



Sex Investment Ratio and Split Sex Ratio in the Fission-Performing Ant *Cataglyphis tartessica*

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Abstract Inclusive fitness theory predicts that the sex investment ratio should be female biased in social insects with haplodiploidy-generated relatedness asymmetry (between females and males and also among females). However, this ratio should become male biased if related females are competing with each other for resources, as it is predicted by local resource competition hypothesis. This specific situation is expected to occur in ant species that reproduce by fission, where young queens leave their mother colonies on foot to found daughter colonies. We tested this idea using the ant *Cataglyphis tartessica* in Doñana National Park (Spain). This species is monogynous (colonies headed by a single queen), monandrous (queen mate with only one male), and reproduces by fission. Given the similarity between foraging and colony fission distances in this species, a strong local competition for resources should be expected between mother and daughter colonies. In this study, we considered investment in females the sum of the investment in gynes (virgin queens) plus the investment in the worker force that leaves with them to found a new colony. Our results show a male-biased sex investment ratio in *C. tartessica* of 1:8 (numerical ratio gynes/males 1:56), suggesting queen control over sexual production. In addition, we found that, during its

reproductive period, this species exhibits split sex (gyne-male) production as well as split male-worker production, without any evidence of variation in relatedness asymmetry between its colonies, at the population level. An interaction between local resources competition and colony size could explain our results.

Keywords Sex investment ratio · split sex ratio · split haplo-diploid production · colony fission · queen-worker conflict · *Cataglyphis*

Introduction

In colonies of social Hymenoptera there are potential breeding conflicts between queens and workers. This is a consequence of haplodiploidy, the sex-determination system in this group of insects that causes dramatic relatedness asymmetry among colony members (Whiting 1935; Trivers and Hare 1976; Boomsma and Grafen 1990). In monogynous and monandrous colonies of social Hymenoptera (assuming worker sterility and random mating), queens are equally related to their daughters and sons (0.5), but sisters are three times more closely related to one another (0.75) than they are to their brothers (0.25) (Hamilton 1972). Under these conditions, assuming workers control reproduction, kin selection theory (Hamilton 1964) predicts that the sex investment ratio (total energy invested in females divided by total energy invested in males) should be 3:1 in favor of females (Trivers and Hare 1976; Boomsma and Grafen 1990; Bourke 2015).

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On the other hand, a male biased sex investment is expected to happen in species displaying polyandry (queens mate with more than one male) and/or polygyny (more than one fertile queen in the colony), factors both that cause a reduction of relatedness among the members of a colony. When one or both of these factors act in the colonies of a population, with varying intensity, it is possible that a bimodal production of sexuals might occur (Boomsma and Grafen 1990, 1991; Sundström et al. 1996; Heinze et al. 2001; Kümmerli and Keller 2009; Bourke 2015; Meunier et al. 2008 for a review).

However, there are alternatives that enable the occurrence of split sex ratio in the absence of such variation in relatedness between colonies, involving ecological factors as a possible cause (Grafen 1986; Keller and Nonacs 1993; Rosenheim et al. 1996). In others cases, it has been proposed that the queen can force workers to raise male sexuals by limiting the number of female brood (Passera et al. 2001); even more, the split sex ratio observed in colonies of *Bombus terrestris* has been related to the duration time of hibernation – diapause of their queen (Duchateau et al. 2004).

In some monogynous ants, new colonies are the result of mother colonies fissioning into one or more daughter colonies, each one composed by a female reproductive plus a portion of the mother colony's workers (Lenoir et al. 1988; Peeters and Molet 2009; Chéron et al. 2011). In such species, young queens, accompanied by a group of workers (hereinafter, WF – worker force–), leave the mother colony on foot to found the daughter colony. In these queens, flightlessness is associated with a drastic reduction in body size (Amor et al. 2011; Peeters and Aron 2017). As a consequence, they cannot feed the first generation of workers solely using their metabolic reserves, which means they are completely dependent on their WF to provide food for the colony (Peeters 2012). Hamilton (1975) thus proposed that the accompanying WF should be counted as part of female investment.

Another important consequence of fission is that the distance between mother and daughter colonies is rather small, leading to resource competition (nest sites, food) between related queens (Bourke and Franks 1995; Chéron et al. 2011). Under such circumstances, sex investment is expected to be skewed in favour of males, the dispersing sex (because they fly while queens have short non-functional wings), as predicted by the local resource competition hypothesis (Raignier 1972; Pamilo 1991; Bulmer 1983; Boulay et al. 2007).

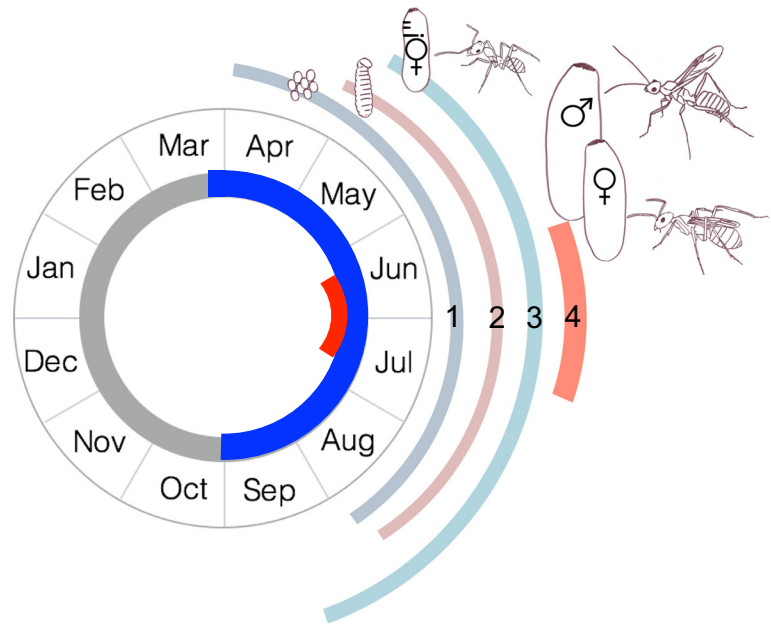
In this study, we examined sex investment ratio patterns in the monogynous and monandrous ant species *Cataglyphis tartessica* (Amor and Ortega 2014). This species lives in sandy habitats throughout southwestern Spain (Jowers et al. 2014). *Cataglyphis tartessica* displays in addition other key features that make it a good study species like being monomorphic and having small colonies of up to 300 individuals (Amor and Ortega 2014). Ants are medium sized (workers average 4.5 mm in length; males are larger than queens), and have a within-colony genetic relatedness among workers not significantly different from 0.75 (Amor et al. 2016). The species begins its annual activity in early spring, dispersing via colony fission in late spring (Amor et al. 2017). Virgin queens and males are only produced during this period (Fig. 1).

Around 30% of colonies reproduce by fission each year (Amor et al. 2011). Mother colonies usually produce just one daughter colony allocating one third of their workers. The daughter colony is located at an average distance of 8.3 m, very similar to its colony foraging distance which is 9.3 m (Amor et al. 2010). During the colony fission, workers transport to the daughter colony (or propagule) other adult workers, eggs, larvae, small cocoons (pupae) of both workers or virgin ergatoid queens (worker-like apterous queens), and big cocoons of virgin brachypterous queens (queens with short non-functional wings); the queen mother remains in the mother colony (Amor et al. 2011) (Fig. 2).

Materials and Methods

The study was conducted in Doñana National Park (southwestern Spain) in late May and June 2010. We excavated all the *Cataglyphis tartessica* nests located in two 10 × 10 m plots, which were separated by 125 m. Colonies were brought to the laboratory where sexuals, workers, and cocoons were counted. Cocoon caste was identified based on cocoon length according to Amor et al. (2011) (workers [$n = 173$]: 4.95 ± 0.2 mm; brachypterous queens [$n = 9$]: 6.09 ± 0.17 mm; and males [$n = 26$]: 7.17 ± 0.33 mm; mean \pm SE; analysis of variance: $F_{2,205} = 770.9$, $P < 0.001$). To estimate the population-level sex investment ratio (total energy invested in females divided by total energy invested in males), the fresh weight of 30 worker cocoons, 11 male cocoons, 7 brachypterous queen cocoons, and 28 adult workers was measured to the nearest 10^{-1} mg.

Fig. 1 Colony life cycle of *C. tartessica*. Seasonal period of foraging activity (in blue), and reproduction (in red). Brood stages of development: 1, eggs; 2, larvae; 3, small cocoons (workers); 4, large cocoons (males); medium cocoons (brachypter females)



Population-level investment in females (queen + WF; x) and in males (y) was estimated as follows:

$$x = \frac{\sum_{i=1}^n (a + b + c)}{n} \tag{1}$$

$$y = \frac{\sum_{i=1}^n (d + e)}{n} \tag{2}$$

where a , b , c , d , and e are the products of the total number of brachypterous queen cocoons, worker cocoons, adult workers, male cocoons, and adult males, respectively, multiplied by the mean of their fresh weight; n is the total number of excavated colonies. We used the mass of male cocoons as an approximation of adult male mass.

Due to the difficulty to find a substantial number of propagules within the random field sampling plots of the present work, the demographic composition of the propagules (queen + WF) obtained in this study was compared with that of 36 propagules (produced by 34 fission events) obtained in another study (Amor et al. 2011).

Instead of having a brachypterous queen, sometimes *C. tartessica* colonies have an ergatoid queen. Ergatoid queens are apterous gynes very similar in size and appearance to workers; they are visually indistinguishable from them at the pupal stage. Because the workers

carrying out fission do not discriminate between ergatoid queen cocoons and worker cocoons (in contrast to what is seen with brachypterous queen cocoons, which are all transported to the daughter nest [Amor et al. 2011]), they were ignored in this study.

All statistical analyses were carried out using STATISTICA 12.0 software. We performed an one-way ANOVA to test the relationship between colony size and the production of sexuals. We tested the occurrence of split sex ratios and bimodal patterns of male-worker production with a Pearson’s Chi-squared test. We carried out a Mann-Whitney U test to examine the worker production in colonies with males before and after male production.

Results

A total of 59 *Cataglyphis tartessica* colonies were collected from the two plots (42 and 17). Six were queenless but contained brachypterous queen cocoons, suggesting they were recently formed daughter colonies (or propagules). Two colonies were found without cocoon production, one of them with 29 adult males (Table 1). The remaining 51 colonies contained worker cocoons or male cocoons, and, in only three, both (Fig. 3). Of the 21 colonies found with sexual cocoons, no colony contained both male and female sexuals (15 colonies contained male cocoons versus 6 with queen

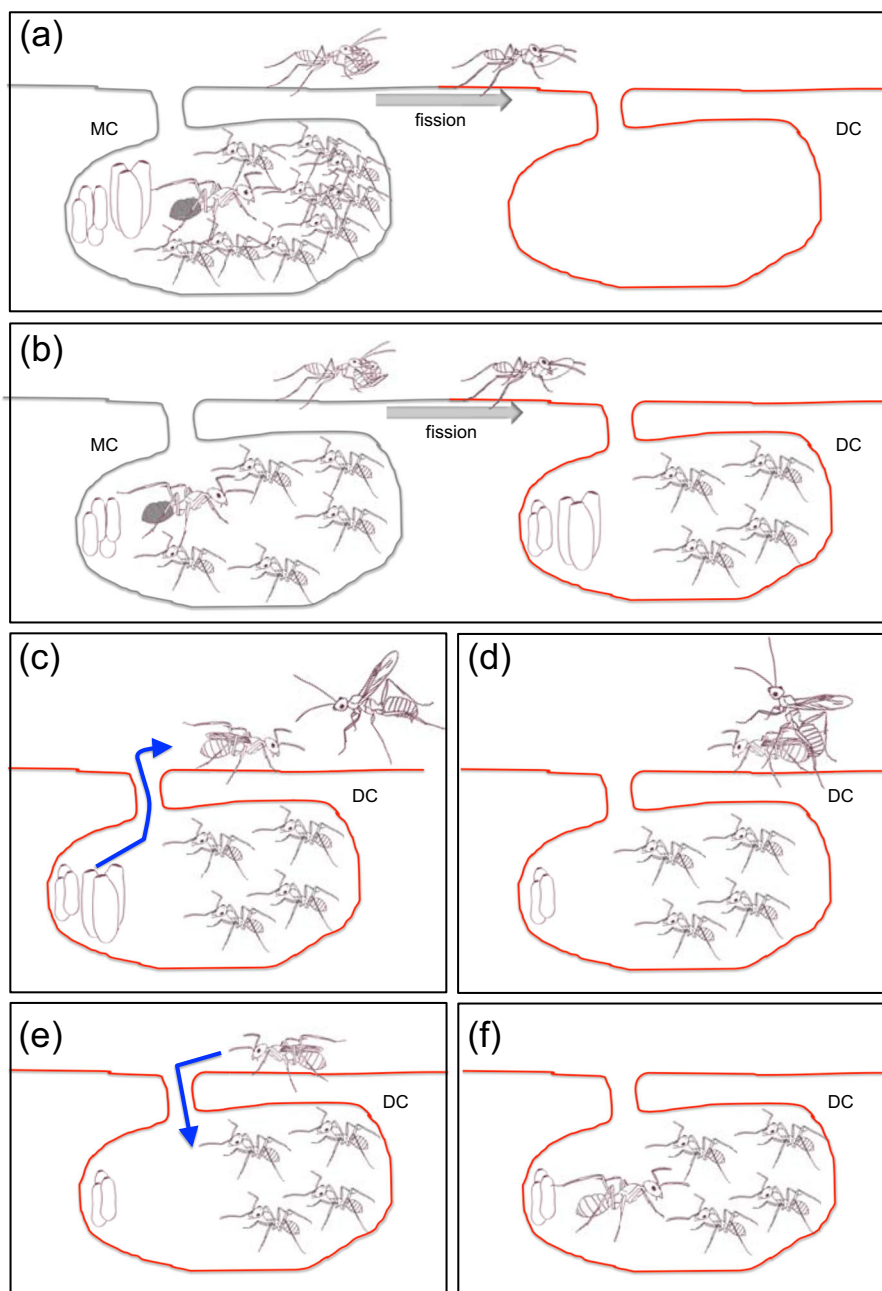


Fig. 2 Schematic drawing of the colony fission in *C. tartessica*. **a** Transport from the mother colony (MC) to the daughter colony (DC, or propagule) of workers, eggs, larvae, small worker cocoons and medium cocoons; **b** the queen mother remains in MC, while 1/3 of workers, some brood and most of medium brachypter cocoons

have been transported to DC; **c** a virgin brachypter female emerges from the cocoon and leaves the nest; **d** she mates with a male who comes flying; **e** after mating, the female returns quickly to the DC; **f** she lost her wings remaining as the new queen of the colony

cocoons; Pearson Chi-squared test: $\chi^2 = 33.43$, $df = 2$, $P < 0.001$), showing strong evidence of split production of sexuals. Moreover, of the 15 colonies with male cocoons, only three also contained worker cocoons (12

colonies with split haploid/diploid production (expected 0) vs 3 colonies without split haploid/diploid production (expected 15); Pearson's Chi-squared test: $\chi^2 = 20.0$, $df = 1$, $P < 0.001$). Among the colonies containing

males, worker cocoons were more common in those with only adult males versus in those with male cocoons (Mann-Whitney U test, $Z = 2.95$; $P = 0.003$), indicating that worker production may resume once the production of males has finished.

Of the three types of colonies observed a) propagules (with brachypterous queen cocoons), b) without males in adult and/or cocoon stage, and c) with males, the latter were the largest (mean number of workers \pm SE; 75.0 ± 13.4 , 109.1 ± 12.2 , and 175.7 ± 34.0 , respectively; one-way anova: $F_{2,56} = 3.451$; $P = 0.038$; Fisher *LSD* post-hoc test: $P = 0.02$). However, these colonies with males were comparatively smaller than fission colonies (sum of mother and daughter colonies) described in Amor et al. (2011): 175.7 ± 34.0 ($n = 20$) vs 297 ± 21.8 ($n = 34$), respectively (mean number of workers \pm SE; one-way anova: $F_{1,52} = 10.0$, $P = 0.003$). No significant difference was found between the categories propagules and colonies without males. Queen type/status (brachypterous queen [B], ergatoid queen [E], or absent queen [QL]) for colonies with males did not differ from colonies producing only workers, excluding the propagule-based colonies (which were all queenless) (4B, 11E, and 5QL vs 13B, 13E, and 6QL, respectively; Wilcoxon matched pairs test: $Z = 1.60$, $P = 0.11$), suggesting queen type/status does not affect the production of males.

The fresh weights obtained were: for adult workers 3.2 ± 0.7 mg (mean \pm SD, $n = 28$); for worker cocoons 3.5 ± 0.9 mg ($n = 30$); for brachypterous queen cocoons 12.0 ± 1.0 mg ($n = 7$); and for male cocoons 18 ± 1.0 mg ($n = 11$). When we calculated the sex investment ratio at a population level (considering female investment as queens + WF):

$$\text{sex investment ratio} = \frac{[\text{investment in female (mg)}]}{[\text{investment in male (mg)}]}$$

$$\text{sex investment ratio} = \frac{40 \pm 120 \text{ mg}}{330 \pm 700 \text{ mg}},$$

we got a result that supports the existence of a male biased sex-ratio of 1/8 in *C. tartessica*. The bias was much more pronounced for the numerical sex ratio: 1/56 (number of gynes/number of males).

Although this study examined a small number of *C. tartessica* propagules, their demographic composition did not differ substantially from that of the propagules described in Amor et al. (2011) (Table 2). The significant difference in the number of brachypterous queen cocoons was likely due to methodological differences. More specifically, in this study, a colony was classified as a propagule if brachypterous queen

cocoons were found in it. In contrast, in Amor et al. (2011), classification was based on observing workers carrying nestmates and brood from the mother colony to the daughter colony, and it was not always possible to find queen cocoons in this latter case.

Discussion

Cataglyphis tartessica is a species of ant with a common life history pattern that comprises two stages: one of colonial growth, starting in early spring, during which only workers are produced, and another of reproductive growth by colony fission in late spring (Amor et al. 2011, 2017). Before the colony fission, *C. tartessica* splits the production of both sexes, one of them philopatric (gynes –virgin queens– that will be part of the propagules) and another dispersing (males) (Amor et al. 2011). Our present results, together with those obtained in Amor et al. (2011), confirms that gyne cocoons and male cocoons do not co-occur in the same colony. Additionally, they show that gynes and males are raised in the largest colonies. This split sex ratio occurs in the absence of the two main causes that could motivate it, assuming worker control: variation in the degree of polyandry and/or polygyny among the colonies of a population, causing relatedness asymmetry among them. Another possible source of variation in relatedness asymmetry among colonies is associated with transient changes in the social structure of the colony (Meunier et al. 2008). An example of it is when the queen is replaced by one of her daughters. This decrease of relatedness among nestmates occurs in the new colonies due to the coexistence of daughter and sister workers of the queen. Hypothetically, this situation, not examined in this study, could lead these colonies to bias in favor of males (Meunier et al. 2008). For such a situation to arise, several assumptions should be satisfied. First, workers must be able to detect within-colony variation in relatedness (Boomsma et al. 2003). Second, to reach the size of a male-producing colony, the queen will have firstly to produce a high number of new workers, which takes time, leading to a gradual approach to 0.75 of relatedness among nestmates. The gradual death of the founding workers of the new colony will also contribute to this approach. Third, the daughter workers of the current queen must allow the elimination, by their aunt workers via policing behavior, of diploid eggs with which they are strongly related, allowing only

Table 1 Mean (\pm SE) number of workers, males and brood composition of the different type of colonies of *C. tartessica*. W: adult workers; Wc: worker cocoons; Bc: brachypter queencocoons; Ma: adult males; Mc: male cocoons. Types of colony marked with * have not replicates ($n=1$)

Type of colonies	n	W	Wc	Bc	Ma	Mc
Only Wc	32	111.7 \pm 12.2	87.2 \pm 12.5	–	–	–
Wc+Bc	6	75 \pm 13.8	24.3 \pm 5.9	3.3 \pm 1.2	–	–
Wc+Ma	4	138 \pm 40.6	77.7 \pm 27.6	–	12.2 \pm 10.8	–
Wc+Mc	1*	41	10	–	–	1
Wc+Ma+Mc	2	151 \pm 20.5	16.5 \pm 15.5	–	40 \pm 5	32.5 \pm 1.5
Ma+Mc	11	226.45 \pm 55.4	–	–	29 \pm 7.6	50 \pm 11
Only Mc	1*	92	–	–	–	7
Only Ma	1*	101	–	–	29	–
No brood	1*	26	–	–	–	–
Total	59					

male production, which would imply a cost in resources difficult to manage.

Although the most commonly evoked explanation for the existence of split sex ratio is the presence of variation in relatedness among colonies within a population, this split does not always occur under such conditions (Meunier et al. 2008). In *Formica selysi*, Rosset and Chapuisat (2006) found that the queen can constrain

worker manipulation by laying diploid eggs in some colonies and haploid eggs in others without correlation with variations in relatedness between colonies. Keller and Nonacs (1993) argue that the queen control over worker manipulations is easier in small colonies. On the other hand, it has been proposed that split sex ratio may arise in ant colonies headed by only one singly mated queen, and under queen control in a high conflict

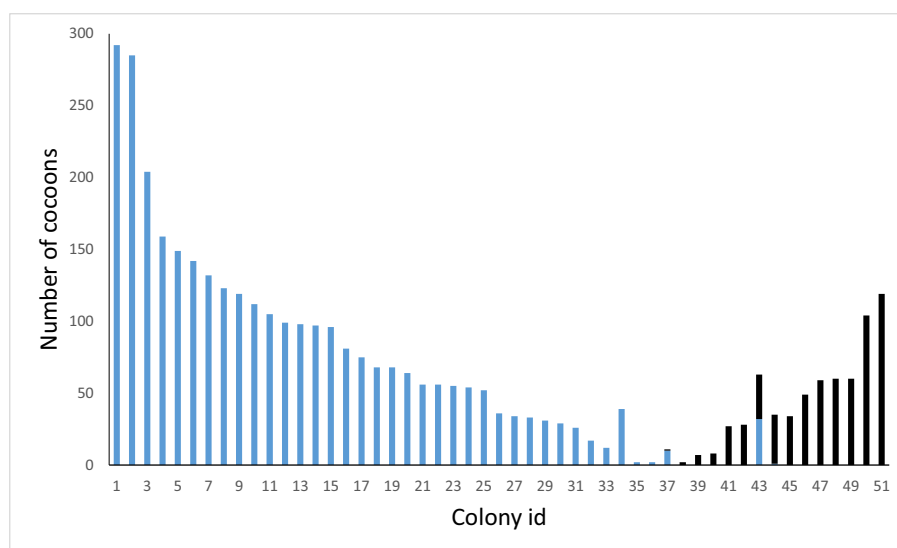


Fig. 3 Split haplo-diploid production in *C. tartessica*. Colonies with male (black) and/or worker (blue) cocoons found in 51 colonies excavated in late spring in Doñana National Park, Spain. In only three of them worker and male cocoons co-occurred

(colony 37, with 10 worker cocoons and 1 male cocoon; colony 43, with 32 worker cocoons and 31 male cocoons, and colony 44 with 1 worker cocoon and 34 male cocoons)

Table 2 Comparison of the demographic composition of fission propagules of *C. tartessica* in this study ($n=6$ propagules) versus that in Amor et al. (2011) ($n=36$ propagules). Males are absent from the propagules. Adult workers (W), worker cocoons (Wc), and brachypterous queen cocoons (Bc) (Analysis of variance $F_{3,38}=3.77$; $P=0.02$)

	This study	Amor et al. 2011		
	Mean±SD	Mean±SD	<i>F</i>	<i>P</i>
W	75±32.8	91.1±39.8	1.96	0.17
Wc	24.3±14.6	17.6±19.7	0.63	0.43
Bc	3.3±2.8	1.6±1.8	4.16	0.048

situation (Kümmerli and Keller 2009). Thus, an extreme biased-production of gynes and males by the queen in different colonies will force workers to rear gynes or males, respectively, as it has been suggested to occur in *Solenopsis invicta* (Vargo 1996) and *Pheidole desertorum* (Helms 1999). Small colony size could lead to a conflictive in terms of survival for species that reproduce by fission. Given the small size of *C. tartessica* colonies, with about three hundred workers, the non-production of males in colonies undergoing fission reduces costs, allowing these colonies to invest in a larger size (gynes and workers) of the propagule. Other species of ants that reproduce by fission like *Aphaenogaster senilis* and *Eciton burchellii*, with thousands of workers, do not split sex ratio (Boulay et al. 2007; Schneirla 1971). Following the same line of argument, the pressure to reach a competitive colony size could be behind the correlation found between the split haplo-diploid production and colony size. So, while the larger colonies would compete to produce males that will inseminate the gynes in new propagules, the medium-sized colonies would invest in worker production.

We also found a sex investment ratio, at population level and counting the worker force of the propagules as investment in reproductive females, of 1:8, biased in favour of the dispersing sex (numerical ratio gynes/males 1:56). This bias, similar to most species that reproduce by fission (Boulay et al. 2007; Schneirla 1971; Percy and Aron 2006), follows the prediction of the local resource competition hypothesis (Clark 1978; Silk 1984; Song et al. 2016). Thus, in order to reduce competition between daughter and mother colonies, the queen responds by investing preferentially in

male offspring. Thus, the interaction between local resource competition, under which colony productivity is maximized via male-biased production, and small colony size, with the aim of producing a daughter colony of viable size, could be the key to the interpretation of our results in *Cataglyphis tartessica*.

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