



Qualitative bias in offspring investment in a superorganism is linked to dispersal and nest inheritance



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How parents invest resources in offspring is a central aspect of life history. While investment strategies have been well studied in solitary organisms, comparatively little has been done on social species, including the many that reproduce by fission. Under colony fission, a parent colony divides resources (individuals) to form two or more offspring colonies. Because individuals differ in characteristics (e.g. size), there is opportunity for both quantitative and qualitative bias in their allocation. In this study we investigated the qualitative aspect of offspring investment during colony fission. Colonies of the ant *Cataglyphis cursor* fission into multiple offspring colonies as part of their lifecycle, and the distribution of workers is quantitatively biased. We found that investment is also qualitatively biased in terms of worker size and worker genetic characteristics (patrilines). This bias was mainly between the offspring colony that inherited the original nest and offspring colonies that dispersed to new nesting sites. In 74% of cases, dispersing colonies contained larger workers, and the distribution of genetic patrilines was biased in two of six cases in a manner that cannot be explained by the observed variation in worker size between patrilines. Fission also led to a reduction in diversity in offspring colonies compared to the parent colony, in terms of both worker size (70% of cases) and genetic diversity (40% of cases). These patterns are probably the result of differing dispersal probability between workers of different patrilines and of different size. This differential allocation may be adaptive because larger workers may be of disproportionate value to dispersing colonies, and their loss an acceptable cost to the colony inheriting the nest. © 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

How individuals allocate resources during reproduction is a central focus of life history theory. While there can be advantages to producing larger offspring (Krist, 2011; Marshall & Keough, 2008), parents with finite resources face a trade-off between offspring size and number (Smith & Fretwell, 1974), and the vast literature exploring the influence of varied quantitative investment on offspring characteristics indicates that the optimal investment strategy is context dependent (Bernardo, 1996; Burgess, Bode, & Marshall, 2013). Less attention has been paid to the importance of qualitative variation in investment, although some authors have suggested this may be of at least equal importance (Krist, 2011;

Mousseau & Fox, 1998; Nager, Monaghan, & Houston, 2000). For example, differential deposition of hormones in avian eggs can influence offspring phenotype and behaviour (reviewed in Gil, 2008; Groothuis, Müller, von Engelhardt, Carere, & Eising, 2005), and indeed, the available evidence suggests that variation in the composition of invested resources may have diverse effects in a wide range of species (De Fraipont, Clobert, John, & Meylan, 2000; Gil, 2008; McGraw, Adkins-Regan, & Parker, 2005).

Theoretical and empirical studies of offspring investment have focused on solitary organisms (Stearns & Hoekstra, 2005), while the vast and often ecologically dominant social fauna has suffered a dearth of attention. Social insect colonies are superorganisms, and new colonies are created through one of two different modes that differ strongly in the manner in which resources are allocated. Under independent colony foundation (ICF) young queens depart

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alone from the parent colony, disperse and mate on the wing, and start new colonies on their own. Under this strategy, the quantity and quality (e.g. size, energetic resources) of individual sexual offspring (dispersing queens and males) produced by the colony will be the main determinant of colony reproductive success. In contrast, under dependent colony foundation (DCF, also known as swarming, budding or colony fission), young queens start new colonies with the help of nestmate workers (reviewed in: Cronin, Molet, Doums, Monnin, & Peeters, 2013; Peeters & Molet, 2010). These queens leave the parent colony accompanied by numerous workers and are continuously helped and protected. Colony reproductive success in this case depends largely on the number and characteristics of workers (e.g. age, size and genetic lineage) allocated to the new colonies. However, despite the abundance and ecological importance of species employing DCF (Cronin et al., 2013), and the growing body of theoretical (Bulmer, 1983; Cronin, Loeuille, & Monnin, 2016; Crozier & Pamilo, 1996; Rangel, Reeve, & Seeley, 2013) and empirical (Amor et al., 2011; Briese, 1983; Chéron, Cronin et al., 2011; Cronin, Fédérici, Doums, & Monnin, 2012; Fernández-Escudero, Seppä, & Pamilo, 2001; Gotwald, 1995; Lenoir, Quérard, Pondicq, & Berton, 1988; Seeley, 1996; van Veen & Sommeijer, 2000) literature on the quantitative aspects of reproductive allocation during DCF, studies on qualitative variation during DCF in social insects have been largely restricted to assessing the potential for nepotism, for which no convincing evidence has been found (Breed, 2014; Heinze, Elsishans, & Hölldobler, 1997; Rangel, Mattila, & Seeley, 2009; Solís, Hughes, Klingler, Strassmann, & Queller, 1998).

In addition to the number of workers, an important consideration under DCF is the characteristics of the workers allocated to offspring nests. Workers are not identical entities, but can differ in a variety of ways including genetic makeup, experience, age and morphology. These factors are not necessarily independent, as for example some degree of genetic determination of worker morphology has been demonstrated in several species of ants (Fraser, Kaufmann, Oldroyd, & Crozier, 2000; Hughes, Sumner, Van Borm, & Boomsma, 2003; Jaffe, Kronauer, Kraus, Boomsma, & Moritz, 2007). Trait variation among workers means that they are not of equivalent fitness value for a new colony, and the number of workers allocated may thus be an incomplete measure of reproductive investment. Furthermore, because social organisms are subject to selection at multiple levels (Gardner & Grafen, 2009; Hölldobler & Wilson, 2009), the optimal allocation strategy from a colony perspective may not be the same as that from an individual perspective. A range of benefits to having a genetically diverse workforce has been demonstrated in social insects (Baer & Schmid-Hempel, 1999; Hughes & Boomsma, 2004; Seeley & Tarpay, 2007; Ugelvig, Kronauer, Schrempf, Heinze, & Cremer, 2010), and we might thus expect allocation to favour the maintenance of genetic diversity in newly produced colonies. However, despite the lack of evidence for nepotism, individual selection could potentially favour the association of workers with more closely related full-sister gynes (young queens), leading to reduced genetic diversity and thus the opposite pattern to that expected by colony level selection.

In this study, we investigated the potential for qualitative bias in reproductive allocation during DCF in a superorganism, using the thermophilic ant *Cataglyphis cursor*. This species reproduces exclusively via colony fission (a term we use here synonymously with DCF, following Cronin et al., 2013), with a parent colony producing on average four (range 2–7) offspring colonies containing a highly variable number of workers (Chéron, Cronin et al., 2011; Cronin et al., 2012; Lenoir et al., 1988). Workers exhibit continuous variation in size (Cagniant, 1983; Clémencet & Doums, 2007), an important trait in thermophilic ants because it is linked with

heat resistance and thus affects foraging behaviour and interspecific scramble competition (Cerdá, 2001; Cerdá & Retana, 1997). Colonies are headed by a single queen, mated with on average 5.6 ± 1.3 males (range 4–8; Percy, Aron, Doums, & Keller, 2004), and thus contain multiple worker patriline (Chéron, Monnin, Fédérici, & Doums, 2011; Percy et al., 2004). In addition, although queens produce workers sexually and males by arrhenotokous parthenogenesis as in most Hymenoptera, this species is unusual in that new gynes (i.e. young virgin queens) can be produced either sexually or via thelytokous parthenogenesis (Doums et al., 2013; Percy et al., 2004).

Our investigation focuses on worker size and genetic patriline. From both of these perspectives, there are reasons to expect the pattern of allocation will deviate from our null hypothesis that workers are randomly distributed. First, worker size in ants is positively associated with higher longevity (Porter & Tschinkel, 1985), resilience to starvation (Heinze, Foitzik, Fischer, Wanke, & Kipyatkov, 2003), foraging efficiency (e.g. temperature resistance, Cerdá & Retana, 1997; Cerdá & Retana, 2000; Clémencet, Cournault, Odent, & Doums, 2010) and colony defence (Hölldobler & Wilson, 1990). However, as size increases so does production cost, and only well-established colonies may be able to produce the large workers they need. Newly founded colonies may thus benefit disproportionately from the presence of larger workers compared to larger, established colonies. We might therefore expect larger workers to be preferentially allocated to small colonies and/or colonies that disperse to new nesting sites (where a new nest must be excavated), with their corresponding depletion in the parent colony. Second, from a genetic standpoint, bias could arise if workers exhibit nepotistic tendencies and preferentially associate with gynes of their own patriline during fission for inclusive fitness purposes. However, in *C. cursor*, this can only occur in colonies with sexually produced gynes, because parthenogenetically produced gynes are equally related to all workers regardless of patriline. If nepotism does occur, we might therefore expect differences in patriline distribution of workers between sister colonies (i.e. offspring colonies derived from the fission of the same parent colony) containing sexually produced gynes from different patrilines. Alternatively, workers of different patrilines in bees and ants may exhibit different dispersal propensities (Kryger & Moritz, 1997; Seppä, Fernández-Escudero, Gyllenstrand, & Pamilo, 2008), and this could lead to bias in the distribution of patrilines between the offspring colony that inherited the nest and those that dispersed to new nesting sites. Finally, size-based allocation of workers may be confounded by genetic effects if these factors are related. Although genetic variation has not been convincingly linked to differences in worker size in two previous studies in *C. cursor* (Eyer, Freyer, & Aron, 2013; Fournier, Battaille, Timmermans, & Aron, 2008) this pattern has been demonstrated in other ant species (Evison & Hughes, 2011; Fraser et al., 2000; Hughes et al., 2003; Jaffe et al., 2007; Rheindt, Strehl, & Gadau, 2005) and we reassessed this possibility here.

METHODS

We used 54 offspring colonies of *C. cursor* from a previous study (Chéron, Cronin et al., 2011). These colonies were collected as products of the fission of 14 parent colonies in the field at Argelès-sur-Mer in southern France. 'Parent' and 'offspring' colonies refer to colonies before and after fission, respectively. That is, each parent colony divided into several offspring colonies, and offspring colonies derived from the same parent colony are thus 'sister' colonies. In *C. cursor* the queen of the monogynous parent colony (i.e. the mother queen) is retained in approximately half of all reproducing colonies (Chéron, Cronin et al., 2011) so that one of the resulting

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