Oecologia (2012) 168:361–369
DOI 10.1007/s00442-011-2098-6

BEHAVIORAL ECOLOGY - ORIGINAL PAPER

The influence of intraspecific competition on resource allocation during dependent colony foundation in a social insect

Adam L. Cronin · Pierre Fédérici · Claudie Doums · Thibaud Monnin

Received: 17 November 2010 / Accepted: 13 July 2011 / Published online: 11 August 2011
© Springer-Verlag 2011

Abstract Organisms face a trade-off between investment in fewer, larger offspring, or more, smaller offspring. Most organisms can adjust investment through variation in the size and number of offspring in response to factors such as resource availability and competition. In some social animals, established colonies divide into groups of individuals that become autonomous, a process known as colony fission (also dependent colony foundation in social insects). Resource allocation under fission can be fine-tuned by adjusting the number of new groups (offspring number) and the number of individuals in each new group (offspring size). We assessed the influence of competition on resource allocation during fission in the ant *Cataglyphis cursor*, by allowing colonies to fission in experimental enclosures of high or low conspecific colony density. The pattern of colony fission was similar to that observed in the field: each fissioning colony produced a few new nests comprising a highly variable number of workers and a single queen, the old queen was often replaced, and new queens were produced in excess. The number of new nests produced depended on the available workforce in the parent colony but was not affected by differences in colony density. Comparison with data from fission under natural field conditions, however, indicates that colonies in enclosures produced fewer, larger new nests, suggesting that resource investment patterns during fission are indeed subject to extrinsic factors. The density of conspecific colonies in the immediate surroundings may be an unreliable estimate of competition intensity and other factors should be considered.

Keywords Colony fission · Ant · Trade-off · Offspring investment · *Cataglyphis cursor*

Communicated by Jérome Casas.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2098-6) contains supplementary material, which is available to authorized users.

A. L. Cronin (✉) · P. Fédérici · C. Doums · T. Monnin
Laboratoire Écologie & Évolution UMR 7625,
Université Pierre et Marie Curie, 7 quai St Bernard,
75252 Paris, France
e-mail: adamcronin@gmail.com

Present Address:
A. L. Cronin
United Graduate School of Agriculture,
Iwate University, 3-18-8 Ueda, Morioka 020-8550, Japan

C. Doums
École Pratique des Hautes Études, Paris, France

Introduction

For a given quantity of resources, many organisms face a trade-off between producing fewer, larger, offspring or more, smaller, offspring (Smith and Fretwell 1974). The benefits of biasing investment toward larger or more offspring depend on environmental factors, such as climate, resource availability, temperature and competition (Brockelman 1975; Parker and Begon 1986; Sibly et al. 1988; Fox and Czesak 2000; Fischer et al. 2003; Marshall et al. 2006; Allen et al. 2008). In most organisms, investment can be varied through adjustments in the size and number of offspring, for example through creating fewer or smaller seeds or eggs, permitting some adaptation to extrinsic factors (e.g., Stanton 1984; Fox et al. 1997; Fox and Czesak 2000; Einum et al. 2002). Investment in each offspring is nonetheless constrained by physical limits on individual size, and resources must be allocated at the time

of offspring production (e.g., number and size of eggs or seeds to produce), well before dispersal.

Reproductive investment may be subject to different rules in organisms such as plants reproducing via stolons (e.g., spider plant *Chlorphytum comosum*) and in some animal societies. In a range of social vertebrates (e.g., African wild dog *Lycaon pictus*) and social insects (e.g., honeybees *Apis mellifera*), reproductive units are not lone individuals but groups. In a process known as fission (also called dependent colony foundation or DCF in social insects; Peeters and Molet 2010), established groups divide into two or more new groups which then become autonomous. Reproductive investment in each offspring can be quantified as the number of individuals assigned to each new group. Investment in each group is relatively unrestricted (without limits on individual size), and, furthermore, the size and number of new groups can be adjusted to suit environmental conditions right up to dispersal. This capacity to readily alter the size of new groups presumably permits fissioning groups a great deal of investment flexibility.

Competition is an important influence on offspring investment because offspring are vulnerable to competition from established adults, and competitive environments can bias investment toward larger offspring in a range of taxa (Stanton 1984; Fox and Mousseau 1996; Hendry et al. 2001; Fischer et al. 2003; Marshall et al. 2006; Allen et al. 2008; Bashey 2008). Competition is particularly important in organisms that tend to saturate their environment, such as ants (Andersen 1992, 2000; Boulay et al. 2010; Parr and Gibb 2010). In many ant species, new colonies are started by lone queens after dispersal (independent colony foundation or ICF). These queens face severe risks from predation, desiccation, and competition from established colonies, and it is estimated that only around 1% succeed (Tschinkel 2006; Hölldobler and Wilson 2009). This high rate of failure has probably led to the evolution of DCF in a large number of taxonomically scattered groups (Peeters and Molet 2010): new groups established in this manner have enough workers to build and defend the nest, rear brood, and forage efficiently, and are relatively good competitors from the very beginning (Peeters and Ito 2001). These benefits come at a cost to dispersal range, however, as ant workers are not winged and, unlike ICF queens, DCF performing groups must disperse on foot. This restricted dispersal can lead to local resource competition among related colonies (Bourke and Franks 1995). To date, however, only a few studies have specifically examined colony reproduction via DCF in ants (e.g., Amor et al. 2011; Chéron et al. 2011), and fewer still have examined the response of colony reproduction to different extrinsic factors (but see Molet et al. 2008; Boulay et al. 2010).

The DCF performing ant *Cataglyphis cursor* (Hymenoptera: Formicidae: Formicinae) is found in open habitats on the north side of the Mediterranean basin. Colonies contain around 700 workers (Lenoir et al. 1988; Clémencet and Doums 2007), and are headed by a single, multiply-mated queen who is the only egg-layer. This species is particular, however, in that both queens and workers can reproduce via thelytokous parthenogenesis (Cagniant 1976; Pearcy et al. 2004a). In south-eastern France, sexual brood (queens and males) are produced during spring, and gynes (new queens, which may be sexually or parthenogenetically produced) mate at the nest entrance with unrelated males (Lenoir et al. 1988; Clémencet et al. 2005; Cronin et al. 2011). A subset of the workers then transport one or more gynes, a number of workers and some brood to previously selected sites to start 2–7 new nests (Chéron et al. 2011). Transports can occur back to the parent colony, and new nests may even be reabsorbed by the parent colony if they prove for some reason to be inviable (Chéron et al. 2011). The number and size of new nests produced by colonies of *C. cursor* can be highly variable for a given initial colony size, and allocation of resources among newly formed groups is biased. This variation probably reflects a diversified bet hedging strategy (Chéron et al. 2011).

Although DCF likely improves the competitive ability of new nests relative to ICF, some new groups produced during DCF by *C. cursor* can contain relatively few workers, and these nests could face significant competition from other colonies in close proximity. Populations of *C. cursor* can contain many colonies (up to 1,100 cols/ha, Lenoir et al. 1990; 268 colonies in an area of 9,905 m^2, Chéron et al. 2011), and it is possible that competition influences the process of resource allocation during DCF (e.g., Pearcy and Aron 2006). Here, we test the hypothesis that colonies of *C. cursor* vary investment (size and number of new nests formed) in response to the competitive environment (Sibly et al. 1988; Bourke and Franks 1995; Allen et al. 2008), by comparing the products of DCF in experimental enclosures of high and low conspecific colony density. We anticipated that a stronger competitive environment would lead to increased investment in offspring size at the cost of offspring number (Brockelman 1975; Fox et al. 1997; Einum et al. 2002; Allen et al. 2008), and hence the production of larger (and thus fewer) new nests for a given colony size.

Materials and methods

Experimental enclosures

Ten experimental enclosures of 10.8 m^2 each were established on the grounds of the Mediterranean Garden of Mas

de la Serre (Laboratoire Arago, Observatoire Océanologique de Banyuls-sur-mer, Université Pierre et Marie Curie) in south-eastern France (42°28.43′N, 3°6.96′E). Enclosures consisted of a circular, vertical, metal chamber 1 m high filled to a height of approximately 0.5 m with a 1:1 sand:earth mix. Netting suspended by plastic poles prevented predation by birds, and enclosure walls had smooth faces preventing ants from escaping. This containment strategy is possible because *C. cursor* is naturally cursorial and lacks the propensity to climb. The site was on a terraced south-facing hill sparsely covered with olive trees. Because only ten enclosures were available, the experiment was performed once in 2009 and then repeated in 2010 to increase sample size.

Collection of colonies

We obtained colonies of *C. cursor* from beachside dune systems from two sites in south-eastern France; near Argelès-sur-mer (42°34.33′N, 3°2.62′E), and near Saint Cyprien (42°39.30′N, 3°2.00′E). Colonies were designated either as 'focal' or 'competitive' colonies. The former could reproduce by DCF and were the focus of the study, whereas the latter could not reproduce and were used to manipulate colony density. Focal colonies were collected at Argelès-sur-mer and chosen when observations indicated the presence of multiple males and/or gynes at the nest entrance, suggesting colony division was about to occur (the presence of males indicates sexual calling by unmated gynes and was a reliable indicator of gyne presence). Suitable colonies were identified via regular monitoring of nests in the days prior to excavation. Competitive colonies were excavated from Saint Cyprien, located 9.5 km north of Argelès-sur-mer. Using colonies from a different population excluded the possibility that competitive and focal colonies were related (Clémencet et al. 2005). Competitive colonies were excavated without monitoring behaviour prior to collection: it was not important if competitive colonies were preparing to fission or not as colonies were modified before introduction to the enclosures (see below). Focal colonies were excavated between 31 May and 3 June 2009 and between 30 May and 2 June 2010, while competitive colonies were excavated between 25 and 31 May 2009 and between 26 May and 2 June 2010. All colonies were maintained in plastic boxes ($\sim 15 \times 20 \times 10$ cm) with water, sugar and dried crickets until installed in enclosures.

Details of focal colonies are summarized in Table 1. It should be noted, however, that brood numbers should be regarded as approximations, as brood, particularly small larvae and eggs, can be lost during excavation. Focal colonies at the time of initial excavation comprised 421–1,796 (870 ± 331, mean $\pm$ SD) workers, and 8–63 (24 ± 15) gynes, similar to previous data from the field (mean workers: 676 ± 440, Lenoir et al. 1988; 731 ± 456, Chéron et al. 2011). The number of workers and gynes did not differ between years (Mann–Whitney: $U = 27$, $z = -1.701$, $p = 0.089$ and $U = 25.5$, $z = -1.814$, $p = 0.063$, respectively; Table 1). The number of workers was positively correlated with the total number of sexual brood (gynes + males + sexual pupae: Pearson's $r = 0.75$, $p < 0.001$, $n = 20$) as shown by Pearcy and Aron (2006), but not the number of gynes ($r = -0.19$, $p = 0.597$, $n = 20$).

Experiment

Two treatments were performed in each year: in the first set of enclosures, focal colonies were installed on their own (low density LD), while in the second set of enclosures, focal colonies were accompanied by two competitive colonies (high density HD). Each treatment had a sample size of five in each year. Enclosures were 10.8 m^2, equating to a colony density of 0.28 colonies per m^2 in HD enclosures and 0.09 colonies per m^2 in LD enclosures. In a previous study, we mapped all colonies ($n = 268$) from our focal colony collection site at Argelès-sur-mer and determined a mean colony density of 0.03 colonies per m^2 (Chéron et al. 2011). Density varied locally so that 60.4% of colonies had no neighbor within a 1.85 m radius (corresponding to the size of the enclosures), while 39.6% had one to five neighbors (and thus a higher density than in the LD treatment). Only 7.5% of field colonies had two or more neighbors within a 1.85 m radius and thus experienced a density equal or higher than of HD enclosures. Therefore, our LD and HD treatments are realistic approximations of natural low and high density conditions.

Focal colonies were paired roughly by colony size (number of workers) and randomly assigned to each treatment. The focal colony in enclosure 10 in 2009 was modified (workers were removed) to fit in with the established allocations (see Table 1). Enclosures used for HD treatments in 2009 were used for LD treatments in 2010. No competitive colonies had gynes when excavated, though some had sexual brood (large cocoons). To standardize the effect of colony density and competition among HD enclosures, all competitive colonies were modified from initial sizes to a standard of 350 workers, one queen, and no brood before installation into enclosures. No brood were included as very few brood were recovered from some colonies during initial excavation.

Colonies were installed in enclosures on 3 and 4 June 2009 and 2 and 3 June 2010 as follows: colonies were transferred to smaller plastic boxes ($\sim 15 \times 15 \times 8$ cm) the night before installation, containing a piece of egg carton to act as substrate for nesting and a hole to permit ants to exit (which was taped closed until colonies were installed). Early the following morning, colonies were taken to the enclosures

Table 1 Composition of focal colonies of *C. cursor*

Treatment	Year	Enclosure	Colonies at onset of the experiment				Colonies at end of the experiment		
			Workers	Brood P/L/SP	Gynes	Males	Workers	New nests	Production mode
HD	2009	1	421	400/0/25	17	9	558	1	P
HD	2009	4	475	200/40/0	22	1	381	1	P
HD	2009	6	1,002	70/450/0	19	29	807	4	P
HD	2009	8	980	200/50/39	10	56	1,019	4	P
HD	2009	9	536	25/50/35	43	2	314	2	S
HD	2010	2	918	0/50/110	16	25	664	3	P
HD	2010	3	816	171/40/42	9	54	559	2	P
HD	2010	5	1,149	32/600/56	63	15	581	3	S
HD	2010	7	1,016	192/200/70	18	18	866	3	P
HD	2010	10	750	50/6/29	25	30	398	2	P
LD	2009	2	919	500/150/5	16	14	1,038	2	P
LD	2009	3	1,294	200/200/30	22	22	1,187	3	?
LD	2009	5	802	160/0/20	9	11	732	2	S
LD	2009	7	446	0/50/1	11	1	333	1	P
LD	2009	10	450	15/30/23	12	27	345	1	P
LD	2010	1	1,041	0/130/106	31	26	666	3	P
LD	2010	4	824	11/50/45	19	34	517	3	P
LD	2010	6	1,796	1/200/165	25	69	1,328	3	P
LD	2010	8	999	0/100/27	46	15	814	3	P
LD	2010	9	768	118/200/58	48	2	656	2	P

The compositions of focal colonies are shown when they were transplanted into the enclosures at the onset of the experiment and when collected at the end of the experiment. The former includes number of workers, brood (*P* pupae, *L* larvae, *SP* sexual pupae), gynes and males. The latter includes pooled number of workers in all new nests, number of new nests excavated, and mode of production of gynes found in new nests. The focal colony in enclosure 10 was modified prior to introduction to enclosures from 883 workers and 60 larvae to 450 workers and 30 larvae. The latter was used in all calculations. One new nest in enclosure 8 in 2009 was not discovered until later and may have produced additional workers

and a small hole sufficient to contain the box was excavated. Boxes were inserted into these holes, which were then covered with a terra-cotta pot-plant tray (20 cm) and a thin layer of earth. Focal colonies were installed in the center of enclosures with competitive colonies placed near walls opposite each other (in HD enclosures).

Because focal colonies were collected on the basis of the presence of active males at the nest entrance and/or gynes, it is very likely that mating had taken place prior to nest excavation in the field. However, to ensure that all females had the maximum opportunities to mate, males were introduced to the enclosures on an almost daily basis for the first 2 weeks of the experiment. One to three males, which had been collected during the previous few days at Argelès-sur-mer where they were patrolling around nest entrances to mate with gynes, were placed in each enclosure. These males were observed patrolling the enclosures though no actual matings were seen.

Colonies were left in the enclosures for 20–21 days in 2009 and 19 to 20 days in 2010. Enclosures were monitored for the creation of new nests approximately every 2 days throughout this period. New nests were detected by foragers returning to the nest and/or by workers digging soil at the nest entrance. Most were established within the first few days of the experiment. New nests were marked, and monitored for activity until the end of the experiment when they were excavated. All occupants were censused and placed in ethanol for later genetic analyses. Queens from all excavated colonies were dissected to determine insemination and ovarian status. The timing of excavations was based on the absence of construction of any new nests during the preceding week, and completion of colony foundation activity in concurrently monitored field colonies at Argelès-sur-mer. Field data suggest colony fission is complete after 7 days (Chéron et al. 2011), and thus it seems safe to assume that fission was complete in the enclosures when nests were excavated.

Genetic analyses

All queens recovered at the end of the experiment were genotyped using 12 microsatellite markers developed for

C. cursor: Ccur11, Ccur26, Ccur46, Ccur 51, Ccur 58, Ccur61, Ccur 63, Ccur 65, Ccur76, Ccur89, Ccur 99 and Ccur 100; (Doums et al., unpublished; Pearcy et al. 2004b). DNA was extracted from the head of queens and head + thorax of workers using a QIAgen DNAeasy kit (Valencia, CA) and resuspended in 150 µl of elution buffer. Polymerase chain reactions (PCR) were carried out in a 10-µl volume containing 1 µl of DNA solution, 0.15 µl of dNTP 40 mM, 0.75 U of Taq polymerase (QIAgen), 1 µl Buffer 10×, and either: 10 µM each primer co-amplified as (Ccur26, Ccur46, Ccur76) or (Ccur11, Ccur63, Ccur89), or (0.10 µM of Ccur 51, 0.10 µM of Ccur 58, 0.25 µM of Ccur 65 and 0.15 µM of Ccur 99) or (0.75 µM of Ccur 61 and 0.20 µM of Ccur 100). The amplified fluorescent fragments were visualized using an automated ABI Prism 310 Sequencer, and allele sizes were estimated using Genescan 3.2.1 (Applied Biosystems).

Genetic differentiation is detectable over distances as short as a few kilometres in *C. cursor* (Clémencet et al. 2005), and thus in HD enclosures we were able to differentiate between queens from focal (Argelès-sur-mer) and competitive (Saint Cyprien) colonies based on genotype data. We employed the program WHICHRUN (Banks and Eichert 2000) to assign queens of excavated colonies to source populations based on known gene frequency data for each population (Doums, unpublished) in 2009. As no competitive queens were lost in 2009, competitive colony queens were paint-marked on the thorax prior to establishment in enclosures in 2010, and all were recovered. We assessed where possible whether new queens were most likely to have been sexually or parthenogenetically produced by comparing genotypes of queens in new nests (assuming thelytokous parthenogenesis with central fusion; Pearcy et al. 2004a, 2006).

Statistics

Statistics were carried out in the 'R' statistical package, version 2.11.1 for Windows (R Development Core Team 2010). General linear models and mixed models were employed as appropriate (see "Results"). We initially fitted a full model including all explanatory variables and subsequently removed variables by stepwise deletion. Significance values are reported for terms added to this minimum adequate model. All means are quoted as (arithmetic mean ± standard error) unless otherwise noted.

Results

In HD enclosures in 2009, focal colonies and any new colonies produced by focal colonies were unambiguously distinguished from competitive colonies using population gene frequencies in WHICHRUN. In 2010, competitive colonies were distinguished by the presence of marked queens, all of which remained at the time of collection. Hereafter, colony number and composition refer exclusively to focal colonies and the new nests they produced by colony fission except where otherwise noted. In the following account, we use the term 'focal colony' to refer to the situation at the onset of the experiment, before fission occurred, and 'new nest' to the situation at the end of the experiment, whether fission occurred or not. Thus, each enclosure initially contained one focal colony, and at the end of the experiment contained one or more new nests.

Number of new nests produced and effect of colony density

At the end of the experiment, we excavated between one and four new nests (mean = 2.35 ± 0.88) from each enclosure. It was not possible to determine with certainty which were 'offspring' nests and which was the original parent nest because: (1) none of the nests remained at the initial installation site, and (2) in at least some cases the original queen was replaced (see below). This is in agreement with data from the field (Chéron et al. 2011). We thus considered all nests excavated at the end of the experiment equally as products of DCF ('new nests'). Colony fission occurred (two or more new nests were excavated) in six of the ten enclosures in 2009 (mean new nests = 2.1 ± 1.2; range 2–4) and in all enclosures in 2010 (mean = 2.7 ± 0.5; range 2–3; Fig. 1; Table 1).

All focal colonies containing over 500 workers fissioned whereas those with fewer workers did not. This suggests that the number of workers was an important trigger for colony fission in the enclosures. In contrast, the number of worker pupae was highly variable and is probably not important in the decision to divide or not (e.g., the colony in enclosure 1 in 2009 contained 421 workers and 400 pupae, but did not fission, whereas the colony in enclosure 9 in 2009 with 536 workers and 25 pupae did). The number of gynes was also highly variable and gynes were always produced in excess (range 9–63 gynes for one to four new nests; Table 1).

The relationship between the size of the colony before fission and the number of new nests produced by colony fission is summarized in Fig. 2, which indicates a positive linear relationship in both HD and LD treatments. We analyzed this relationship with a GLM implemented in R, with year, enclosure, treatment, colony size (initial number of workers) and number of gynes as initial explanatory variables. Initial tests employing Poisson errors indicated under-dispersion and thus we remodeled the GLM with quasi-Poisson errors. The minimum adequate model comprised only treatment and colony size, and indicated a

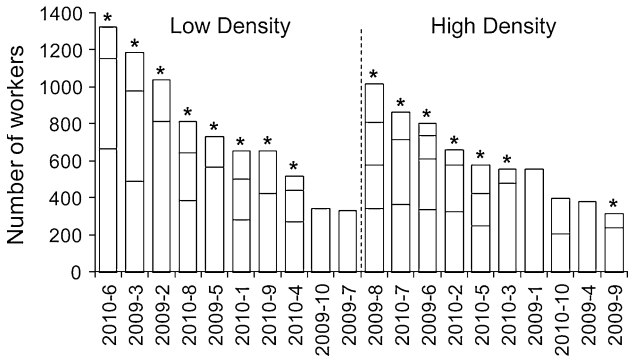

Fig. 1 Number of *C. cursor* workers in new nests in each enclosure as excavated at end of experiment. *Stacked bars* indicate size (number of workers) of individual nests. *Numbers* at the base of each *column* indicate year and enclosure number. *Asterisks* indicate significantly skewed number of workers among new nests in the same enclosure, using Nonacs (2000) B statistic at $p < 0.05$. One nest in enclosure 8 in 2009 was not excavated until 2010 and thus the number of workers recorded may not accurately reflect the number just after fission. This colony was excluded from analyses of survivorship and new nest size

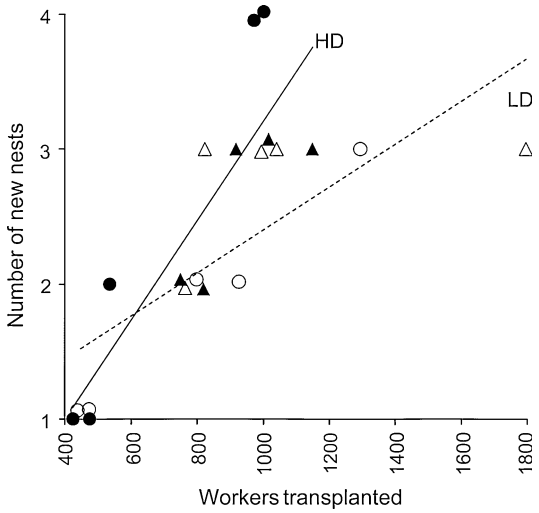

Fig. 2 Relationship between initial number of workers in focal colonies and the number of new colonies produced. Colonies in high density (*HD*) enclosures are shown in *black* (*solid line*) while low density (*LD*) treatments are in *white* (*broken line*). Data from 2009 are indicated by *circles* while those from 2010 are indicated by *triangles*. For clarity, a few overlapping points have been slightly repositioned

highly significant effect of colony size ($t_{16} = 3.06$, $p = 0.008$), the slope of the relationship being higher in the HD enclosures (significant interaction between colony size and treatment; $t_{16} = 2.30$, $p = 0.035$; Fig. 2). However, the interaction was not significant after the removal of the outlier colony with the highest colony size (the colony in enclosure 6 in 2010, on the far right of Fig. 2), and colony size was then the only significant effect in the model without the outlier ($t_{17} = 5.75$, $p < 0.001$; minimum adequate model comprising colony size only).

Composition of new nests

In the field, new nests typically contain several gynes when they are founded and monogyny is restored within a week (Chéron et al. 2011). In our experiment, all new nests contained a single queen when excavated, and dissections revealed that all queens were inseminated and had well-developed ovaries. This supports our assumption that colony fission was completed by the end of the experiment.

We inferred the mode of production of gynes from genetic data (Electronic Supplementary Material) assuming thelytokous parthenogenesis with central fusion (see Pearcy et al. 2004a, 2006). Queens were considered produced by parthenogenesis when they had the same genotype at all loci (or differences at one or two loci that could be explained by recombination under thelytoky) and were otherwise considered sexually produced. The mode of production could be assessed in all but one colony (enclosure 3 in 2009) where it was unclear. These data indicate that, in all enclosures in which production mode could be inferred, all new nests contain either only parthenogenetically produced or only sexually produced queens. All queens were parthenogenetically produced in three of five cases in 2009 and nine of ten cases in 2010 (75% overall; Table 1). Genetic data also indicate that in at least 7 of 20 enclosures (3, 5 and 9 in 2009, and 4, 6, 8 and 9 in 2010), queen replacement had occurred, as no genotype present could be that of the mother of the remaining queens.

The number of workers in new nests recovered from each enclosure is summarized in Fig. 1. One new nest in enclosure 8 in 2009 was overlooked when collecting colonies (smallest nest in enclosure 8, 2009; Fig. 1) and was collected later than the other nests, and thus had time to produce additional workers. This enclosure's data were therefore excluded from calculations of worker numbers below. In enclosures in which fission occurred, there were 2–4 new nests per enclosure, each comprising 66–817 workers (mean 278 ± 170; $n = 40$ new nests from 15 enclosures). The allocation of workers among new nests in the fissioning enclosures was analyzed using Nonacs B statistic of reproductive skew (Nonacs 2000), with the number of workers representing 'individual benefits'. This analysis indicated that allocation of workers to new nests was skewed in all cases except for enclosure 10 in 2010 (Fig. 1). We explored possible factors affecting worker number in new nests using a mixed model implemented in R, with worker number as the dependent variable, treatment and enclosure as fixed effects and original (focal)

colony as a random factor (excluding enclosure 8 in 2009). There were no significant effects ($p > 0.05$).

Variation in colony size during the experiment

Focal colonies varied in size over the course of the experiment. The number of workers recovered at the end of the experiment (pooled from all new nests) on average exhibited a 21% decline (−49 to +33%; Table 1) compared to the number of workers at the time of transplantation, and this rate did not differ between HD and LD treatments (−24 and −19%, respectively; Mann–Whitney: $U = 30$, $z = -1.225$, $p = 0.221$).

Competitive colonies did not divide, and indeed could not, as any gynes had been removed. One competitive colony in enclosure 8 in 2009 failed or was destroyed, while all other competitive colonies diminished in size by 37% on average. This was higher than the average loss in focal colonies but is unsurprising given the absence of brood in competitive colonies at the start of the experiment. The old queen remained in all competitive colonies at the time of collection.

Discussion

Parental organisms can derive greater fitness from directing investment of limited resources into increased offspring size rather than increased offspring number in some contexts, such as where offspring face competition (Brockelman 1975; Fox et al. 1997; Einum et al. 2002; Allen et al. 2008). We tested this effect in an ant reproducing via colony fission by transplanting colonies of the ant *C. cursor* into experimental enclosures where we manipulated colony density. Most transplanted colonies fissioned, and did so in a manner akin to that observed in unmanipulated field colonies: they produced several new nests, biased resource allocation (i.e., worker number) among these nests, restored monogyny in all new nests and often replaced the initial queen. However, in this experiment, an environment with higher initial intraspecific colony density (presence of competitive colonies) did not give rise to larger fission products, suggesting fissioning colonies were not influenced by differences in the initial competitive environment. The absence of any effect of our treatment could also be explained by colonies being unaware of the presence of competitive colonies or unable to respond to the threat they posed, yet these possibilities are unlikely for the following reasons. Colony densities in our treatments were representative of those in the field: 60% of field colonies experienced a lower density than that in our LD treatments whereas 40% experienced a higher density, while only 7.5% of colonies in natural conditions experienced densities equal or higher than those in our HD enclosures. Given the relatively small area of enclosures, especially relative to the normal foraging area of this species of up to 130 m^2 (Lenoir et al. 1990), it therefore seems safe to assume that colonies were very soon as aware of each other's presence as those in the field. Similarly, it is unlikely that colonies were unable to respond to any threat represented by competitive colonies because focal colonies were not limited to initial impressions of the competitive environment but could adjust investment on an ongoing basis throughout the experiment: observations of fission in the field suggest that transporting workers of *C. cursor* can move workers and brood back to the parent nest during the colony fission process in natural populations (Chéron et al. 2011). Entire new nests can potentially be reabsorbed by the parent colony during this process and relocated to another new nest afterwards. The lack of a colony density effect may be explained by the fact that colonies of *Cataglyphis* ants compete for forage over an area of tens of meters away from the nest (Lenoir et al. 1990), such that local colony density around the nest may be relatively unimportant. Indeed, *C. cursor* does not defend a territory like many other ants, and intra-specific scramble competition with neighboring colonies occurs throughout the foraging area (Lenoir et al. 1990; Cerdá et al. 1997).

The flexible nature of the fission process in *C. cursor* presumably lends colonies the capacity to adapt resource allocation to variation in a range of extrinsic factors. While our treatment did not influence the pattern of fission, some support for this adaptability comes from a comparison between our data and fission under natural conditions in the field. Chéron et al. (2011) studied colony fission in 19 colonies of *C. cursor* under natural conditions at the same site from which focal colonies were sourced for our experiment. Their study was undertaken concurrently (in 2009) and approximately 12 km from our enclosures. Climatic conditions were thus similar though our site was more shaded and approximately 70 m higher. The mean size of fissioning colonies, inferred in both cases from fission products as this was the only method available for field colonies, was similar (enclosures: 741 ± 278, $n = 15$ vs. field: 731 ± 456, $n = 19$; $t_{32} = 0.07$, $p = 0.940$). Nonetheless, colonies in enclosure produced fewer new nests than field colonies (2.8 ± 0.7, $n = 16$ vs. 4.0 ± 11.3, $n = 19$; $t_{33} = -3.39$, $p = 0.002$), the average size of new nests in the enclosures was larger (284 ± 107 workers, $n = 15$ vs. 190 ± 129 workers, $n = 19$; $t_{32} = 2.26$, $p = 0.031$), and colonies in enclosures allocated more workers to their smallest new nest (145 ± 58, $n = 15$ vs. 76 ± 46, $n = 19$; $t_{32} = 3.91$, $p < 0.001$). In addition, colonies with fewer than 500 workers did not fission in the

enclosures whereas this did occur in the field. Larger colonies in the enclosures also tended to produce more new nests whereas those in the field produced larger new nests. Colonies in enclosures thus allocated resources differently to those in the field, suggesting that extrinsic factors can indeed elicit plastic responses in resource allocation during colony fission.

Our data do not permit us to attribute causality to particular factors underlying the differences between fission in the field and in enclosures, but we can speculate upon some possibilities. In addition to competition with foreign conspecifics, ant colonies are subject to competition between new nests created during fission (i.e., local resource competition or LRC; Bourke and Franks 1995) because dispersal distances under DCF are constrained by dispersal on foot (Peeters and Ito 2001; Peeters and Molet 2010). Chéron et al (2011) concluded that LRC is unlikely to be severe in field colonies of *C. cursor*, as foreign conspecific colonies were closer on average than fission products. However, mean dispersal distance in the field was on average 7 m, greatly exceeding that possible in the enclosures. LRC may thus be a more potent concern in the confined environment of the enclosures, where foraging area is also limited, placing constraints on the number of new nests produced. A further possibility is that absolute density of nests (i.e., focal and competitive colonies) in both treatment and control enclosures greatly exceeded that in the field once fission had begun. At the end of the experiment, LD and HD enclosures contained 2.3 ± 0.8 nests (i.e. 0.21 nests/m^2) and 4.4 ± 1.0 nests (2.5 ± 1.1 new nests derived from focal colonies plus 1.9 ± 0.3 competitive colonies, i.e., 0.41 nests/m^2), respectively. This is higher than in the field where only 7.5 and 1.1% of colonies had at least two and four neighbors within a 1.8 m radius, respectively. An effect of very high absolute density could potentially swamp any treatment effect, but the available data do not allow us to disentangle this possibility from that of LRC.

Our study provides a rare opportunity to examine pre- and post-fission colony composition, permitting us to examine survivorship of gynes and, to some degree, replacement of old queens. *C. cursor* is strictly monogynous, and thus the maximum number of post-fission gynes (new queens) is restricted by the number of new nests produced (excess queens are killed). However, the number of queens produced prior to colony division was very high relative to the number of new colonies produced. This over-production of gynes may serve as a form of insurance in case of predation or other accidents during transport of gynes to new nests. However, it also raises the possibility of a larvae/adult conflict for caste determination as observed in Meliponine bees (Ratnieks 2001; Wenseleers and Ratnieks 2004) and in *C. floricola*, where it has been proposed as the basis for the evolution of ergatoids (wingless, worker-like queens; Amor et al. 2011). A further possibility is a strategy of intra-specific parasitism: colonies may be more vulnerable to intrusion by unrelated individuals during emigration or colony fission, and excess gynes could gain high benefits from becoming queen in an unrelated colony.

Queen replacement occurred in at least 35% of enclosures during the fission process. Field data (Chéron et al. 2011) suggest that the rate of queen replacement in naturally fissioning colonies in the population used in this study was also high, at 53% ($n = 19$). Because of asexual reproduction, queens are effectively able to perpetuate themselves, while workers could also favor new parthenogenetically produced queens over old queens depending on the long-term costs of asexuality. Our data indicate the proportion of sexually produced (vs. parthenogenetic) queens in new nests was 20%. In contrast, a previous study reported the proportion of sexually produced gynes in another population was <4% (Pearcy et al. 2004a). Comparative data on initial (pre-fission) frequencies of sexual and parthenogenetically produced queens are unavailable at present, but it would be of interest to explore the relative success of each form during colony fission and inheritance.

Our study concurs with field data demonstrating a high variation in investment in new nests both between and within colonies. In the absence of other rationale for generating such variation, this supports Chéron et al.'s (2011) conjecture that *C. cursor* follows a diversified bet hedging strategy (Olofsson et al. 2009). In addition, our study suggests that, while colonies relocated to enclosures retain this investment diversity, they can adjust average investment toward fewer, larger new nests, implying the influence of extrinsic factors (e.g., Rosenheim et al. 1996). LRC among new nests produced during colony fission may be a significant factor in constraining the number of new nests produced under highly constrained dispersal such as within our enclosures. Further studies of environmentally contingent investment strategies in other DCF species may help identify causal factors and reveal interesting parallels with offspring investment in other organisms.

Acknowledgments We would like to thank the Laboratoire Arago (Observatoire Océanologique de Banyuls-sur-mer, Université Pierre et Marie Curie) for permitting this study to take place on the experimental grounds of the Mediterranean Garden of Mas de la Serre, and the Coast Conservation Office ("Conservatoire du littoral") for allowing the collection of 'competitive' colonies in a protected bird nesting area in Saint Cyprien. We are very grateful to Laurent Belkadi, Nathalie Guillory, Claudy Haussy, David Laloi, Jean-Christophe Lenoir and Claire Tirard for help in erecting the enclosures. We also thank Mathieu Molet for help collecting and installing colonies and Peter Nonacs, Alain Lenoir and three anonymous referees for helpful comments on this and an earlier version of the manuscript. This work was funded by ANR-06-BLAN-0268.

References

Allen RM, Buckley YM, Marshall DJ (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. Am Nat 171(2):225–237. doi:10.1086/524952

Amor F, Ortega P, Jowers MJ, Cerdá X, Billen J, Lenoir A, Boulay R (2011) The evolution of worker–queen polymorphism in *Cataglyphis* ants: interplay between individualand colony-level selections. Behav Ecol Sociobiol 65:1473–1482. doi:10.1007/s00265-011-1157-7

Andersen AN (1992) Regulation of momentary diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. Am Nat 140(3):401–420

Andersen AN (2000) A global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC, pp 25–34

Banks MA, Eichert W (2000) WHICHRUN (Version 3.2) a computer program for population assignment of individuals based on multilocus genotype data. J Hered 91:87–89

Bashey F (2008) Competition as a selective mechanism for larger offspring size in guppies. Oikos 117(1):104–113. doi:10.1111/j.2007.0030-1299.16094.x

Boulay R, Galarza JA, 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

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Brockelman WY (1975) Competition, the fitness of offspring, and optimal clutch size. Am Nat 109:677–699

Cagniant H (1976) Distribution, écologie et nid de la fourmi *Cataglyphis cursor* Fonscolombe (Hyménoptères Formicidae). Vie Milieu 26:265–276

Cerdá X, Retana J, Cros S (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. J Anim Ecol 66(3):363–374

Chéron B, Cronin A, Doums C, Fédérici P, Haussy C, Tirard C, Monnin T (2011) Unequal resource allocation among colonies produced by fission in the ant *Cataglyphis cursor*. Ecology 92(7):1448–1458. doi:10.1890/10-2347.1

Clémencet J, Doums C (2007) Habitat-related microgeographic variation of worker size and colony size in the ant *Cataglyphis cursor*. Oecologia 152(2):211–218

Clémencet J, Viginier B, Doums C (2005) Hierarchical analysis of population genetic structure in the monogynous ant *Cataglyphis cursor* using microsatellite and mitochondrial DNA markers. Mol Ecol 14(12):3735–3744

Cronin AL, Monnin T, Haussy C, Doums C (2011) Opportunities for mate choice in the fission performing ant *Cataglyphis cursor*. Ecol Entomol. doi:10.1111/j.1365-2311.2011.01291.x

Einum S, Hendry AP, Fleming IA (2002) Egg-size evolution in aquatic environments: does oxygen availability constrain size? Proc R Soc Lond B 269:2325–2330. doi:10.1098/rspb.2002.2150

Fischer K, Brakefield PM, Zwaan BJ (2003) Plasticity in butterfly egg size: why larger offspring at lower temperatures? Ecology 84:3138–3147

Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369

Fox CW, Mousseau TA (1996) Larval host plant affects fitness consequences of egg size variation in the seed beetle *Stator limbatus*. Oecologia 107(4):541–548

Fox CW, Thakar MS, Mousseau TA (1997) Egg size plasticity in a seed beetle: an adaptive maternal effect. Am Nat 149(1):149–163

Hölldobler B, Wilson EO (2009) The super-organism. the beauty, elegance and strangeness of insect societies. Norton, New York

Hendry AP, Day T, Cooper AB (2001) Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. Am Nat 157(4):387–407

Lenoir A, Nowbahari E, Querard L, Pondicq N, Delalande C (1990) Habitat exploitation and intercolonial relationships in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Acta Oecol 11(1):3–18

Lenoir A, Quérard L, Pondicq N, Berton F (1988) Reproduction and dispersal in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Psyche 95(1–2):21–44

Marshall DJ, Cook CN, Emlet RB (2006) Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87(1):214–225

Molet M, van Baalen M, Peeters C (2008) Shift in colonial reproductive strategy associated with a tropical-temperate gradient in *Rhytidoponera* ants. Am Nat 172:75–87

Nonacs P (2000) Measuring and using skew in the study of social behavior and evolution. Am Nat 156:577–589

Olofsson H, Ripa J, Jonzén N (2009) Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proc R Soc Lond B 276:2963–2969. doi:10.1098/rspb.2009.0500

Parker GA, Begon M (1986) Optimal egg size and clutch size-effects of environment and maternal phenotype. Am Nat 128(4):573–592

Parr CL, Gibb H (2010) Competition and the role of dominant ants. In: Lach L, Parr C, Abbott K (eds) Ant ecology. Oxford University Press, Oxford, pp 77–96

Pearcy M, Aron S (2006) Local resource competition and sex ratio in the ant *Cataglyphis cursor*. Behav Ecol 17(4):569–574

Pearcy M, Aron S, Doums C, Keller L (2004a) Conditional use of sex and parthenogenesis for worker and queen production in ants. Science 306:1780–1783

Pearcy M, Clémencet J, Chameron S, Aron S, Doums C (2004b) Characterization of nuclear DNA microsatellite markers in the ant *Cataglyphis cursor*. Mol Ecol Notes 4(4):642–644

Pearcy M, Hardy O, Aron S (2006) Thelytokous parthenogenesis and its consequences on inbreeding in an ant. Heredity 96:377–382

Peeters C, Ito F (2001) Colony dispersal and the evolution of queen morphology in social Hymenoptera. Annu Rev Entomol 48:601–630

Peeters C, Molet M (2010) Colonial reproduction and life histories. In: Lach L, Parr C, Abbott K (eds) Ant ecology. Oxford University Press, Oxford, pp 159–176

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ratnieks FLW (2001) Heirs and spares: caste conflict and excess queen production in *Melipona* bees. Behav Ecol Sociobiol 50:467–473

Rosenheim JA, Nonacs P, Mangel M (1996) Sex ratios and multifaceted parental investment. Am Nat 148(3):501–535

Sibly R, Calow P, Smith RH (1988) Optimal size of seasonal breeders. J Theor Biol 133(1):13–21

Smith CC, Fretwell SD (1974) Optimal balance between size and number of offspring. Am Nat 108(962):499–506

Stanton ML (1984) Seed variation in wild radish-effect of seed size on components of seedling and adult fitness. Ecology 65(4):1105–1112

Tschinkel WR (2006) The fire ants. Harvard University Press, Cambridge

Wenseleers T, Ratnieks FLW (2004) Tragedy of the commons in *Melipona* bees. Biol Lett 271:S310–S312