

Research article

Size-dimorphism in the queens of the North American ant *Leptothorax rugatulus* (Emery)

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Summary

With recent findings of an unexpected variability in the reproductive behaviour of ant sexuals, their morphology has become an area of major evolutionary interest (Heinze and Tsuji, 1995). Here we report on the occurrence of two queen morphs in *Leptothorax rugatulus* (Hym., Formicidae): Microgynes (small queens), exceeding worker-size only marginally, and macrogynes, which are, typically for the subgenus *Myrafant*, about twice as big as their workers. The frequency distribution of queen-size is clearly bimodal, in contrast to worker- and male-size. The average size of queens is highly correlated with the size of daughters in field-collected colonies, whereas within colonies no correlation between the average queen-size and the size of workers or males exists. This gives additional support that size-dimorphism is due to a specific, transmissible size reduction of the microgynes which could be based on genetics, the environment or both. This reduction is quasi-isometric, with a slightly smaller thorax-to-head ratio in microgynes, and scanning electron microscopy does not reveal any significant degeneration of the pterothorax, ocelli or number of ommatidia. The frequency of microgynes at different sample sites is highly variable, correlating well with the prevailing social structure in the respective subpopulations. Indeed, the majority of macrogynes is found in monogynous colonies, while microgynes abound in polygynous ones, which is strong evidence for an alternative dispersal tactic. However, the expected correlation to altitude or latitude was not found and further investigations are needed to reveal proximate and ultimate causes of this prevalent polymorphism between two types of female ant reproductives.

Introduction

In recent years the reproductive behaviour of ants, including their dispersal, has proven much more variable than anticipated previously (Heinze and Tsuji, 1995). Currently it might even be debatable whether the majority of species are restricted to the classical ant life-history of new colonies being founded independently by single queens after mating and dispersal flight. The social structure of ants seems to be very flexible and environment-dependent (e.g., Herbers, 1986) and in an increasing number of species facultative polygyny has been shown.

Polygynous colonies can only form by multiple-queen founding (pleometrosis), colony fusion or by adoption of gynes into existing colonies, thus the social structure is reliably linked to the mode of reproductive behaviour (Keller, 1991) and it has to be accepted that the latter is variable, as well. Pleometrosis rarely leads to primary polygyny (Hölldobler and Wilson, 1977, 1990; Bourke and Franks, 1995) and fusion of mature, queenright colonies has almost never been observed. Therefore, the main reason for polygyny is the adoption of young queens into established colonies. This alternative tactic comprises different phenomena: gynes might try to enter alien colonies to exploit the existing work force or they might be readopted into their natal colonies (not necessarily without conflict of interests) to share reproduction within these colonies and/or to disperse later with some of the workers. In many of these species, as dispersal between habitats is expected to be never completely abandoned (Hamilton and May, 1977), dependent and independent colony founding coexist, their relative frequencies determined by the ecology of the species under study (Rosengren and Pamilo, 1983; Bourke and Heinze, 1994). Intraspecific morphological adaptations of the queens to dependent colony foundation vary from a mere reduction in the amount of their body weight (Tschinkel, 1996) to worker-like morphs without flight capability (Buschinger and Heinze, 1992).

The readaption process, on the other hand, facilitates the evolution of individuals which save the investment in storage tissue and try to enter alien colonies and exploit the existing workforce in order to reproduce. Such individuals would be expected to retain their dispersal capability to reach unrelated colonies to parasitize. Consequently, purely size-reduced queens (microgynes) might constitute specialized social parasites (Buschinger, 1990; Bourke and Franks, 1991), but might just as likely be a transitory form in the evolution of readoption (Ross and Keller, 1995). Reported from a variety of species, the occurrence of queen size dimorphism in the genus *Leptothorax* is especially interesting because this well-studied taxon provides some of the best-documented examples of social parasitism (reviewed by Buschinger, 1986) and of readoption (e.g., Buschinger, 1968). Within this genus queen size dimorphism with a clear bimodality has so far only been shown for one population of *L. spinosior* (Hamaguchi and Kinomura, 1996), although there is circumstantial evidence for it in several species (Herbers, 1984; Seifert, pers. comm.).

Here we report on the occurrence of a queen size dimorphism in the North American species *Leptothorax rugatulus* (Emery). Due to its abundance, this species might provide an important model system to study queen size dimorphism in Formicoxenines.

Materials and methods

Leptothorax rugatulus was mainly found in habitats ranging from oak-pine woodland to fir forest and thus it is restricted to mountain ranges in the southern part of its distribution. In two consecutive years 513 complete colonies and 67 colony fragments of *L. rugatulus* were collected at 36 sites from 14 populations in Arizona, New Mexico and Colorado (Table 1). The population described by Möglich (1978) at lower altitude in a mixed oak-juniper woodland seems to have gone widely extinct, as only two colonies could be found during several days of collecting. *Leptothorax*

Table 1. *Leptothorax rugatulus* was sampled from 14 different populations, which are separated by desert habitat in southern Arizona and New Mexico. Each population was named after a nearby geographic landmark. Apart from the number of collected colonies and collection sites the predominant type of vegetation and the geographic location and elevation of each population are given

| Name | Geographical latitude (north)/ longitude (west) | Elevation [m] | Vegetation type | Sample size [number of colonies] | Number of collecting sites |
|---------------------------|---|---------------|---|----------------------------------|----------------------------|
| Chiricahua Mountains | 32°00' / 109°15' | 1860 – 2630 | oak dry forest – mixed coniferous forest | 366 | 17 |
| Cibola National Forest | 34°35' / 106°12' | 2380 | juniper-pine forest | 9 | 1 |
| Emory Pass | 32°50' / 107°50' | 2230 | mixed coniferous forest | 12 | 1 |
| Gila National Forest | 33°55' / 108°22' | 2450 | open pine forest | 12 | 1 |
| Huachuca Mountains | 31°36' / 110°25' | 2400 | pine forest | 20 | 1 |
| Jack Peak | 32°35' / 108°27' | 2450 | open pine forest | 16 | 1 |
| Lincoln Forest | 32°50' / 106°00' | 2360 | mixed coniferous forest | 5 | 1 |
| Magdalena Mountains | 34°25' / 107°30' | 2500 | mixed coniferous forest | 10 | 1 |
| Manzano Wilderness | 34°45' / 106°20' | 2040 | open oak-pine forest | 30 | 1 |
| Mount Graham | 32°42' / 109°45' | 2100 – 3000 | oak-pine forest – mixed coniferous forest | 25 | 3 |
| Mount Lemmon | 32°30' / 111°00' | 2250 | oak-pine forest – mixed coniferous forest | 24 | 2 |
| Warner Gulch | 34°10' / 106°10' | 2000 | pine forest | 5 | 1 |
| Round Mountain | 40°30' / 105°25' | 1800 | open pine mixed forest | 16 | 1 |
| Roosevelt National Forest | 40°40' / 105°20' | 1750 – 2200 | pine forest/ pine-fir forest | 30 | 4 |

rugatulus nests mainly under stones and in rock crevices from which the small and well-defined colonies can easily be aspirated. In two 100 m²-plots in the main study population (Chiricahua Mountains) the nest densities were 0.02 and 0.46 per square meter respectively, as determined by systematically searching the leaf litter, turning every stone and exploring all perceivable crevices.

Individuals were collected with an aspirator and the queens present were counted and their size preliminarily estimated under a stereomicroscope. The majority of the colonies were brought back alive to the laboratory, where most were kept under artificial dark-/light rhythms in standard laboratory nests (Buschinger, 1974).

Observation of foraging activity indicated that *L. rugatulus* is active at daytime with an activity peak around 14:00, thus counted worker numbers are underestimates due to missing foragers.

Maximum thorax width and length, as well as maximum head width of 285 queens were measured under a stereomicroscope at 50× magnification and a size index computed: to weigh head and thorax equally, the square root of the product of thorax length and width was added to head width and the sum was divided by two. In the 91 males and 34 gynes measured, the wings impeded an accurate measurement of thorax length and thus the mean of thorax and head width was used as a size estimator, as it was done for the 162 measured workers. All measurements were taken from live specimens by video-recording or by immobilizing specimens under a microscope slide. The accuracy of measurements was estimated by repeating a subsample of 15, which resulted in an average deviation of 1.7%. To check whether different queen size resulted in (and thereby probably also was caused by) different egg size, the volume of 200 eggs (100 of small and 100 of large queens) was estimated by measuring egg length and diameter under a microscope (measurement error: 0.01 mm) and calculating the volume of the corresponding cylinder.

The reproductive status of 89 queens of different sizes from monogynous and polygynous colonies was investigated by dissection (Buschinger and Alloway, 1978); their ovaries were checked for developing eggs, the presence of yellow bodies, and sperm in the spermatheca.

As the attempt to directly measure the flight capability of gynes proved unsuccessful, indirect, morphological evidence of differences in dispersal behaviour was sought. Therefore, three micro- and macrogynes were investigated under the scanning electron microscope with special emphasis on thorax structure, ommatidia and the compound eyes. Furthermore, wing load (defined as body mass per unit of wing area) of males, micro- and macrogynes were measured. Body mass of mature sexuals was directly recorded on a Mettler MT5 microbalance. In order to determine exactly the wing area, one fore- and one hindwing of each individual were spread out on a microscope slide and photographed. The wing area could then be inferred from the weight of the corresponding cut-out prints.

Results

L. rugatulus proved to be a facultatively polygynous species, with an average of 2.7 (\pm S.D. 4.3) queens per colony. Only one of the 89 dealated queens investigated showed no sign of present or former reproductive activity and two queens were not inseminated. A sample of dealated queens parasitised by tapeworm cysticercoids (Heinze et al., in press), which neither were inseminated, nor showed reproductive activity, was excluded from this analysis. Both, micro- and macrogynes generally had eight ovarioles, while workers had only two.

11.3% of the colonies were found queenless, 50.1% were monogynous and 38.6% contained more than one queen. The initial crude categorization of queens yielded 636 microgynes, 541 macrogynes and 202 individuals that could not be classified unambiguously. The subsequent measurements confirmed the initial estimates. Only 7.2% of all analysed nests contained both small and large queens, while

in 13.8% of the nests all queens were microgynes and in 52.8% all were macrogynes. In the remaining cases (26.2%) at least one queen could not be classified unambiguously, thus these could not be classified as containing both or only one morph and were not taken into further account. Colony size averaged 95 (± 85) workers and worker number was weakly correlated with the number of queens (Spearman's $r_s = 0.37$; $p < 0.001$; $N = 308$). A partial correlation analysis of colony size and the number of small queens present in the colony (controlled for overall queen number) yielded a negative coefficient ($r = -0.38$; $p < 0.001$; $N = 308$).

The relative frequencies of small and large queens varied greatly among populations and corresponded well with the predominant social structure; in subpopulations with relatively many microgynes, polygyny was much more common and average queen number higher than in those which comprised mostly macrogynes. In fact, microgynes occur much more often in polygynous colonies (84.6%), while macrogynous queens were predominantly found in monogynous colonies (64.3%; significant difference: $\chi^2 = 56.2$; $df = 1$; $N = 342$; $p < 0.001$). However, neither the frequency distribution of polygyny nor of microgyny was significantly influenced by altitude or latitude, or a combination of both (multiple regression analysis, $B_1 = 0.021 \pm \text{S.E. } 0.023$ and $B_2 = -0.291 \pm 1.875$, $r^2 = 0.075$).

In queens, all three morphological measurements showed a bimodal frequency distribution and the calculated size coefficient (Fig. 1) did not differ from two overlapping normal distributions (Kolmogorov-Smirnov-test: $z_1 = 1.02$; $p_1 = 0.24$ and $z_2 = 0.59$; $p_2 = 0.87$). In contrast, the size of males and workers was unimodally distributed (Fig. 2) and did not differ significantly from a single normal distribution (respectively $z_m = 0.80$; $p_m = 0.54$ and $z_w = 0.70$; $p_w = 0.72$). Also, body size of these two groups was not significantly higher in macrogynous than in microgynous nests (t-test, respectively $t_m = 0.14$, $df = 25$, $p_m = 0.89$; $t_w = 0.17$, $df = 40$, $p_w = 0.87$), which

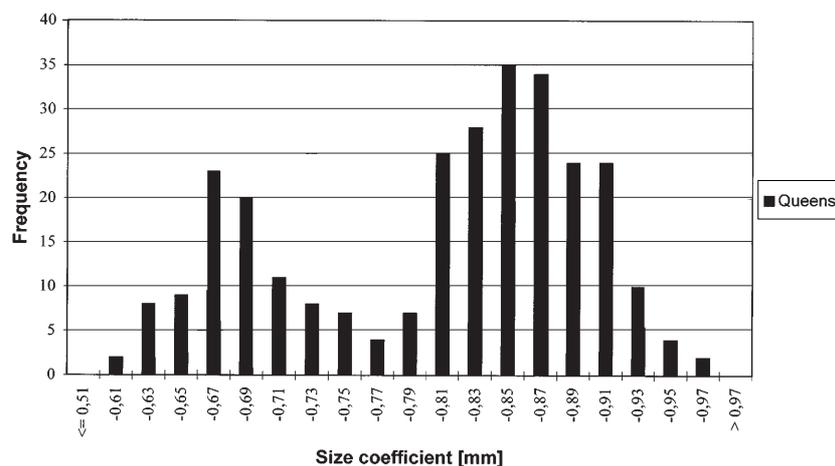


Figure 1. Queen size in *Leptothorax rugatulus* clearly is bimodally distributed. The employed size index, which also serves as x-axis, integrates head width, thorax length and thorax width to estimate body size. Each of the parameters shows a bimodal frequency distribution itself. The size index corresponds well to queen dry weight in the few cases measured so far

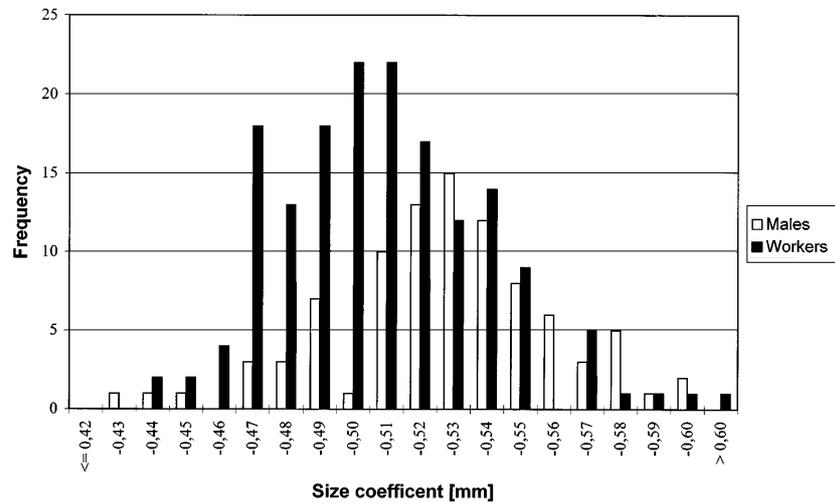


Figure 2. Size distribution of workers and males in *Leptothorax rugatulus*. Both size distributions do not differ from a normal distribution. Note that workers are more variable in size than males and some extreme deviations have been observed, which were not included in this analysis

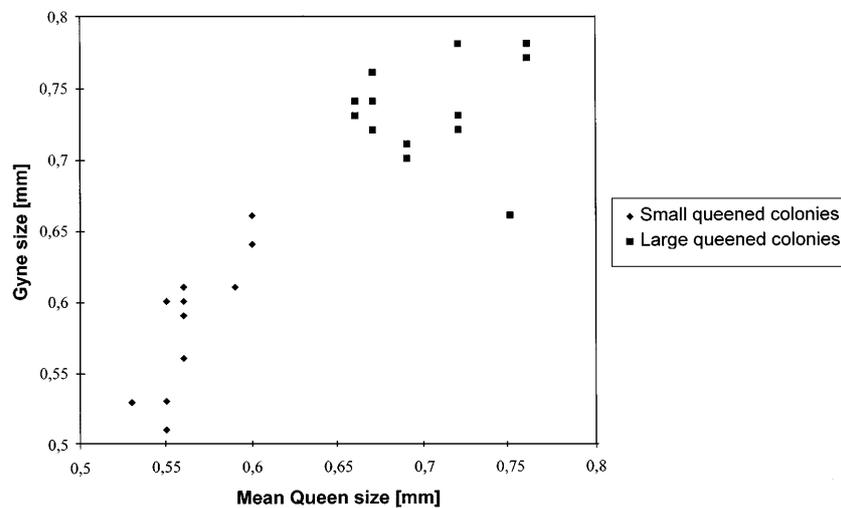


Figure 3. The relationship between the mean size of the queens in a colony and the size of the gynous produced by these colonies. Small queened colonies produce significantly smaller daughter gynes than large queened colonies. Overall there is a good correlation between mean queen size of a colony and the gynes it produced (Spearman's $r_s = 0.85$, $p < 0.001$, $n = 33$)

corroborates well with the fact that there was no significant difference in egg size between macrogynes and microgynes (t-test for unequal variances, $t=0.46$, $df=11$, 12 , $p=0.652$; Levene's test for equality of variances $F=9.40$, $p=0.007$). The body size of produced gynes however, showed a significant difference ($t_g=11.98$, $df=31$, $p_g < 0.001$): colonies with large queens produced macrogynes, the female sexual offspring of small queens was significantly smaller. This dependency is best expressed as a regression (Fig. 3; $B=1.0175 \pm 0.0860$, $r^2=0.8188$).

The investigation using the scanning electron microscope did not reveal any significant structural degeneration of flight-relevant organs in microgynes: all three ocelli were fully developed in both morphs and the number of ommatidia was reduced isometrically to size: (macrogyne: 171, 193 and microgyne: 123, 128). The structure of the thorax of both morphs did not differ significantly: both contained the full complement of sclerites and sutures. Additionally, the examination of the wing joints indicated no crucial differences between macrogynes and microgynes. The thorax-head ratio, however, is slightly correlated to body size ($r=0.63$, $p<0.001$, $n=285$).

In contrast, the wing load differed not only between males and females but also strongly between micro- and macrogynes despite a relatively small sample size (one-way ANOVA $F=275.5$; $df=2, 29$; $p<0.0001$) and the values did not overlap (Fig. 4). As expected males had the lowest wing load, but surprisingly the values for microgynes were much lower than for macrogynes.

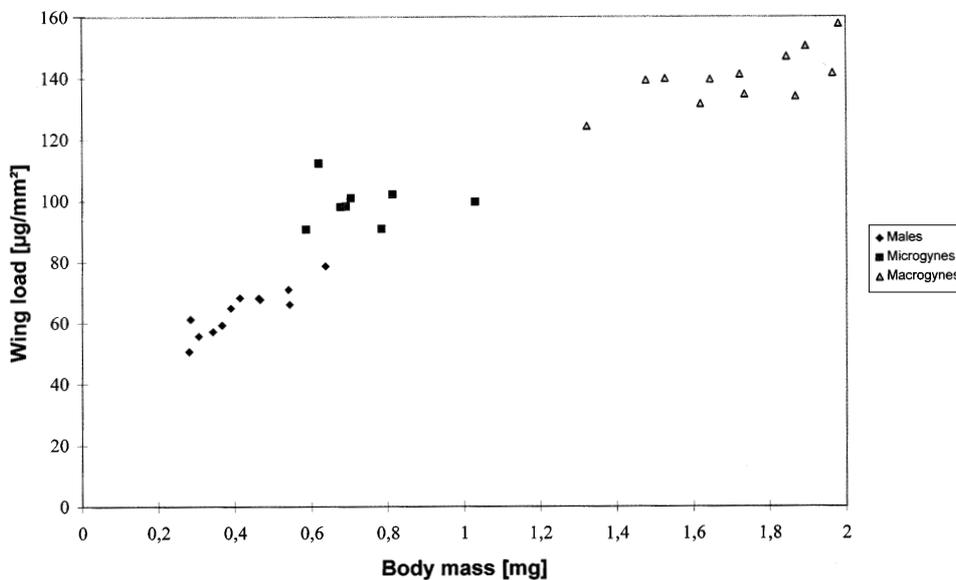


Figure 4. Wing load was calculated from the wing area and fresh body mass, the latter also being used here as abscissa. There is no overlap in the values for males, small and large queens. Wing load was lowest for males, as these lack body reserves for colony founding, and highest for large gynes, which is presumably due to their large body reserves

Discussion

Apart from collecting some basic biological data on this widely distributed but poorly investigated *Leptothorax* species it could be shown that its high variability in queen size is due to a clearly bimodal queen size distribution and not a random phenotypic fluctuation based on developmental noise. This justifies the application of the terms macrogyne and microgyne despite the fact that the two distributions show some overlap. It is also a good indication that the parameter “queen size” is subject to disruptive selection which is presumably brought about by two different life-history strategies of the female reproductives in *Leptothorax rugatulus*. This hypothesis is further supported by the facts that only the queens exhibit such dimorphism and that the size seems to be transmitted from mothers to daughter gynes, while the size of workers or males is not significantly higher in small-queened colonies than in large-queened. As egg size is not different between macrogynes and microgynes, the high correlation between queen mothers and daughters is not brought about by quantitative maternal effects via egg mass. However, currently it cannot be distinguished whether this transmissibility of queen size is due to genetic or “cultural” effects (Keller and Ross, 1993).

The close interdependence between the size of the queens and the social structure of their colonies is strong evidence for different reproductive tactics with the microgynes being adopted into existing colonies, resulting in secondary polygyny (Hölldobler and Wilson, 1977, 1990; Bourke and Franks, 1995), and macrogynes founding their colonies mainly on their own, giving rise to monogynous colonies. It has been shown in a number of *Leptothorax* species that two alternative modes of reproduction exist, namely independent colony founding and dependent colony founding via readoption and budding (Bourke and Heinze, 1994; Heinze, 1995). As budding with workers prohibits a dispersal flight and does not require the queen to bear much storage tissue, this has led to a worker-like queen morph in some species (e.g., Heinze, 1989).

Microgynes also lack extensive body reserves relative to the size of their workers. Thus the coexistence of macro- and microgynes could be perceived as an intermediate stage in the adaptation to a disruptive selection regime caused by alternative modes of reproductive behaviour (Ross and Keller, 1995). The costs of a large body size have been reduced, on the other hand the flight capability has been retained, which might be due to either the necessity to take part in nuptial flights in order to mate, or evolutionary inertia as morphological traits generally evolve more slowly than behaviour and social structure.

The success of the two tactics is believed to be climate dependent (Herbers, 1993; Heinze and Hölldobler, 1994), thus the apparent lack of any correlation between the morph frequency and the climate-associated factors altitude and latitude is unexpected, although it has to be stressed that microclimatic parameters were not recorded. Also, other environmental factors such as the availability of nest sites or habitat patchiness might be more important ecological correlates affecting colony founding modes (Herbers, 1993; Bourke and Heinze, 1994).

The recent finding of a population of *Leptothorax spinosior* from southern Japan with a similar queen size dimorphism to that of *L. rugatulus* (Hamaguchi and Kinomua, 1996) provides an interesting possibility to compare ecological correlates

of the queen dimorphism. Despite similarities in the distribution of queen size, in the close association between queen morph and colony structure and in the high transmissibility of body size from mothers to daughter gynes, the two species occur in a completely different habitat. While queen dimorphic *L. rugatulus* populations inhabit montane forests, microgynes of *L. spinosior* were found in a population on the riverside. Probably nesting resources are in both cases patchily distributed, however, it is important to compare the habitat characteristics in more detail, with special emphasis on nesting resources.

On the other hand, the dispersal capability of the *L. rugatulus* microgynes appears not to be inferior to that of the macrogynes, as they possess a fully functional pterothorax, a complete visual apparatus and a lower wing load. Consequently, they are not necessarily forced to mate in the vicinity of their natal colony and seek readoption as has been suggested for other ants with alternative dispersal tactics (Heinze, 1989, 1993; Sundström, 1995). It is therefore conceivable that the microgynes of *L. rugatulus* seek adoption in non-related colonies after successful mating and dispersal on the wing. This would classify them as intraspecific social parasites, an intermediate stage in the evolution of interspecific social parasitism (Bourke and Franks, 1991) which is quite abundant in this tribe Formicoxenini (Buschinger, 1986). Good evidence for that hypothesis has been provided by comparative work in the genus *Myrmica* (Bourke and Franks, 1991; Elmes, 1991a). In this case, the queen size dimorphic *Myrmica ruginodis*, which also resembles *L. rugatulus* with respect to frequency and shape of the queen size distribution (Elmes, 1991b), is likely to constitute an example of an intermediate stage in the evolution of true social parasitism (Bourke and Franks, 1991).

However, there is only one aspect in this study which might be taken as weak evidence in favour of intraspecific social parasitism in *L. rugatulus*: morphologically, no evidence for a reduced fertility of microgynes is found, however, the number of microgynes in a nest, when controlling for overall queen number, is negatively correlated with colony size. A possible explanation for these findings is an overproduction of sexuals by microgynes at the cost of the whole colony.

In contrast, the fact that there is only a small percentage of mixed colonies in nature and that a number of colonies of *L. rugatulus* with only microgyne queens have been prospering for over a year now in the laboratory provides stronger evidence against this hypothesis. In this respect it is essential to know the degree of relatedness between queens in mixed nests and whether microgynes produce a higher gyne/worker ratio.

A third possible scenario that can explain the occurrence of microgynes has been proposed in the genus *Solenopsis*. In monogynous populations of *Solenopsis geminata* (McInnes and Tschinkel, 1995) and *Solenopsis invicta* (Tschinkel, 1996) it has been shown that gynes with specifically less body reserves disperse in spring to usurp queenless colonies. However, it is unlikely that in *L. rugatulus*, as a facultatively polygynous species in which queenless colonies are rarer, the same explanation holds. Nevertheless, the timing of the nuptial flights of micro- and macrogynes needs to be compared.

Overall, there is good evidence that the size dimorphism of *L. rugatulus* queens is related to alternative reproductive tactics and that microgyny is a way of reducing costs of the investment into queens. At present it is not completely clear whether

microgyny constitutes an early stage of a morphological adaptation to dependent colony founding via readoption and budding, or a transitional stage in the evolution of social parasitism. A dispersal polymorphism seems most likely at the moment, however, this has to be proven by further investigations.

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