided the convex hull into eight angular sectors centred at the parent. We computed a probability distribution over these eight sectors or directions by normalizing the 2D sector areas. Finally, we summed the per-colony distributions for each parent-offspring pair to calculate the expected counts for each sector for all pairs. To determine whether or not the model provides a good fit to the data, we subtracted the expected from the observed values and examined whether or not the resulting residuals were normally distributed, using a Shapiro–Wilk test (Shapiro and Wilk 1965). In addition, we tested for isolation by distance, the correlation between the Euclidean genetic and geographical distances between each pair of nests, using a Mantel test with 9,999 permutations (GenAlEx, Peakall & Smouse 2006).

We constructed an estimated composite life table using mortality data from the annual census of the population and, as a measure of fecundity, the number of offspring colonies for parents of a given age from this study. Data on mortality were the number of colonies of a given age that died in three transitions from 1992 to 1993 (shown in Gordon & Kulig 1998), 1999 to 2000 and from 2009 to 2010. These intervals were chosen to be as equally spaced as possible, with the 1992–1993 interval as the earliest one with sufficient colonies of known age old enough to die, based on observations that began in 1981. Colonies aged 26 or older in 2010 were grouped together because these were estimated to be mature, at least 5 years old, when the census began in 1985, and thus could be older.

We adjusted our estimate of age-specific fecundity (m_x) to correct for the 101 of 247 offspring for which we could not assign a parent. Because there was no apparent trend in age-specific fecundity (Fig. 1, S3), we assumed that offspring whose parents were not identified were equally likely to have a parent of any age. We estimated the probability of having offspring in each age class whose parents were not identified (101 offspring without a parent identified and/or 22 age classes of possible parents aged 4 or older). To estimate the overall age-specific fecundity, we then incremented m_x equally for all ages by adding this proportion to the age-specific fecundity for each year,

We calculated population growth rate and generation time in two ways, by constructing an age-structured population matrix, and also using the instantaneous rates calculated directly from the life table. The estimates of age-specific survivorship l_x and fecundity m_x were used to parameterize a post-breeding transition matrix model (Caswell 2001), with age classes 1 to 26, assuming that females cannot begin to produce winged reproductives until they are 4 years old. Assuming a stable age distribution, we analysed the projection matrix using the Microsoft Excel Add-In POPTOOLS (Hood 2010) to calculate the population growth rate (λ), annual population growth rate (r), net reproductive rate (R_0) and generation time (T). The value of (λ) was determined by finding the dominant eigenvalue of the age-structured projection matrix. We used this model to calculate generation time (T) as $R_o = \lambda^T$ where $\lambda = e^{rT}$; this is an extrapolation of the time step between successive generations of the age-structured population. We also calculated the generation time (T) directly from the life table, not taking into account age structure (May 1976); this is the mean generation time for a cohort.

To display the age distribution of parents, we found the proportion of colonies of each age for which offspring were identified. We calculated this proportion as the number of offspring identified for colonies of each age, divided by the number of times that colonies of that age were included in a test as possible parents.

We compared reproductive output in 1 year with our estimate of lifetime reproductive success. Previous work suggested that reproductive output may be correlated from 1 year to the next (Wagner & Gordon 1999). Very few offspring colonies are produced in any given year that a comparison between reproductive output of a group of colonies in 1 year and the small number of offspring colonies produced by that group of colonies only in that year would not be meaningful. We compared the number of gynes produced in 29 colonies for which winged reproductive numbers were measured in 1997 (Wagner & Gordon 1999) with the number of offspring colonies ever founded by daughter reproductives of those colonies. We used Spearmann's rank correlation test to test for a correlation between the number of daughter reproductives produced by a colony in 1997 and the number of offspring colonies ever founded any time until 2010 by its daughter reproductives.

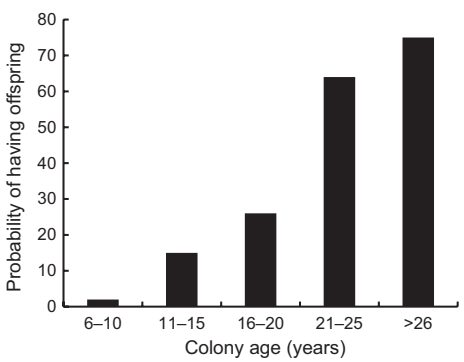


Fig. 1. Probability of having offspring, by colony age. Each bar shows the proportion of colonies of the indicated age class that had any offspring colonies founded by daughter reproductives.

Results

HETEROZYGOSITY OF LOCI

Genotypes were determined at five microsatellite loci for 4824 individuals. All five loci exhibited high genetic diversity. The average number of alleles per locus was 26 and ranged from 16 to 35 with a combined expected heterozygosity of 0·82. In dependent-lineage populations (Helms Cahan *et al*. 2002; Julian *et al*. 2002; Volny & Gordon 2002b; Helms Cahan & Keller 2003), all workers are interlineage hybrids, so the observed level of heterozygosity exceeds the level expected from the overall worker allele frequencies. All loci exhibited an excess of heterozygosity with F_{is} values ranging from −0·06 to −0·47 (p-values <0·05; Table S2). The slightly lower heterozygosity level found in locus Pb6 could be due to the relatively higher frequency (0·024 and 0·011 for J1 and J2 respectively) of null alleles, or amplification artefacts that might have altered the true allele frequencies at this locus.

PROBABILITY OF CORRECTLY IDENTIFYING PARENTS

The accuracy of parentage assignment algorithms depends strongly on the reliability of marker information used in relationship inference (Wang 2009), as well as on allele number and sample size of the potential parental pool. Highly polymorphic markers are more important for inferring the number of parents and individual parent assignment than the number of markers used in the analysis itself (Sefc & Koblmöller 2009). Because our loci showed so many alleles, 16–35 (Table S1), exclusion probabilities were high at the five loci that we analysed. Although highly variable markers can result in genotyping errors due to microsatellite slippage, COLONY2 takes into account possible errors due to genotyping errors and allele dropout (Wang 2004, 2009). Because the lineages had similar numbers of alleles and heterozygosities (Tables S1 and S2), the exclusion probabilities were the same for both lineages; estimates at a single locus ranged from 0·35 to 0·75 when only information from offspring was available (P_{E2}), 0·53– 0·86 if the genotype from one parent was known (P_{E1}), and 0·72– 0·97 if a pair of individuals chosen at random from the population are excluded as both parents of an offspring (P_{E3}). Overall, the combined exclusion power for the five microsatellite loci was very close to 1 for all estimates in both lineages (Table S1), indicating that our parentage analysis is supported by high statistical power.

IDENTIFICATION OF PARENT-OFFSPRING COLONY PAIRS

Of 199 possible parent colonies, there were 49 colonies (~25%) that had offspring colonies on the site. The mean (SD) number of offspring colonies founded by daughter queens was 2·94 (1·85). Numbers of offspring colonies founded by daughter queens ranged from 1 to 8 (Fig. 2). Parents were assigned to 146 of 247 offspring colonies. Many generations of colonies were represented (Fig. 3, Fig. S1). One colony had great-great grand-offspring, whereas six colonies were great grandmothers and 16 colonies were grandmothers.

COLONY LIFE HISTORY AND DISPERSAL

The offspring were distributed throughout the site, showing no tendency for offspring to be nearest neighbours of their parents (Fig. 3). The mean (SD) distance from parent to offspring colonies was 154·4 (80·1) m, and ranged from 11·5 to 365·6 m. There was no effect of year of founding on distance to offspring (F = 1·06, df = 22, 123, p = 0·39; Fig. S2). There was also no effect of mother colony on distance to offspring (F = 1·36, df = 48, 97, p = 0·09).

There were no apparent differences in the distance and directions taken by successful founding queens relative to their parent colonies (Fig. S3). More parent-offspring pairs appear in the east-west direction because the site is rectangular, with its long side in the east-west direction. There was no apparent difference in the dispersal distances and directions of the two lineages (Fig. S3). The observed distribution of colonies by angular sectors did not differ from a random distribution; the Shapiro–Wilk test failed to reject the null hypothesis that the residuals are normally distributed (W = 0·9418, p = 0·63). On the scale of hundreds of metres considered here, there was no correlation between genetic and geographical distance (Mantel correlation test r = 0·028, p = 0·03), indicating that after the mating aggregation, newly mated queens do not tend to disperse back towards their natal nest or those of close relatives.

On the basis of our estimate of age-specific fecundity and mortality, we developed an estimated life table for this population (Table S3, Fig. 4). Using the matrix model, the dominant eigenvalue equivalent to asymptotic growth rate (λ) is 1·069 (r = 0·067 year^{-1}), the estimated rate of growth of the population Ro, is 1·69, and the estimated average generation time, or time in which the population is replaced, is 7·81 years. The value of generation time from the life table analysis was similar, 7·18 years, and the value of R_0 was the same, 1·69.

The longer a colony survives, the more likely it is to produce any offspring founded by a daughter queen (Table S3, Fig. 4, Fig. S4). Of 46 colonies that were 4–5 years old in 2010, the year that colonies were sampled, none had any offspring on the site. It appears that a colony reproduces at a steady rate throughout its life, so the probability of having offspring colonies increases with colony

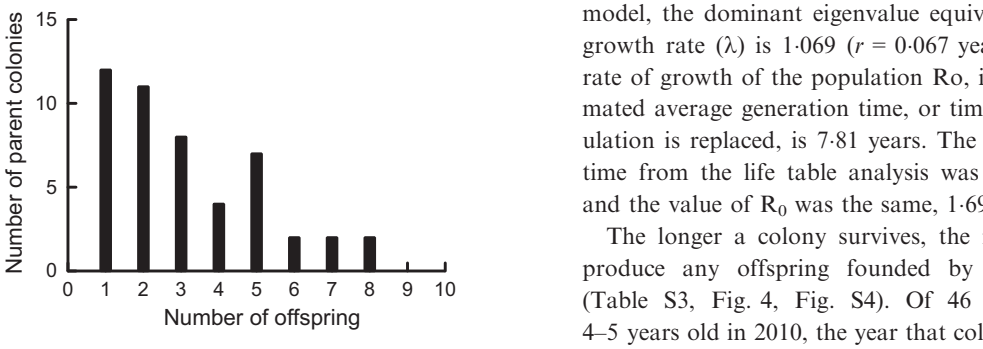


Fig. 2. Distribution of number of offspring colonies. The figure shows offspring numbers only for those colonies that had one or more offspring colonies.

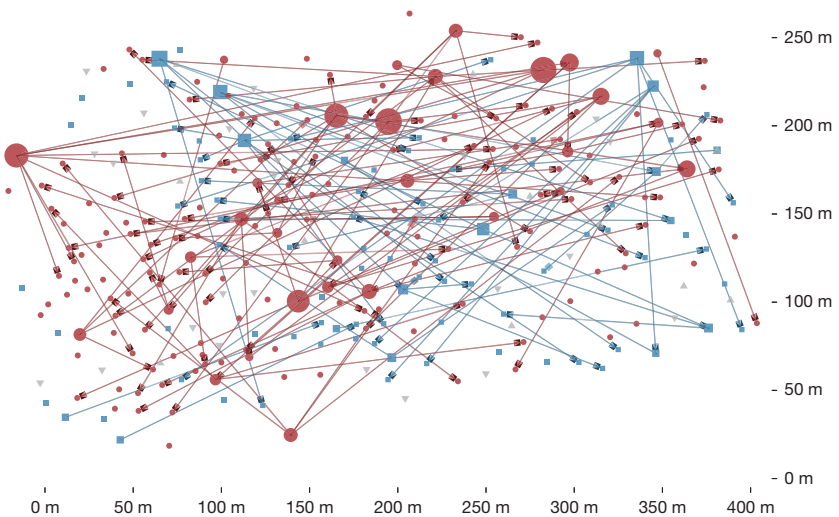


Fig. 3. All parent-offspring pairs. Parents are shown linked to offspring by arrows. Red and circles, J1 lineage; Blue and squares, J2 lineage. The size of the circles and squares indicates number of offspring; the smallest size had no offspring. Upward-pointing triangles represent colonies that were too young to be parents. Downward-pointing triangles represent colonies that were not genotyped. North is at the top of the figure.

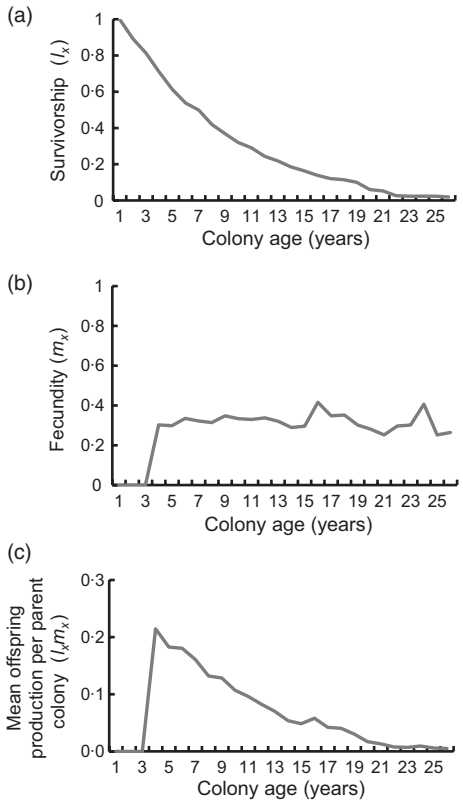


Fig. 4. (a) Survivorship as a function of colony age. (b) Fecundity as a function of colony age. (c) Mean offspring production per parent ($l_x m_x$) as a function of colony age. Values of l_x and m_x are given in Table S3.

age (Fig. 1). The overall probability that a colony of 6–30 years old would have offspring is 0·22. The proportion of colonies of each age whose daughter queens founded colonies that year ranged from 0·03 to 0·08, and there was no apparent decline with age (Fig. 1, Fig. 4, Fig. S4).

The number of colonies for which a parent was identified appears to track the total number of new colonies (Fig. S5). The proportion of new colonies for which a parent was identified is largest for the last 6 years of our study; this is not surprising because younger colonies are more likely to have surviving parents. The proportion of all newly founded colonies whose parent was identified increased from 0·2 in 1987 to 0·9 in 2005 and 2007 (Fig. S5).

There was no relation between the number of daughter reproductives produced by a colony in 1997 and the number of offspring colonies we identified as produced by that colony any time before 2010 (Spearmann's rank correlation test, $n = 29$, $r = -0{\cdot}053$, $t = 0{\cdot}28$, two-tailed $p = 0{\cdot}78$). There was also no correlation when the outlier with 35 daughter reproductives was excluded (Spearmann's rank correlation test, $n = 28$, $r = -0{\cdot}228$, $t = -1{\cdot}29$, two-tailed $p = 0{\cdot}25$) (Fig. 5).

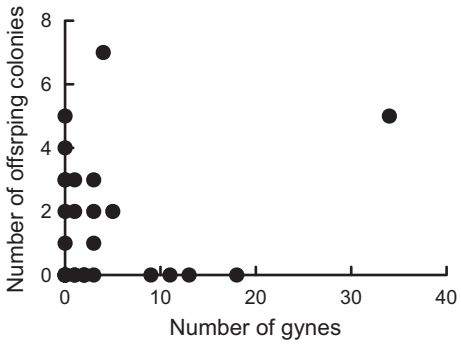


Fig. 5. Relation of reproductive output and realized reproductive success. The figure shows the number of offspring colonies ever produced by a colony, and the number of daughter reproductives produced by that colony in 1997.

Discussion

To our knowledge this is the first time it has been possible to identify, in a natural population, parent and offspring ant colonies. These results make it possible to examine population trends in colony life history. Our results provide estimates of the female component of the lifetime reproductive success of colonies. This is the starting point for future investigation asking whether variation in reproductive success is related to phenotypic variation among colonies in behavioural and ecological traits.

With a population size of 300 colonies and five highly polymorphic loci, our genetic analysis was able to provide consistent, robust estimates of offspring number. Our analysis is missing several pools of potential offspring or parent colonies on the site, including the offspring colonies founded by reproductives that dispersed off the site and parent colonies from off the site that have offspring on the site. The numbers in these two pools are probably not identical, because the distances parent colonies send reproductives to a mating aggregation may not be the same as the distances that newly mated queens disperse from the mating aggregation to found new colonies. The mating aggregations occur at different locations each year, and the reproductives disperse from the mating aggregation in all directions. In addition, some parent colonies must have died before sample collection in 2010. As our estimates of age-specific mortality are consistent with those from previous work (Gordon 1991; Gordon & Kulig 1998), there is no evidence for age bias in the parent colonies that died before sample collection.

The life table provided here is an estimate, based on a sample of the colonies alive in 1 year. We found a high reproductive rate of 1·69. This is consistent with the rapid growth of the population during the years 2003–2010. For these years, we were able to identify most of the parents of the offspring colonies, and we used these data to estimate colony fecundity. The life table may underestimate population growth rate because it does not include offspring that dispersed off the site. In any case, the population growth rate is not constant. During the 25 years of the study, population size at the site has varied greatly, from about 250 colonies in the early 1990s (Gordon & Kulig 1996, 1998) to more than 300 colonies following an increase in population growth in the late 1990s (Sanders & Gordon 2004). It

is likely that population size will continue to fluctuate; for example, it appears that in 2012 severe drought greatly decreased population growth (Gordon pers. obs.).

Several features of our results suggest that our sample provides useful estimates of relative lifetime reproductive success in colonies founded by daughter reproductives. We found a mean dispersal distance of about 150 m, higher than the mean distance indicated in a previous study using a smaller sample of colonies and a measure of isolation by distance rather than distances between known parent-offspring pairs (Suni & Gordon 2010). This mean dispersal distance of 150 m, which is truncated by the size of our 200 × 400 m study site, is still low enough that we were able to identify a parent for many of the offspring colonies on the site. The proportion of new colonies whose parents were identified was 0·8 or higher since 2003, with the exception of 2004 (Fig. S5). This means that relatively few colonies on the site are founded by the daughter reproductives from more distant colonies off the site in the surrounding areas. The proportion of new colonies whose parents were identified is highest in more recent years, which is to be expected because more parents of the colonies on the site are still alive and thus included in our sample. The proportion of new colonies whose parents were identified is consistent over recent years, despite fluctuations in the numbers of new colonies due to changing ecological conditions (Sanders & Gordon 2004), showing that the number of offspring identified tracks the total number produced. Finally, many colonies were related to each other (Fig. 3, Fig. S1); a total of 19 of the colonies identified as offspring were also parents of other colonies, and there were many grandparents and even great grandparents. In addition, offspring founded by daughter reproductives were distributed all over the site (Fig. 3).There was no tendency for daughter reproductives to disperse from the mating aggregation back towards their natal nest; genetic and geographical distances were not correlated. These results, as well as the absence of any year-to-year trends in dispersal distance (Fig. S3) indicate that our sampling method is similarly effective from year to year in estimating relative reproductive success. Further sampling of parent-offspring pairs in the area surrounding the site is needed to elucidate the metapopulation dynamics of this population.

Here we estimate the female component of reproductive success and ignore contributions of males. There is no evidence that some colonies specialize in male production (Gordon & Wagner 1997, Wagner & Gordon 1999), so it is unlikely that the lifetime reproductive success of some colonies occurs only through the queen's sons. This suggests that variation among colonies in numbers of offspring founded by daughter colonies reflects true variation in lifetime reproductive success.

As in other ant species, colonies of harvester ants live within hundreds of metres of their conspecific relatives (Pedersen & Boomsma 1999; Sundström, Keller & Chapuisat 2003; Hardy, Pearcy & Aron 2008). However, colonies compete only with their nearest neighbours for food (Gordon 1992; Gordon & Kulig 1996). We found no tendency for parent and offspring colonies to be located adjacent to each other on the site (Fig. 3), suggesting that because of random dispersal, local competition for foraging area between parent and offspring colonies, or between sibling colonies is rare in harvester ants (Queller 1992; Rodrigues & Gardner 2012). Although colonies of polydomous ant species often live near close relatives (Hardy, Pearcy & Aron 2008), further studies are needed to determine whether or not dispersal far from relatives is the rule for other monogynous, monodomous species such as *P. barbatus*.

Our results suggest that some colonies may fail to reproduce year after year. Relatively few of the colonies, about 25%, had offspring on the site each year. This is similar to the proportion of mature colonies that produce winged reproductives in a given year, about 30% (Gordon & Wagner 1997; Wagner & Gordon 1999). If most colonies do not even produce winged reproductives in a given year, then it is not surprising that they have no offspring that year. Some of the colonies for which we found no offspring may have offspring outside the site. However, the distribution of offspring number (Fig. 2) shows that of the few colonies that had offspring, many had more than one (Fig. 3) and a surprisingly large proportion were grandmothers and great grandmothers (e.g. Fig. S1). This is consistent with the possibility that some colonies are part of successful families that have many offspring, while other colonies have none. In other ant populations, colonies also vary in reproductive output (Beshers & Traniello 1994; Foitzik, Achenbach & Brandt 2009; Boulay *et al*. 2010). We found that only 26% of colonies 16–20 years old, after 10–15 years of reproductive maturity, had produced offspring on the site (Fig. 1). Although most very old colonies, 21 years old or older, did have offspring, there are few such colonies on the site. It may be that all colonies eventually have offspring, or instead that colonies that do not produce offspring are also unlikely to survive to grow old. To distinguish these possibilities it will be necessary to continue to trace reproductive success for another 10–15 years, until more of the colonies now on the site grow old.

There is no apparent relation of reproductive success and colony age (Fig 1, Fig. 4, Fig. S4). Once a colony begins to produce, at age 4 or 5 years, it may continue to do so for 20 years. This is consistent with previous work in this population that showed no effect of colony age on reproductive output (Wagner & Gordon 1999). Theoretical work suggests that the conditions that favour allocation to female reproductive production could persist throughout a colony's lifespan (e.g. Nonacs 1993). Long-term data on individually labelled colonies of many species are needed to determine whether or not the absence of reproductive senescence is common in ants.

Our results provide no evidence that reproductive output, measured in numbers of gynes produced, is correlated

with lifetime reproductive success, measured in number of offspring colonies by the time the colony was 19 years or older (Fig. 5). Although a colony that produces no winged reproductives clearly cannot have offspring, it is not necessarily the case that a colony that produces more winged reproductives has more offspring. Previous work showed that male production by a given colony was correlated in 1995 and 1997 (Wagner & Gordon 1999). We do not know whether the colonies that produced more daughter reproductives in 1997 tend to produce more of them year after year. In this population about 99% of the gynes at the mating aggregation do not found colonies (Gordon & Kulig 1996). The colonies that produce the successful 1% of reproductives may not be the ones that produce the most daughter reproductives. Because the proportion of reproductives that are successful is so low, data would be needed on many colonies for many years to detect a relation, if there is one, between number of reproductives produced and realized reproductive success.

This study provides an estimate of the female component of lifetime reproductive success for a social insect colony, making it possible to evaluate colony life history and the demography of a population of colonies. Our results show that in a population of harvester ant colonies, long-lived colonies continue to reproduce throughout their lifetime. Many generations live in the same population, but it appears that offspring rarely compete directly for foraging area with their parents. This first measure of ant colony reproductive success reveals a surprisingly large range among colonies in fitness, and provides an opportunity to investigate the ecological causes of that variation. Previous work suggests that microhabitat has no effect on colony survival (Gordon 1993, Gordon & Kulig 1996). However, the age and proximity of nearest conspecific neighbours influence survival (Gordon & Kulig 1996) and reproductive output (Wagner & Gordon 1999), and colony differences in behaviour (Gordon *et al.* 2011) may influence colony reproductive success. Further work will make it possible to learn how reproductive output, dispersal and survival are related to realized reproductive success, and why some colonies are able to produce more offspring than others.

Acknowledgements

We thank Sam Crow, Andrew Merrell, Noa Pinter-Wollman and Shelby Sturgis for their help with collecting samples for this project. We are grateful to Mike Greene, LeAnn Howard, Lis Nelis, Steve Palumbi, Ward Watt and Gozde Yucel for assistance and advice, and to Jinliang Wang for his assistance with the use of COLONY software. We thank Raziel Davison, Steve Palumbi, Noa Pinter-Wollman and anonymous reviewers for comments on the manuscript. The work was supported by NSF grant IOS-0718631 to D.M.G, the Stanford Office of the Dean of Research, and the Stanford Emergence of Cooperation project.

References

Albright, R., Mason, B., Miller, M. & Langdon, C. (2010) Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 20400–20404.

Altmann, S.A. (1991) Diets of yearling female primates papio-cynocephalus predict lifetime fitness. *Proceedings of the National Academy of Sciences of the United States of America*, **88**, 420–423.

Anderson, K.E., Wheeler, D.E., Yang, K. & Linksvayer, T.A. (2011) Dynamics of an ant-ant obligate mutualism: Colony growth, density dependence and frequency dependence. *Molecular Ecolology*, **20**, 1781–1793.

Bargum, K., Helantera, H. & Sundstrom, L. (2007) Genetic population structure, queen supersedure and social polymorphism in a social Hymenoptera. *Journal of Evolutionary Biology*, **20**, 1351–1360.

Beshers, S. & Traniello, J.F.A. (1994) The adaptiveness of demographic distributions of the fungus growing ant *Trachymyrmex septentrionalis*. *Ecology*, **75**, 763–775.

Boulay, R., Galarza, J.A., Chéron, B., Hefetz, A., Lenoir, A., Van Oudenhove, L. & Cerdá, X. (2010) Intraspecific competition affects population size and resource allocation in an ant dispersing by colony fission. *Ecology*, **91**, 3312–3321.

Brian, M.V., Clarke, R.T. & Jones, R.M. (1981) A numerical model of an ant society. *Journal of Animal Ecology*, **50**, 387–405.

Caswell, H.(2001) *Matrix Population Models: Construction, Analysis, and Interpretation*.Sinauer Associates Sunderland, MA. 722 pp.

Chapuisat, M., Bocherens, S. & Rosset, H. (2004) Variable queen number in ant colonies: No impact on queen turnover, inbreeding, and population genetic differentiation in the ant *Formica selysi*. *Evolution*, **58**, 1064–1072.

Chapuisat, M., Goudet, J. & Keller, L. (1997) Microsatellites reveal high population viscosity and limited dispersal in the ant *Formica paralugubris*. *Evolution*, **51**, 475–482.

Chapuisat, M. & Keller, L. (1999) Extended family structure in the ant *Formica paralugubris*: The role of the breeding system. *Behavioral Ecology and Sociobiology*, **46**, 405–412.

Crawford, N.G. (2010) SMOGD: Software for the measurement of genetic diversity. *Molecular Ecology Resources*, **10**, 556–557.

Crozier, R.H. & Pamilo, P. (1996) *Evolution of social insect colonies. Sex allocation and kin-selection*. Oxford University Press, Oxford, UK. 320pp.

Damman, H. & Cain, M. (1998) Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *Journal of Ecology*, **86**, 13–26.

Foitzik, S., Achenbach, A. & Brandt, M. (2009) Locally adapted social parasite affects density, social structure, and life history of its ant hosts. *Ecology*, **90**, 1195–1206.

Foitzik, S., Strätz, M. & Heinze, J. (2003) Ecology, life history and resource allocation in the ant, *Leptothorax nylanderi*. *Journal of Evolutionary Biology*, **16**, 670–680.

Fournier, D., Aron, S. & Milinkovitch, M.C. (2002) Investigation of the population genetic structure and mating system in the ant *Pheidole pallidula*. *Molecular Ecology*, **11**, 1805–1814.

Frederickson, M.E. (2006) The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia*, **149**, 418–427.

Frere, C.H., Kruetzen, M., Mann, J., Connor, R.C., Bejder, L. & Sherwin, W.B. (2010) Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19949–19954.

Gordon, D.M. (1991) Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist*, **138**, 379–411.

Gordon, D.M. (1992) How colony growth affects forager intrusion in neighboring harvester ant colonies. *Behavioral Ecology and Sociobiology*, **31**, 417–427.

Gordon, D.M. (1995) The development of an ant colony's foraging range. *Animal Behaviour*, **49**, 649–659.

Gordon, D.M. & Kulig, A.W. (1996) Founding, foraging and fighting: Colony size and the spatial distribution of harvester ant nests. *Ecology*, **77**, 2393–2409.

Gordon, D.M. & Kulig, A.W. (1998) The effect of neighboring colonies on mortality in harvester ants. *Journal of Animal Ecology*, **67**, 141–148.

Gordon, D.M. & Wagner, D. (1997) Neighborhood density and reproductive potential in harvester ants. *Oecologia*, **109**, 556–560.

Gordon, D.M., Guetz, A., Greene, M.J. & Holmes, S. (2011) Colony variation in the collective regulation of foraging by harvester ants. *Behavioral Ecology*, **22**, 429–435.

Goropahnaya, A.V., Seppa, P. & Pamilo, P. (2001) Social and genetic characteristics of geographically isolated populations in the ant *Formica cinerea*. *Molecular Ecology*, **10**, 2807–2818.

Hammond, R.L., Bourke, A.F.G. & Bruford, M.W. (2001) Mating frequency and mating system of the polygynous ant, *Leptothorax acervorum*. *Molecular Ecology*, **10**, 2719–2728.

Hardy, O.J., Pearcy, M. & Aron, S. (2008) Small-scale spatial genetic structure in an ant species with sex-biased dispersal. *Biological Journal of the Linnean Society*, **93**, 465–473.

Hedrick, P.W. (2005) A standardized genetic differentiation measure. *Evolution*, **59**, 1633–1638.

Helms Cahan, S. & Julian, G.E. (2010) Shift in frequency-dependent selection across the life-cycle in obligately interbreeding harvester ant lineages. *Evolutionary Ecology*, **24**, 359–374.

Helms Cahan, S. & Keller, L. (2003) Complex hybrid origin of genetic caste determination in harvester ants. *Nature*, **424**, 306–309.

Helms Cahan, S., Parker, J.D., Rissing, S.W., Johnson, R.A., Polony, T.S., Weiser, M.D. & Smith, D.R. (2002) Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. *Proceedings of the Royal Society of London, Series B*, **269**, 1871–1877.

Hood, G. M. (2010) PopTools version 3.2.5. Available on the internet. URL http://www.poptools.org.

Ingram, K.K. & Gordon, D.M. (2003) Genetic analysis of dispersal dynamics in an invading population of Argentine ants, *Linepithema humile*. *Ecology*, **84**, 2832–2842.

Jervis, M.A., Heimpel, G.E., Ferns, P.N., Harvey, J.A. & Kidd, N.A.C. (2001) Life-history strategies in parasitoid wasps: A comparative analysis of 'ovigeny'. *Journal of Animal Ecology*, **70**, 442–458.

Jost, L. (2008) G_{ST} and its relatives do not measure differentiation. *Molecular Ecology*, **17**, 4015–4026.

Julian, G.E., Fewell, J.H., Gadau, J., Johnson, R.A. & Larrabee, D. (2002) Genetic determination of the queen caste in an ant hybrid zone. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 8157–8160.

Keller, L. (1993) The assessment of reproductive success of queens in ants and other social insects. *Oikos*, **67**, 177–180.

Keller, L. & Passera, L. (1990) Fecundity of ant queens in relation to their age and the mode of colony founding. *Insectes Sociaux*, **37**, 116–130.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.H., Hoang, A., Gibert, P. & Beerli, P. (2001) The strength of phenotypic selection in natural populations. *American Naturalist*, **157**, 245–261.

Leibig, J. & Poethke, H.J. (2004) Queen lifespan and colony longevity in the ant *Harpegnathos saltator*. *Ecological Entomology*, **29**, 203–207.

MacKay, W.P. (1985) A comparison of the energy budgets of 3 species of *Pogonomyrmex* harvester ants (Hymenoptera,Formicidae). *Oecologia*, **66**, 484–494.

May, R.M. (1976) Estimating r: A pedagogical note. *American Naturalist*, **110**, 496–499.

Metcalf, C.J.E. & Pavard, S. (2007) Why evolutionary biologists should be demographers. *Trends in Ecology and Evolution*, **22**, 205–212.

Moilanen, A., Sundström, L. & Pedersen, J.S. (2004) MATESOFT: A program for deducing parental genotypes and estimating mating system statistics in haplodiploid species. *Molecular Ecology Notes*, **4**, 795–797.

Molet, M., Van Baalen, M. & Peeters, C. (2008) Shift in colonial reproductive strategy associated with a tropical-temperate gradient in *Rhytidoponera* ants. *American Naturalist*, **172**, 75–87.

Nonacs, P.(1993) The effects of polygyny and colony life history on optimal sex investment. In *Queen Number and Sociality in Insects*, L. Keller (Ed.), pp 110–131. Oxford University Press, London

Pamilo, P. (1981) Genetic organization of Formica sanguinea populations. *Behavioral Ecology and Sociobiology*, **9**, 45–50.

Pamilo, P., Chautems, D. & Cherix, D.(1992) Genetic differentiation of disjunct populations of the ants *Formica aquilonia* and *Formica lugubris* in Europe. *Insectes Sociaux*, **39**, 15–29.

Peakall, R. & Smouse, P.E. (2006) GENALEX 6: Genetic analysis in Excel Population genetic software for teaching and research.. *Molecular Ecology Notes*, **6**, 288–295.

Pearcy, M., Goodisman, M.A.D. & Keller, L. (2011) Sib mating without inbreeding in the longhorn crazy ant. *Proceedings of the Royal Society of London, Series B*, **278**, 2677–2681. doi:10.1098/rspb.2010.2562 Published online

Pedersen, J.S. & Boomsma, J.J. (1999) Multiple paternity in social Hymenoptera: Estimating the effective mate number in single–double mating populations. *Molecular Ecology*, **8**, 577–587.

Qian, Z.Q., Schluns, H., Schlick-Steiner, B.C., Steiner, F.M., Robson, S. K.A., Schluns, E.A. & Crozier, R.H. (2011) Intraspecific support for the polygyny-vs.-polyandry hypothesis in the bulldog ant *Myrmecia brevinoda*. *Molecular Ecology*, **20**, 3681–3691.

Queller, D.C. (1992) Does population viscosity promote kin selection? *Trends in Ecology and Evolution*, **7**, 322–324.

Rodrigues, A.M. & Gardner, ??. (2012) Evolution of helping and harming in heterogeneous populations. *Evolution*, **66**, 2065–2079.

Ross, K.G. (2001) Molecular ecology of social behaviour: Analyses of breeding systems and genetic structure. *Molecular Ecology*, **10**, 265–284.

Ross, K.G., Krieger, M.J.B., Shoemarker, D.D., Vargo, E.L. & Keller, L. (1997) Hierarchical analysis of genetic structure in native fire ant populations: Results from three classes of molecular markers. *Genetics*, **147**, 643–655.

Rousset, F. (2008) GENEPOP'007: A complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources*, **8**, 103–106.

Sanders, N.J. & Gordon, D.M. (2004) The interactive effects of climate and interspecific neighbours on mortality of red harvester ants. *Ecological Entomology*, **29**, 632–637.

Schmidt, A.M., Linksvayer, T.A., Boomsma, J.J. & Pedersen, J.S. (2011) No benefit in diversity? The effect of genetic variation on survival and disease resistance in a polygynous social insect. *Ecological Entomology*, **36**, 751–759 (doi:10.1111/j.1365-2311.2011.01325).

Schrempf, A., Reber, C., Tinaut, A. & Heinze, J. (2005) Inbreeding and local mate competition in the ant *Cardiocondyla batesii*. *Behavioral Ecology and Sociobiology*, **57**, 502–510.

Sefc, K.M. & Koblmöller, S. (2009) Assessing parent numbers from offspring genotypes: The importance of marker polymorphism. *Journal of Heredity*, **100**(2), 197–205.

Shapiro, S.S. & Wilk, M.B. (1965) An analysis of variance test for normality (complete samples). *Biometrika*, **52**, 591–611.

Stopher, K.V., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T. (2008) Individual differences, density dependence and offspring birth traits in a population of red deer. *Proceedings of the Royal Society of London, Series B*, **275**, 2137–2145.

Sundström, L. (1993) Genetic population structure and sociogenetic organisation in *Formica truncorum* (Hymenoptera, Formicidae). *Behavioral Ecology and Sociobiology*, **33**, 345–354.

Sundström, L., Keller, L. & Chapuisat, M. (2003) Inbreeding and sex-biased gene flow in the ant *Formica exsecta*. *Evolution*, **57**, 1552–1561.

Sundström, L., Seppä, P. & Pamilo, P. (2005) Genetic population structure and dispersal patterns in Formica ants – a review. *Annales Zoologici Fennici*, **42**, 163–177.

Suni, S. & Gordon, D.M. (2010) Fine-scale genetic structure and dispersal distance in the harvester ant *Pogonomyrmex barbatus*. *Heredity*, **104**, 168–173.

Takahashi, M.K., Horner, L.M., Kubota, T., Keller, N.A. & Abrahamson, W.G. (2011) Extensive clonal spread and extreme longevity in saw palmetto, a foundation clonal plant. *Molecular Ecology*, **20**, 3730–3742.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**, 2731–2739.

Thorne, B.L., Breisch, N.L. & Haverty, M.I. (2002) Longevity of kings and queens and first time of production of fertile progeny in dampwood termite (Isoptera; Termopsidae; *Zootermopsis*) colonies with different reproductive structures. *Journal of Animal Ecology*, **71**, 1030–1041.

Thurin, N., Sery, N., Guimbretiere, R. & Aron, S. (2011) Colony kin structure and breeding system in the ant genus Plagiolepis. *Molecular Ecology*, **20**, 3251–3260.

Trontti, K., Thurin, N., Sundstrom, L. & Aron, S. (2007) Mating for convenience or genetic diversity? Mating patterns in the polygynous ant Plagiolepis pygmaea. *Behavioral Ecology*, **18**, 298–303.

Tschinkel, W.R. (1987) Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. *Insectes Sociaux*, **34**, 143–164.

Tschinkel, W.R. (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecological Monogragphs*, **63**, 425–457.

Tsuji, K. & Tsuji, N. (1996) Evolution of life history strategies in ants: Variation in queen number and mode of colony founding. *Oikos*, **76**, 83–92.

Volny, V.P. & Gordon, D.M. (2002a) Genetic basis for queen-worker dimorphism in a social insect. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 6108–6111.

Volny, V.P. & Gordon, D.M. (2002b) Characterization of polymorphic microsatellite loci in the red harvester ant, *Pogonomyrmex barbatus*. *Molecular Ecology Notes*, **2**, 302–303.
Wagner, D. & Gordon, D.M. (1999) Colony age, neighborhood density and reproductive potential in harvester ants. *Oecologia*, **119**, 175–182.
Walling, C.A., Pemberton, J.M., Hadfield, J.D. & Kruuk, L.E.B.(2010), Comparing parentage inference software: Reanalysis of a red deer pedigree. *Molecular Ecology*, **19**, 1914–1928; doi:10.1111/j.1365-294X.2010.04604
Wang, J. (2004) Sibship reconstruction from genetic data with typing errors. *Genetics*, **166**, 1963–1979.
Wang, J. (2007) Parentage and sibship exclusions: Higher statistical power with more family members. *Heredity*. **99**, 205–217; doi:10.1038/sj.hdy.6800984
Wang, J. (2009) A new method for estimating effective population sizes from a single sample of multilocus genotypes. *Molecular Ecology*, **18**, 2148–2164.
Wang, J. (2010) COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, **11**, 141–145.
Wang, J. & Santure, A.W. (2009) Parentage and sibship inference from multi-locus genotype data under polygamy. *Genetics*, **181**, 1579–1594.

Received 10 August 2012; accepted 12 November 2012
Handling Editor: Tim Coulson

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Parent-offspring relations in two large families of colonies.

Fig. S2. Dispersal distance from parent to offspring.

Fig. S3. Dispersal direction from parent to offspring

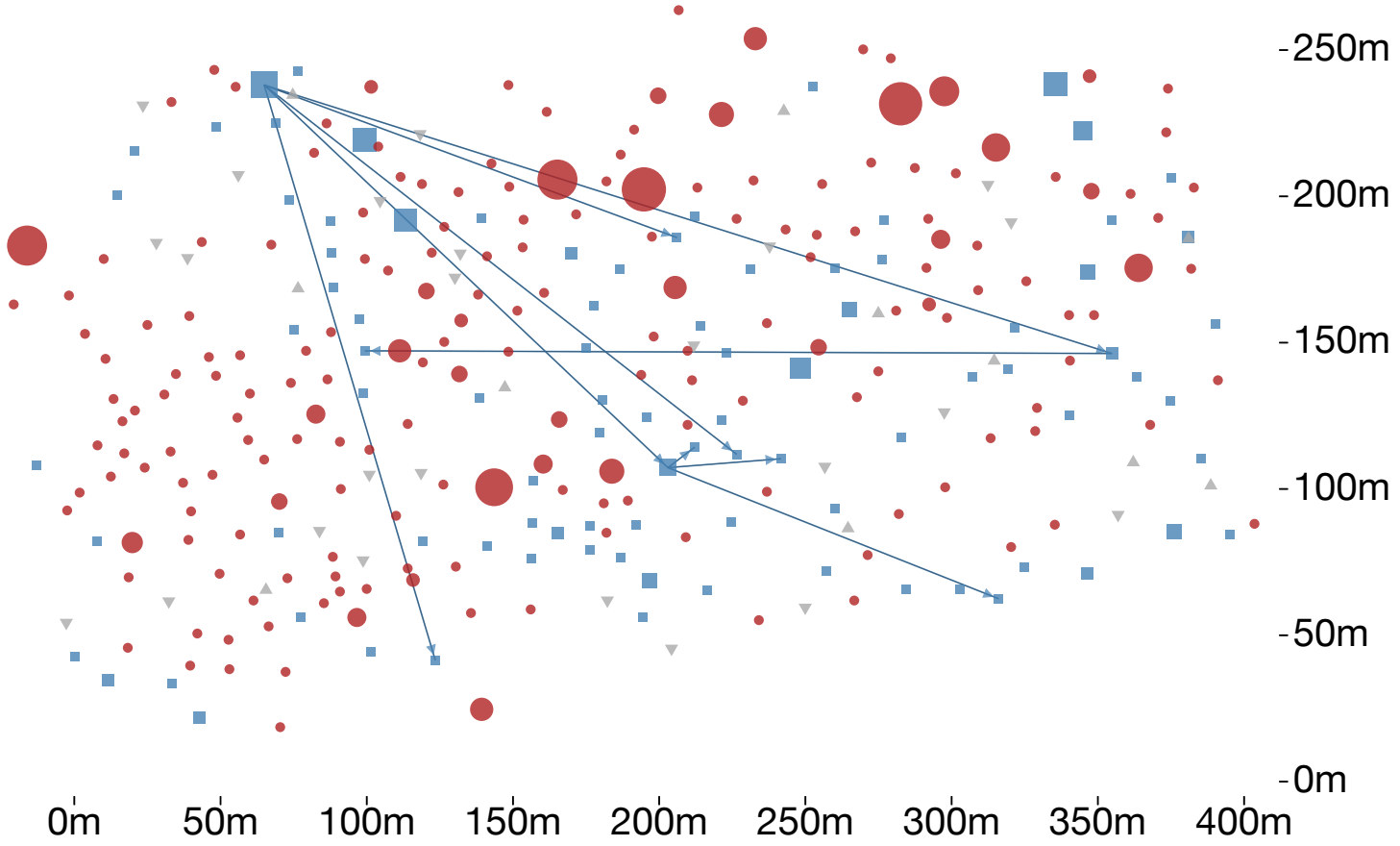
Fig. S4. Fecundity by parent age

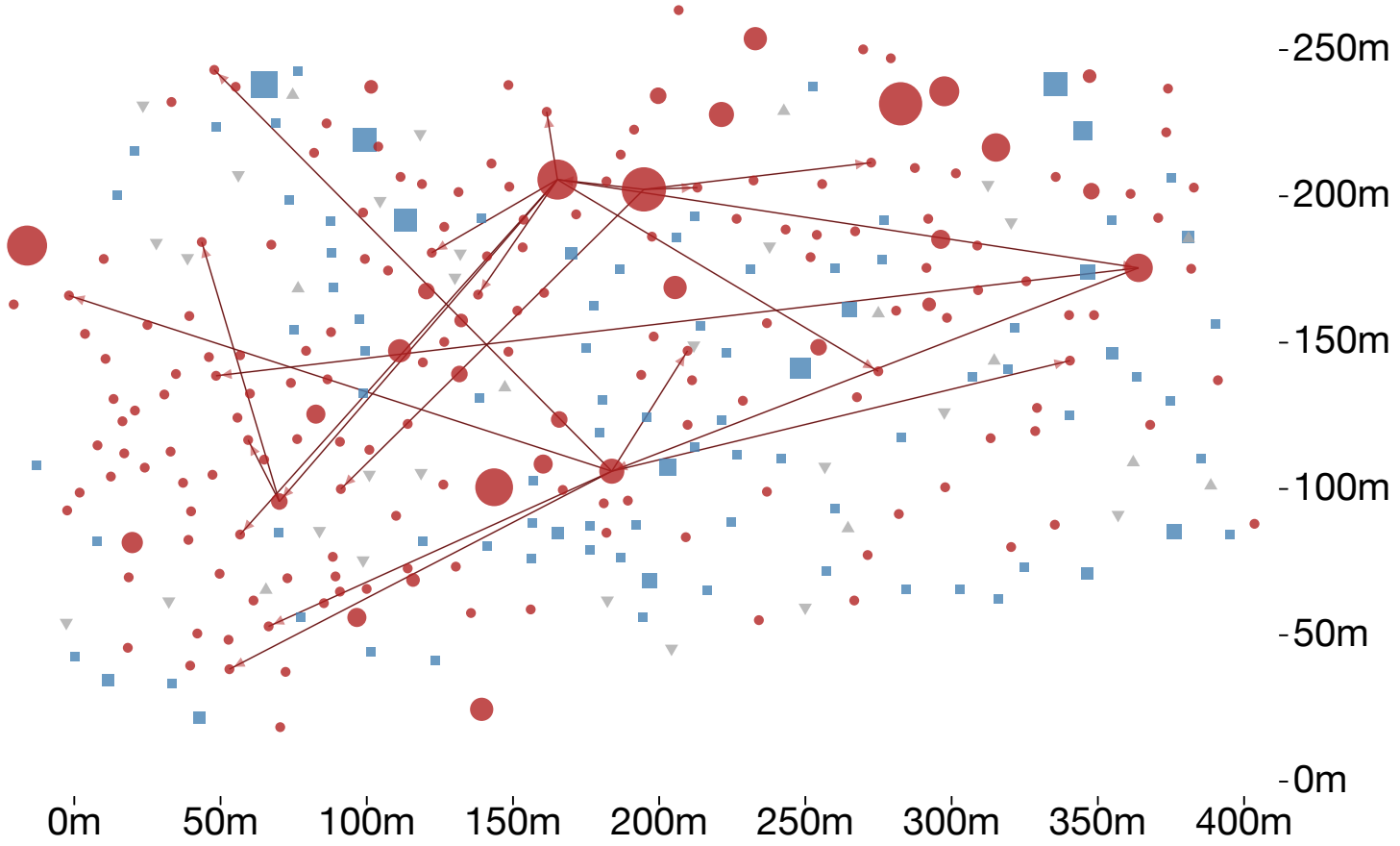
Fig. S5. Proportion of all new colonies on the site each year for which a parent was identified.

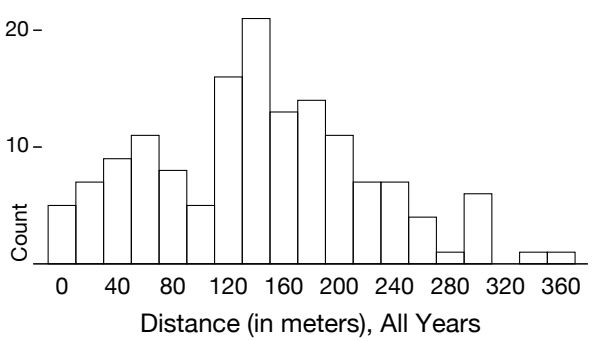
Table S1. Microsatellite loci used in parentage analysis. Primer sequence, Size of detected fragments,Number of alleles, probabilities of parentage exclusion (P_{E1}-one parent known, P_{E2}- no parents known, P_E-two parent exclusion), Frequency of null alleles.Parentage exclusion probabilities ($P_{E1\text{-}3}$) were calculated separately for the J1 and J2 lineages, and the values were always identical to the fifth decimal place.

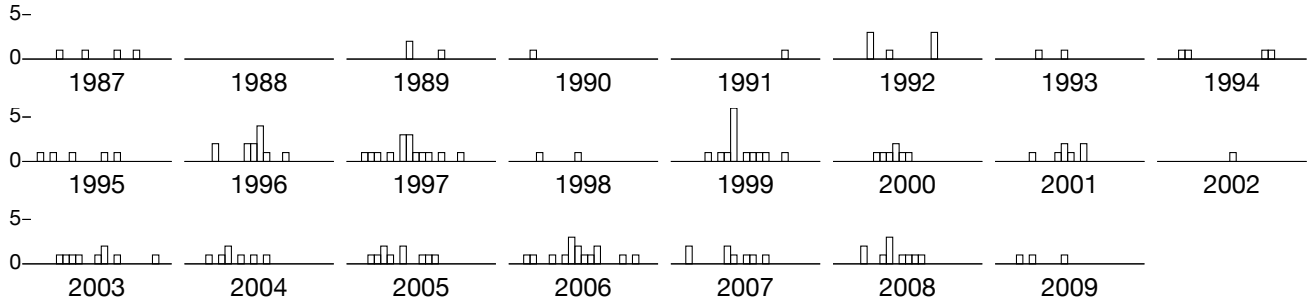
Table S2. Genetic diversity estimates- H_o observed heterozygosity, H_e expected heterozygosity**,** F_{IS}-within-population fixation index**,** $F_{s't}$ among-population fixation index, F_{it} total fixation index, G'_{ST_est} -standardized measure of genetic differentiation, D_{est} -estimator of actual differentiation

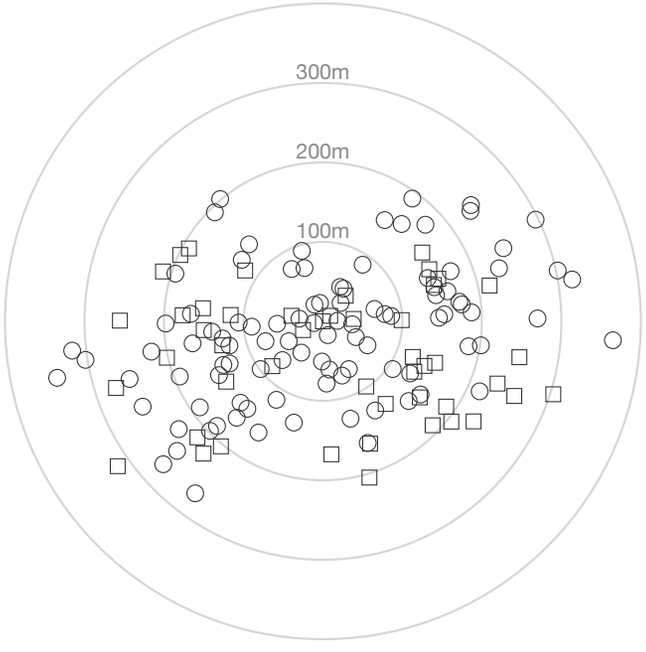
Table S3. Estimated life table


250m
200m
150m
100m
50m
0m
0m
50m
100m
150m
200m
250m
300m
350m
400m

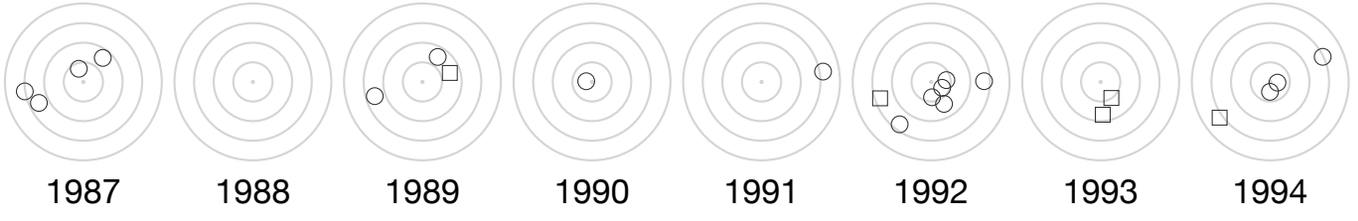

250m
200m
150m
100m
50m
0m
0m
50m
100m
150m
200m
250m
300m
350m
400m


20
10
Count
0
40
80
120
160
200
240
280
320
360
Distance (in meters), All Years

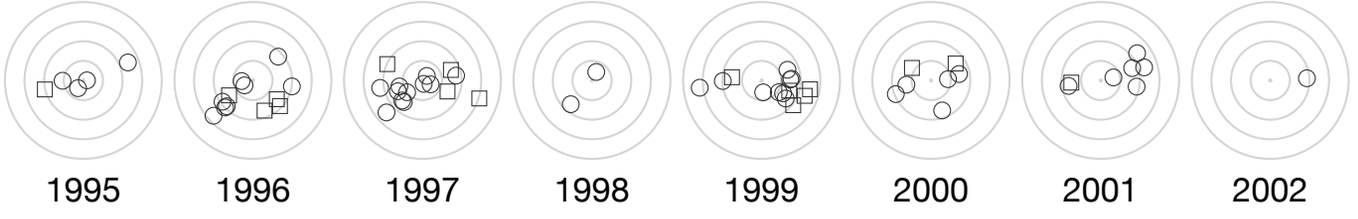

5
0
1987
1988
1989
1990
1991
1992
1993
1994
5
0
1995
1996
1997
1998
1999
2000
2001
2002
5
0
2003
2004
2005
2006
2007
2008
2009



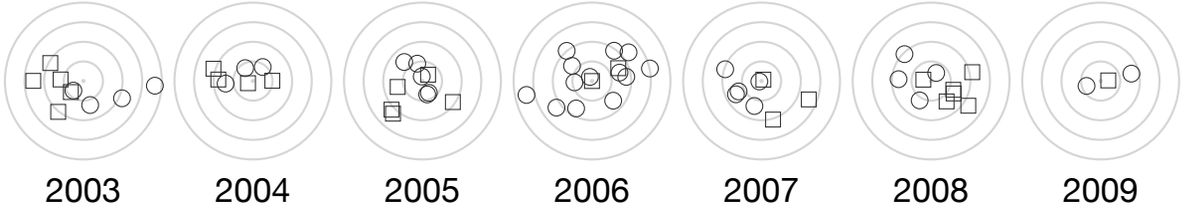
All Years



1987 1988 1989 1990 1991 1992 1993 1994

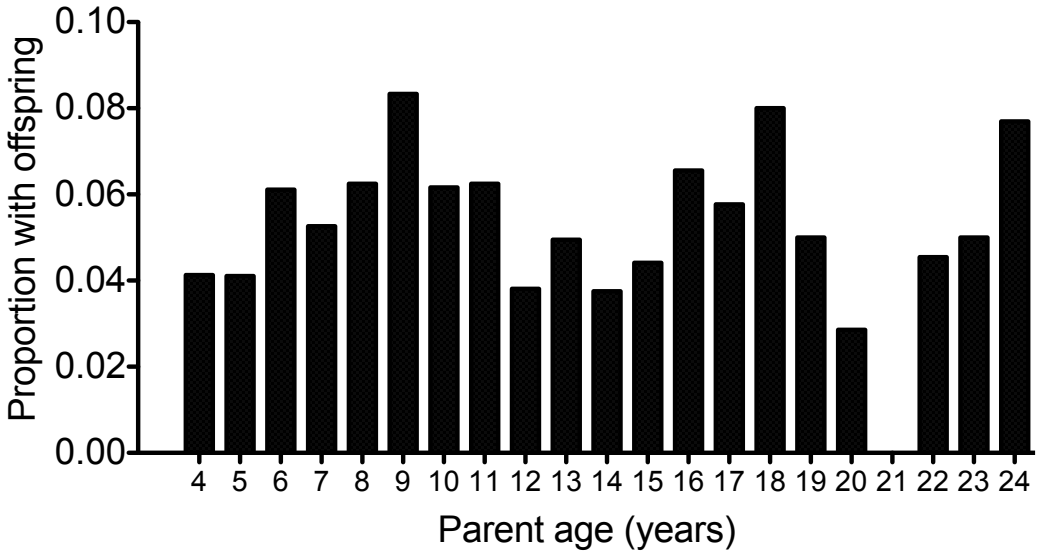


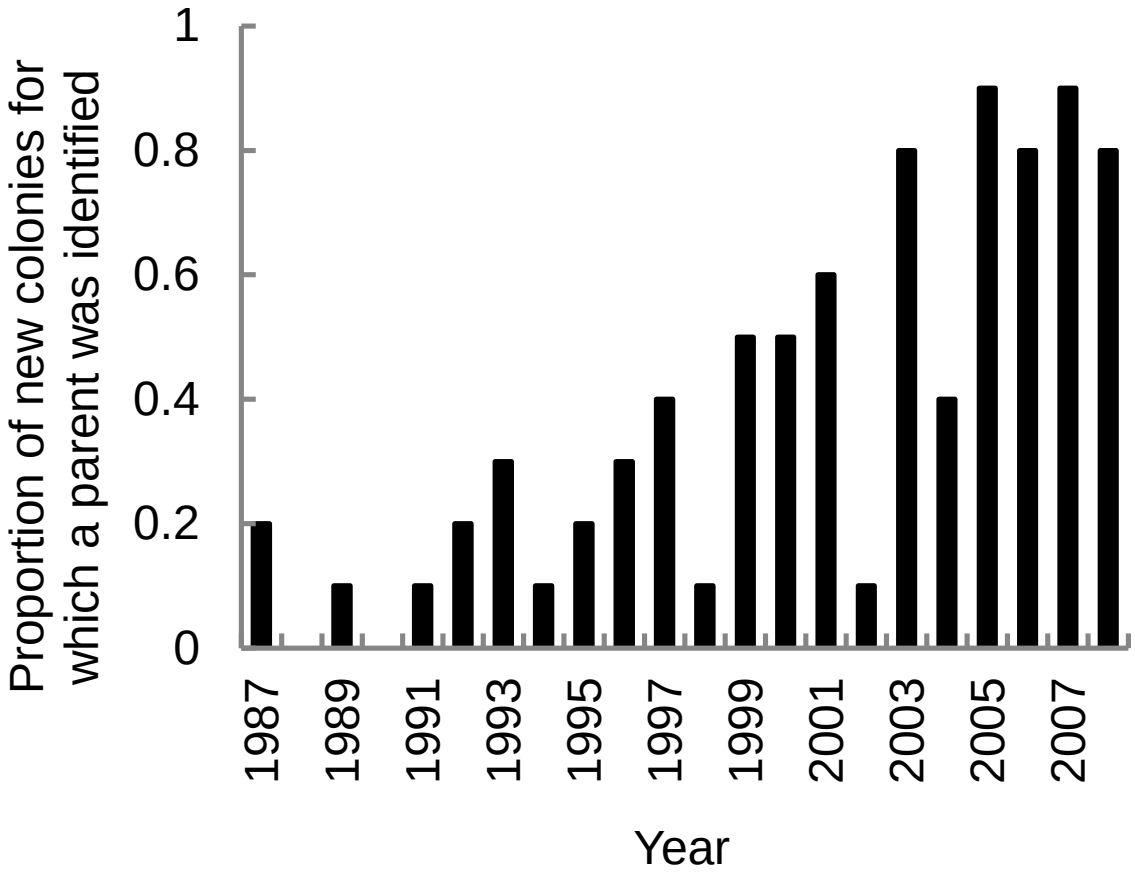
1995 1996 1997 1998 1999 2000 2001 2002



2003 2004 2005 2006 2007 2008 2009

Figure S4


Proportion with offspring
0.10
0.08
0.06
0.04
0.02
0.00
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Parent age (years)


Proportion of new colonies for which a parent was identified
1
0.8
0.6
0.4
0.2
0
1987
1989
1991
1993
1995
1997
1999
2001
2003
2005
2007
Year

SI Figure Legends

Figure S1. Parent-offspring relations in two large families of colonies. Red and circles, J1 lineage; Blue and squares, J2 lineage. The size of the circles and squares indicates number of offspring; the smallest size had no offspring. Upward-pointing triangles represent colonies that were too young to be parents. Downward-pointing triangles represent colonies that were not genotyped. All figures are oriented with north at the top of the figure. 1A, One family of colonies in lineage J1; 1B, One family of colonies in lineage J2.

Figure S2. Dispersal distance from parent to offspring. The histogram on the left shows the frequency distribution for distances from parent to offspring colonies, in meters, for all years, with the distributions for each year shown on the right.

Figure S3. Dispersal direction from parent to offspring. The diagram on the left shows the dispersal distance and direction on polar coordinates, from parent (at the center of the circle) to offspring, for all years, and the dispersal directions for each year are shown on the right. Circles, J1 lineage; Squares, J2 lineage.

Figure S4. Fecundity by parent age. Each bar shows the number of offspring identified for parent colonies of a given age. Total number of colonies of each age are shown in Table S3.

Figure S5. Proportion of all new colonies on the site each year for which a parent was identified.

Table S1. Microsatellite loci used in parentage analysis. Primer sequence, Size of detected fragments, Number of alleles, probabilities of parentage exclusion (P_{E1}-one parent known, P_{E2}- no parents known, P_E-two parent exclusion), Frequency of null alleles. Parentage exclusion probabilities (P_{E1-3}) were calculated separately for the J1 and J2 lineages, and the values were always identical to the 5th decimal place.

Locus	Primer sequences 5' to 3'	Size		Allele number	P_{E1}	P_{E2}	P_{E3}	Freq null
Pb5	F: AACGCGAAAACAGAGCAGATT	168-190	J1	16	0.527	0.349	0.721	0.001
	R: GTCACGAAGGCTAGTGAGCTGT		J2	16				0.000
Pb6	F: GGCAAGAGAGACTCTGTGTGAAA	234-270	J1	33	0.858	0.753	0.968	0.024
	R: GGATATGTGATACAGGCTGACGA		J2	35				0.011
Pb7	F: CGACGATTAATTGAGCCAAGTC	365-395	J1	23	0.540	0.348	0.764	0.000
	R: TTATAATTCGCACGATCCAAGC		J2	23				0.001
Pb8	F: CAAGGAACAGGACGTAGGTGAC	265-395	J1	24	0.680	0.512	0.855	0.002
	R: CTCAACGGAAAGGAAGAGGAAT		J2	26				0.000
Pb9	F: GCATGCAAGCTGATGTTTTATC	232-280	J1	35	0.802	0.670	0.939	0.002
	R: AAAAGCTCAGTTGTCAGCCTGT		J2	35				0.001
Ñ of Loci			J1	25	0.998	0.983	1.000	0.005
			J2	28				0.002

Table S2. Genetic diversity estimates- $\mathbf{H_o}$ observed heterozygosity, $\mathbf{H_e}$ expected heterozygosity, $\mathbf{F_{IS}}$- within-population fixation index, $\mathbf{F_{s't}}$ among-population fixation index, F_{it} total fixation index, $\mathbf{G'_{ST\_est}}$ -standardized measure of genetic differentiation, $\mathbf{D_{est}}$ -estimator of actual differentiation ;

Locus		**H_o**	**H_e**	**F_{is}**	**F_{st}**	**F_{it}**	**G'_{ST_est}**	**D_{est}**
Pb5	J1	0.965	0.747	-0.468	0.122	-0.289	0.325	0.243
	J2	0.976	0.740	-0.558	0.153	-0.319	0.378	0.279
Pb6	J1	0.842	0.931	-0.069	0.156	0.097	0.733	0.684
	J2	0.843	0.928	-0.121	0.190	0.092	0.765	0.71
Pb7	J1	0.726	0.714	-0.278	0.204	-0.016	0.464	0.333
	J2	0.737	0.709	-0.320	0.214	-0.038	0.47	0.336
Pb8	J1	0.976	0.834	-0.356	0.137	-0.169	0.469	0.393
	J2	0.972	0.836	-.0427	0.186	-0.162	0.565	0.474
Pb9	J1	0.971	0.893	-0.279	0.1511	-0.085	0.613	0.549
	J2	0.971	0.901	-0.299	0.171	-0.077	0.666	0.601
Ñ of Loci	J1	0.895	0.822	-0.281	0.153	-0.084	---	0.380
	J2	0.897	0.823	-0.335	0.183	-0.091	---	0.421

Table S3. Estimated life table

Age (years) x	Number of colonies in each age class (2010)	Age specific mortality q_x	Standardized survival rate l_x	Age specific fecundity m_x
1	9	0.1077	1.0000	0.0000
2	10	0.0897	0.8923	0.0000
3	7	0.1273	0.8122	0.0000
4	22	0.1358	0.7089	0.3025
5	15	0.1216	0.6126	0.2982
6	9	0.0727	0.5381	0.3353
7	12	0.1591	0.4990	0.3222
8	4	0.1207	0.4196	0.3145
9	13	0.1324	0.3689	0.3482
10	20	0.0896	0.3201	0.3342
11	21	0.1628	0.2914	0.3301
12	6	0.1053	0.2440	0.3377
13	23	0.1500	0.2183	0.3213
14	16	0.1154	0.1856	0.2895
15	8	0.1500	0.1642	0.2961
16	9	0.1333	0.1395	0.4160
17	3	0.0500	0.1209	0.3482
18	11	0.1250	0.1149	0.3520
19	3	0.4000	0.1005	0.3020
20	8	0.1250	0.0603	0.2806
21	7	0.5000	0.0528	0.2520
22	3	0.1000	0.0264	0.2975
23	8	0.0100	0.0237	0.3020
24	5	0.0100	0.0235	0.4064
25	1	0.1818	0.0233	0.2520
>26	9	0.1077	0.0192	0.2645