Myrmecological News | 20 | 77-85 | Vienna, September 2014

Reconstructing life history in ants: ergatoid queens, facultative monogyny, and dependent colony foundation in *Monomorium algiricum* (Hymenoptera: Formicidae)

Christian Peeters & Alberto Tinaut

Abstract

Ergatoid (= permanently wingless) queens do not disperse individually from their natal colonies, instead they walk with nestmate workers to new nesting sites during the fission of existing colonies. Very few observations of dependent colony foundation are available, and it must often be studied with indirect data. Thirty-five colonies of *Monomorium algiricum* (Bernard, 1955) were excavated at different times of the year. New sexuals (ergatoid queens and males) were found during a short period at the end of summer. Dissection of spermathecae in 331 queens revealed that new gynes mate soon after emergence. Ovarian activity was assessed to distinguish between "old" and newly mated queens. Both monogynous and polygynous colonies were found throughout the year; queens in the latter were less fecund. Sexuals were not produced in some polygynous colonies. The life history of *M. algiricum* is complex due to interactions between extreme seasonality (no foraging and no egg-laying during six months of the year), coexistence between "old" and newly mated ergatoid queens, and the irregularity inherent to colony fission.

Key words: Reproduction, polygyny, seasonality, fission, budding, yellow bodies.

Myrmecol. News 20: 77-85 (online 29 May 2014)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 29 May 2013; revision received 25 November 2013; accepted 25 November 2013
Subject Editor: Chris R. Smith

Christian Peeters (contact author), Laboratoire Ecologie & Evolution, CNRS UMR 7625, Université Pierre et Marie Curie, Paris 75005, France. E-mail: cpeeters@snv.jussieu.fr

Alberto Tinaut, Dept. Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain.
E-mail: hormiga@ugr.es

Introduction

In most ant species, sexuals of both sexes are produced once a year, and dispersal together with mating immediately precedes independent colony foundation (ICF). Many species have shifted away from ICF, and reproductives are totally dependent on nestmate workers to start new colonies (Peeters & Molet 2009). This dependent colony foundation (DCF, also called fission or budding) implies that gynes do not disperse individually; they walk together with workers, hence dispersal is limited. In various species, ergatoid (= permanently wingless) as well as brachypterous (= short-winged) queens have completely replaced winged queens (Peeters 2012). Generally, there is a dramatic decrease in the number of gynes produced annually, however this is counterbalanced by an increased production of workers needed for just-divided colonies to be autonomous. Founding behaviour and reproductive investment are poorly known in species with ergatoid queens. Unlike the conspicuous dispersal flight of species with winged queens, colonies with ergatoid queens often divide unpredictably in time, and it can be difficult to distinguish colony fission from a nest emigration (Cronin & al. 2013). Gynes mate inside or outside the nests, but it is not always known if this occurs before or after colony division. Since direct observations of DCF are infrequent, researchers need to rely on indirect data (Cronin & al. 2013). If a sufficient sample of colonies are collected throughout the year, comparison of colony sizes may reveal the occurrence of colony division. An extra layer of complexity is added in polygynous species, in which different generations of queens can overlap. Since newly produced ergatoid queens remain in their natal colonies, ovarian dissections are required to distinguish them from older queens.

Monomorium is a large cosmopolitan genus (384 species) with surprisingly little published on its reproductive biology, except for the tramp species *M. pharaonis* (Linnaeus, 1758) (references below). *Monomorium algiricum* (Bernard, 1955) (= *Epixenus algiricus* Bernard, 1955) is distributed in southern Spain, although specimens have been collected on the other side of the Mediterranean (in and near Algiers, Algeria). Ergatoid queens were reported in both populations (Bernard 1955, Tinaut & Ruano 1992). In Spain, we collected 35 colonies of *M. algiricum* during different months over five years, and we dissected all queens to determine monogyny or polygyny, and reconstruct the life history.

Material and methods

Thirty-five complete nests of *Monomorium algiricum* were excavated in 2007 - 2012 near Izbor and Lanjarón (Granada province), and Sierra Carbonera (Cádiz province), Spain (Tab. 1). Inhabited chambers occurred mostly at a depth of 30 cm, and never deeper than 55 cm. The mountainous ha-

Tab. 1: Demographic data for 35 colonies of *Monomorium algiricum* collected in different months of the years 2007 - 2012; * queens not dissected, thus no information on their age.

Date	Nest code	Worker adults	Worker pupae	Worker larvae	Eggs	Queens (+ pupae)	Males (+ pupae)
13 / 04 / 2008	C	507	113	546	0	5	0
13 / 04 / 2008	D	228	0	10	> 60	1	0
13 / 04 / 2008	E	1025	0	0	0	1	0
13 / 04 / 2008	F	880	0	0	0	5	0
19 / 04 / 2012	Y	3999	0	31	90	1	0
19 / 04 / 2012	Z	2732	0	3	102	1	0
25 / 04 / 2012	α	2354	0	0	40	8	0
16 / 05 / 2009	G	1878	168	186	> 15	1	0
16 / 05 / 2009	H	235	104	yes	yes	4	0
16 / 05 / 2009	K	265	yes	0	yes	5	0
16 / 05 / 2009	L	508	72	147	> 115	16	0
09 / 08 / 2012	β	2905	395	111	58	10	0
14 / 08 / 2012	γ	1415	204	36	15	1	0
18 / 08 / 2012	δ	3103	117	46	0	5 + 4	113 + 23
19 / 08 / 2012	ε	3971	518	643	65	41	0
29 / 08 / 2011	GG	3821	305	156	0	21	0
31 / 08 / 2011	HH	3270	281	103	0	31	0
02 / 09 / 2011	KK	1066	19	281	62	1 + 5	27 + 7
02 / 09 / 2011	MM	2080	141	266	12	44 + 2	68
09 / 09 / 2011	NN	2734	259	96	0	15	0
16 / 09 / 2011	PP	2373	335	71	0	13	0
20 / 09 / 2011	QQ	3383	614	362	2	14	0
22 / 09 / 2011	RR	829	65	33	13	1	38 + 7
22 / 09 / 2011	SS	1562	112	58	1	18	0
27 / 09 / 2011	TT	1550	210	235	47	33	0
05 / 10 / 2011	UU	3036	222	437	81	11	0
18 / 10 / 2007	A	689	56	0	0	14	0
18 / 10 / 2007	B	1175	18	0	0	10	0
13 / 10 / 2009	AA	1075	0	1	10	1	1
13 / 10 / 2009	BB	2073	0	2	0	1	0
19 / 10 / 2009	CC	1941	0	0	0	24	0
20 / 10 / 2009	DD	2375	0	0	0	4	0
20 / 10 / 2009	EE	2567	0	0	0	1	4
25 / 10 / 2009	FF	1426	0	0	0	5*	0
25 / 10 / 2009	FG	1763	0	0	0	8*	0

bitat (600 m elevation) was open shrubland with scattered small trees (including olives and almonds) and exposed rocky soil. There was a low density of colonies in all localities, and this restricted the size of our samples. Temperatures average 2.2°C for the coldest month (January) and 30.6°C for the hottest month (July); range is -6° to 40°C. Annual rainfall is 340 mm with very dry summers (< 3 mm in June - August). Fieldwork was limited to the period of activity above ground (April - October).

All colonies were transported to the laboratory where adults and brood were promptly counted. Queens (except in colonies A and B) were dissected very soon after field collection (n = 331), and we photographed different stages of ovarian development to allow for comparisons over the years. We determined if the spermatheca was empty or full of sperm, and counted the number of ovarioles. To deduce if oviposition is possible, we noted whether oocytes had yolk and compared the size of the largest yolky oocytes with eggs that had been laid. We inspected "yellow bodies": Every time a mature oocyte is laid as an egg, the follicle cells (surrounding an oocyte) and the trophocytes (nurse cells) accumulate near the base of the ovarioles (Billen 1982, Gobin & al. 1998). With increasing numbers of eggs laid, these deposits become visible as dense, dark yellow aggregates.

We tested several hypotheses to account for differences in the numbers of workers, egg-laying queens and new sexuals across colonies. Pearson correlation coefficient (r) was

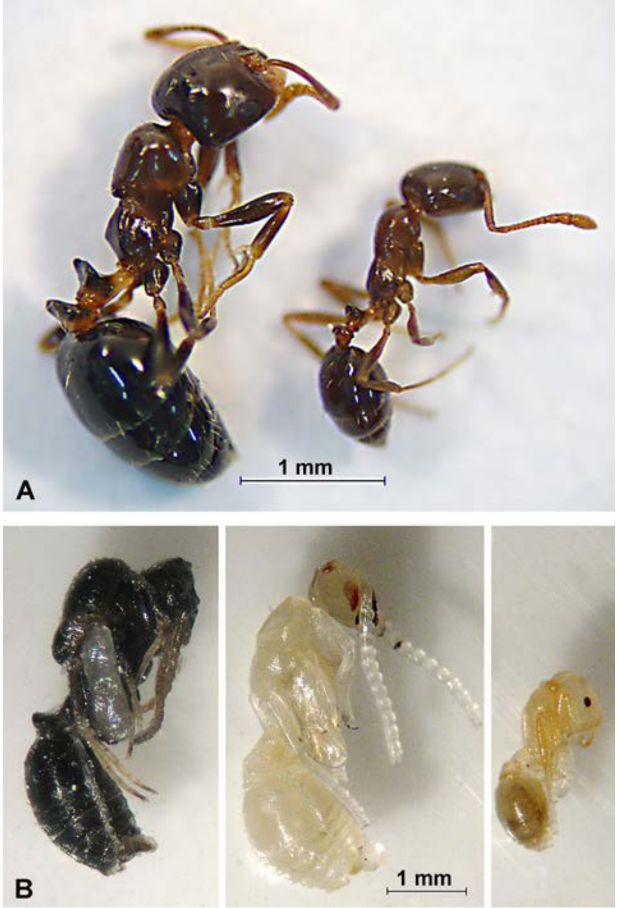

Fig. 1: Caste dimorphism in *Monomorium algiricum*: (A) comparison of ergatoid queen and worker; (B) comparison of pupae of males (two stages of pigmentation) and worker. Note wing furrows in male pupae.

used to analyse the relationship between these variables. Data were tested for normality and homogeneity of variances, transformed when necessary, then either parametric (ANOVA) or non-parametric (Mann-Whitney U) statistics were used.

Voucher specimens have been deposited in the University of Granada (Tinaut's collection, references: 9112 to 9121 and 13479 to 13487), the Museo de Ciencias Naturales de Madrid (references: 75425 for alcohol specimens, 98471 to 98480 for dry specimens), the Natural History Museum in London, and the California Academy of Sciences in San Francisco, USA (images on http://www.antweb.org//specimenImages. do?name=casent0906902).

Results

Basic colony structure and ecology: All queens in *Monomorium algiricum* are ergatoid; their thorax is "worker-like" with a decreased volume and pronounced fusion of flight sclerites. However queens are considerably bigger than workers, both in total length (queens: 2.68 ± 0.13 mm gaster excluded, n = 15; workers: 1.76 ± 0.08 mm, n = 30 (TINAUT & ORTIZ 1988)) and in gaster volume (Fig. 1A). Males are slightly bigger than queens (length excluding gaster: 2.83 ± 0.06 mm, n = 5) and their pupae have wings (Fig. 1B), hence males can be recognized as both pupae and adults.

Importantly, *Monomorium algiricum* forage for only a few months of the year. Due to cold temperatures (see Material and methods), above ground activity stopped completely between November and early April. Similarly in the middle of summer, no ants were seen outside the nests due to extreme heat and dry conditions. Five days were spent in the study areas during July and beginning of August 2012, looking unsuccessfully for foragers. Moreover, nest entrances were blocked or obviously not used, which is evi-

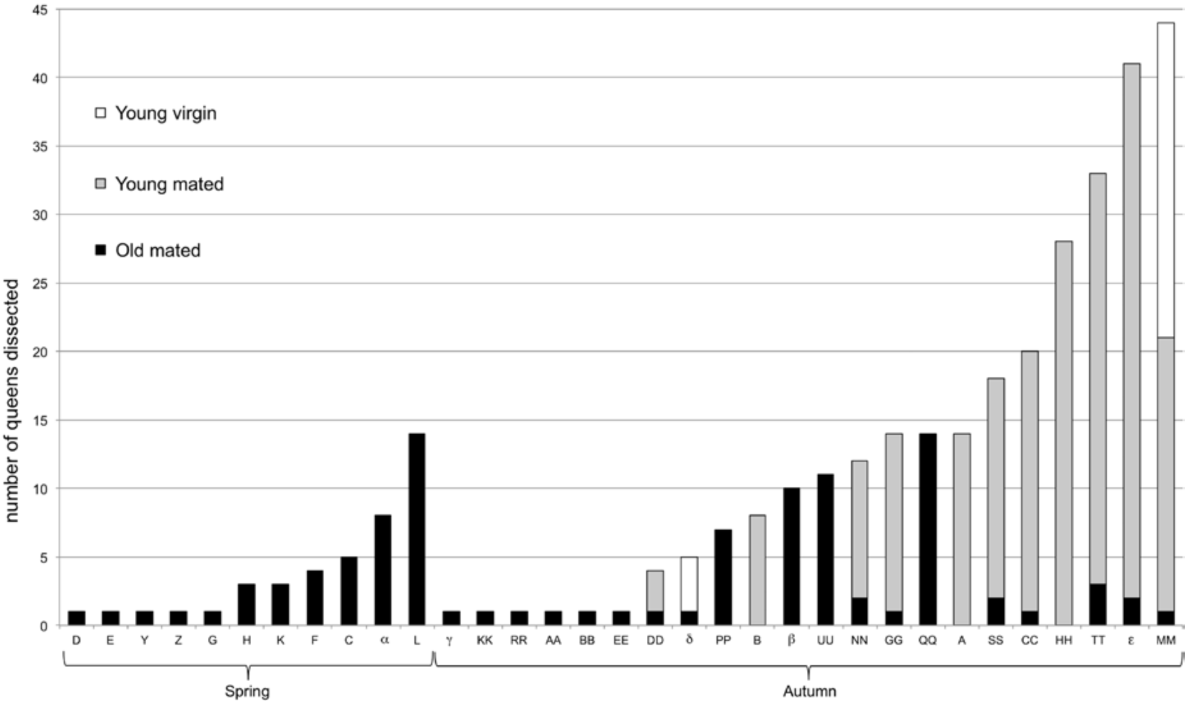

Fig. 2: Numbers of "old" and young (i.e., recently mated) queens in 33 colonies. This distinction is based on the occurrence of large yolky oocytes and dark yellow bodies in 331 queens dissected soon after field collection. Only two colonies had young gynes that were not yet mated.

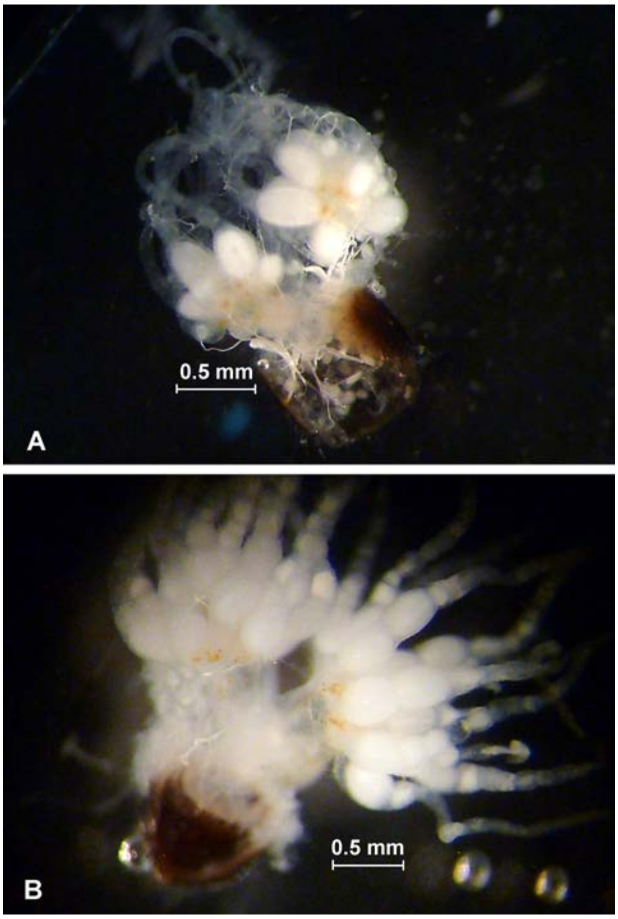

Fig. 3: Comparison of ovarian activity between polygynous and monogynous colonies excavated in early spring: (A) queen from colony alpha (total of eight queens), with short ovarioles and few large yolky oocytes (maximum of one per ovariole); the presence of only few yellow bodies indicates she is young (mated the previous autumn); (B) queen from monogynous colony Y with several medium and large yolky oocytes per ovariole, and also few yellow bodies.

dence of a lack of nocturnal foraging. Accordingly, we can describe colonial structure by reference to two distinct sampling periods: spring (April - May; 11 colonies) and autumn (mid August - October; 24 colonies).

We counted 228 - 3999 workers in spring colonies (1329 ± 377, N = 11; Tab. 1). Similarly, colonies collected in autumn varied from 689 to 3971 workers (2174 ± 194.5, N = 24). Average number of workers was significantly higher in autumn compared to spring nests ($F_{1,33} = 4.87$; $P = 0.03$), and colony sizes were even more distinct if we also consider worker larvae and pupae (Tab. 1). Eleven colonies (both spring and autumn) were monogynous, while 24 colonies (spring and autumn) were polygynous (4 - 41 mated queens; Fig. 2). Both small and big colonies could have a single queen (Tab. 1).

Queen number and ovarian activity: One to sixteen queens were found in the 11 colonies excavated in April - May (Tab. 1), when foraging had started again after the long winter (five months). All dissected queens were mated (N = 42; Fig. 2). Their ovaries consisted of a pair of 14 - 20 ovarioles. Six colonies were polygynous and most queens had medium-large yolky oocytes in most ovarioles (Fig. 3A). Some oocytes were mature (i.e., as large as an egg), indicating these queens can oviposit. In a colony with 16 queens (colony L), ovaries were less active than in colonies H and K, having four and five queens respectively. In the monogynous colony Y, the single queen had ovaries with many large yolky oocytes (Fig. 3B). In another monogynous colony (G), the single queen had a swollen gaster with intersegmental membranes distended ventrally, and dorsal plates two and three fully exposed. Her ovarioles were longer and each had three to four medium and large yolky oocytes. In colonies C (polygynous) and D (monogynous) that were excavated in early spring, none of the queens seemed able to lay eggs yet, despite having dark yellow bodies (Fig. 4). This indicates that ovarian activity stopped during winter, which is confirmed by the presence of few or no eggs and only small larvae in spring colonies (Tab. 1). However, colony C had many larvae and pupae, indicating that brood can overwinter.

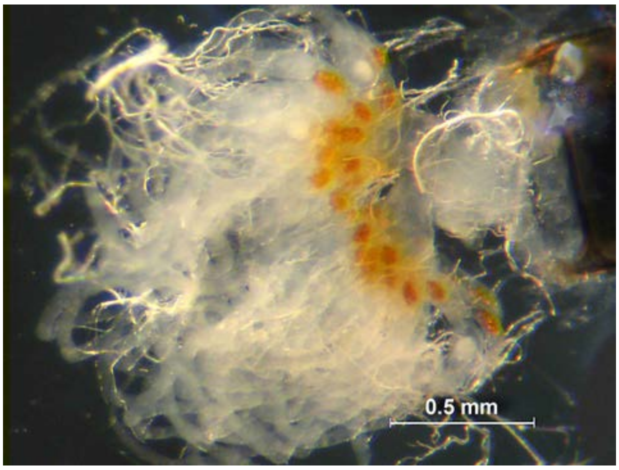

Fig. 4: Monogynous queen with inactive ovaries (no yolky oocytes) at the beginning of spring (colony D). Dark yellow bodies suggest she mated two years earlier; she cannot have mated the previous summer as there was no time to lay many eggs before winter.

Twenty-four colonies collected in August - October had 1 - 41 queens. In six monogynous colonies, all queens had ovaries with large or mature oocytes and dark yellow bodies, similar to spring colonies. Another 18 colonies had many queens, showing considerable variations in ovarian activity. Some queens had very active ovaries and dark yellow bodies, suggesting these were "old" queens mated the previous year or earlier. However the majority of queens showed low to moderate levels of ovarian activity, with short ovarioles containing mostly small or medium yolky oocytes, numerous fat bodies, and scarce or no yellow bodies (Fig. 5). Dissections revealed that all were mated (exceptions in only two colonies, Fig. 2). We interpret these queens to be newly mated and thus young (see below).

Our dissection data suggest that newly mated queens start oogenesis but most do not oviposit until the next spring. Indeed, few or no eggs were found in a majority of autumn colonies (Tab. 1, exceptions are TT and UU). Additional evidence for a decrease in ovarian activity before winter is the presence in autumn colonies of "old" queens with dark yellow bodies but very few yolky oocytes, suggesting that

Fig. 5: Newly mated queen, showing short ovarioles surrounded by fat bodies and very scarce yellow bodies (colony TT). Circle indicates spermatheca filled with sperm.

Fig. 6: Queen with inactive ovaries in autumn (colony CC); one or more large yolky oocytes, as well as yellow bodies, are evidence of past oogenesis.

oogenesis had stopped (Fig. 6). This situation remains until the following spring, as seen in colony D (Fig. 4).

We examined whether worker number in the colonies depends on the time of year (Hypothesis 1) or the number of egg-layers (Hypothesis 2). Colony size varied independently of the numbers of "old" queens (r = 0.234, $P = 0.3$). Since worker numbers were highest in autumn (see above), Hypothesis 2 can be rejected. Next, we analyzed what factors affect the variability in queen number. When only "old" queens are considered, their numbers do not differ significantly between spring and autumn colonies (Mann-Whitney U, $P = 0.15$). However, when all the queens ("old" and young) are considered, numbers are significantly higher in autumn compared to spring colonies (Anova $F_{1,31} = 5.99$, $P = 0.02$). Thus, time of year explains the variability in queen number because sexuals emerge during a distinct period.

Production of sexuals: Unlike most ants where winged gynes are easily recognized and counted, ergatoid gynes emerge wingless (Fig. 1A), hence ovarian dissections are needed to distinguish them from "old" queens. In contrast, ergatoid pupae were conspicuous because they are much bigger than workers. However, only a few queen pupae were found in mid August-beginning September (colonies δ, KK and MM; Tab. 1), and there were no callow gynes (i.e., with lighter pigmentation).

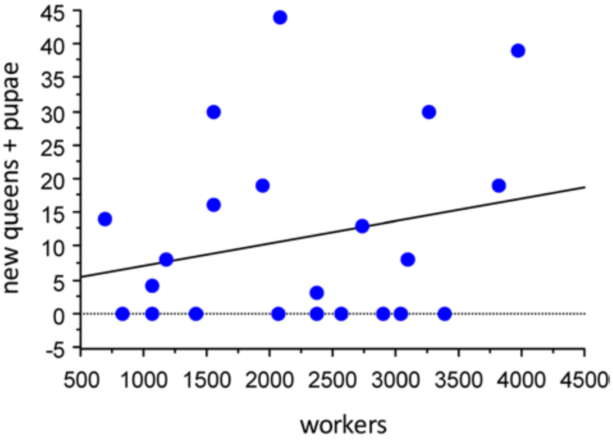

Fig. 7: Relation between worker numbers and numbers of new queens (including pupae) in 22 autumn colonies (equation of the regression $Y = 3.89 + 0.003*X$; r = 0.234; $P = 0.3$).

The higher number of queens in autumn colonies (Tab. 1) is consistent with the finding (based on ovarian dissections) that new queens had recently emerged. Almost all were inseminated, revealing that gynes mate soon after emergence. Colony MM was an exception because 23 queens were virgin. Another 21 queens were mated in this colony but their ovaries were only slightly developed and lacked yellow bodies, except for one individual which we interpret to be the "old" queen (Fig. 2). Thus 43 ergatoid gynes had been reared in colony MM, and there were also two gyne pupae (Tab. 1). Similarly, colony δ had four virgin queens and four queen pupae, together with a mated "old" queen. Dissections indicate that young and "old" queens coexisted in a total of nine colonies.

Our data underestimate male production since we do not know how many flew off before excavation. A large number of males occurred in one August colony, and there were fewer in three September colonies (Tab. 1). Based on our finding that many new gynes had already mated by the end of summer, we conclude that most males had flown off earlier. In total, 16 of 22 colonies collected August - October produced sexuals of one or both sexes (Tab. 1 and Fig. 2). Of these, ten colonies had only gynes, three colonies had only males, and three had both (one had big sexual larvae of unknown sex).

What can explain this variability in the pattern of production of sexuals? We tested worker number (Hypothesis 3) vs. number of reproductive queens (Hypothesis 4). There is almost no correlation (r = 0.234, $P = 0.3$) between worker numbers and the production of gynes (Fig. 7), and no correlation relative to production of males (r = 0.09, $P = 0.5$). Four of four colonies that were highly polygynous (10 - 14 "old" queens) produced no sexuals, whereas six of eleven monogynous colonies produced new gynes, and another four colonies with two to three "old" queens also produced

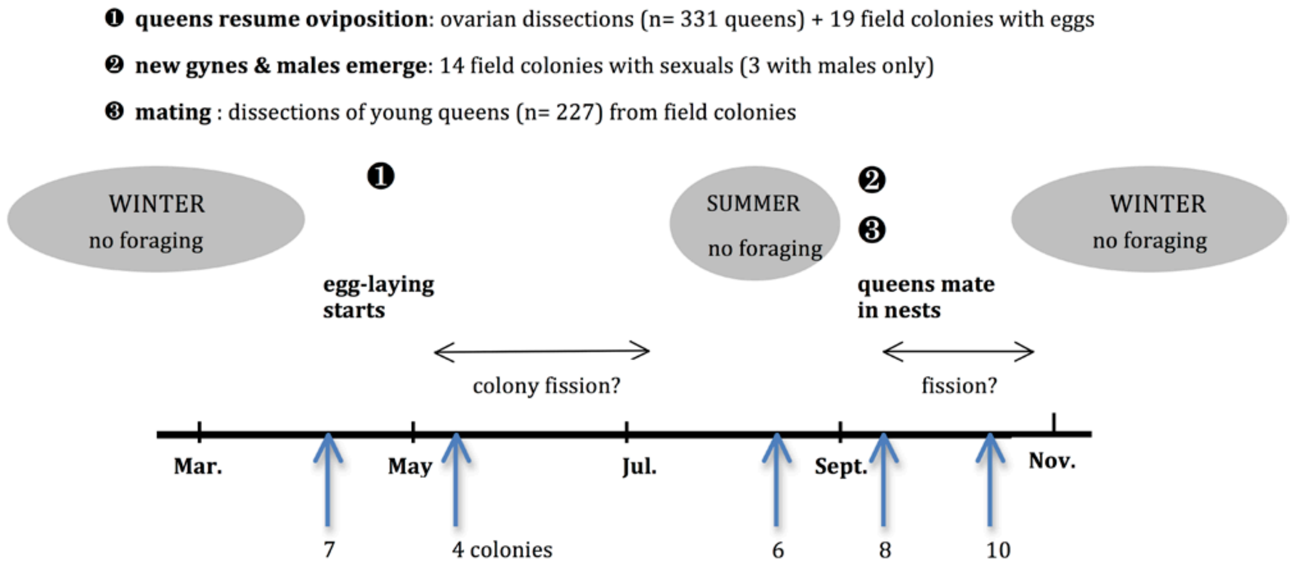

Fig. 8: The annual life cycle of *Monomorium algiricum* is influenced by cold winters and very dry summers, and these determine three key events that may trigger colony fission. Below dateline are the total numbers of colonies excavated in one month (N = 35 collected 2007 - 2012).

gynes. Accordingly, nests with few "old" queens produced significantly more (Mann-Whitney U, $P = 0.002$) sexuals (queens and males) than nests with many "old" queens, thus supporting Hypothesis 4. However, three monogynous colonies produced males only. It is possible that the presence of many egg-laying queens mated the previous year inhibits the rearing of new gynes.

Inferring the occurrence of colony fission: Figure 8 integrates three important yearly events for which we have unambiguous field evidence: (1) queens start or resume egg-laying in spring, leading to an increased number of workers in colonies; (2) new gynes and males emerge in summer; (3) mating occurs soon after emergence. Both an increase in the number of workers in a colony, and many newly-mated queens starting oogenesis simultaneously, are known to trigger colony fission in other social insects (Cronin & al. 2013). This may also be true in *Monomorium algiricum*. Given that we excavated colonies over five years (Tab. 1), inter-annual variations in weather may have had a confounding effect on several life history parameters, e.g., timing of sexual production.

Discussion

The life history of *Monomorium algiricum* is particularly complex due to an interaction of four factors: (I) queens are ergatoid and remain in their natal colonies after mating; (II) strong seasonality causes foraging and egg-laying to stop during five to six months; (III) some colonies are monogynous while others have multiple queens; (IV) colonies multiply by fission, and this causes sudden and unpredictable changes in colony demography and queen number.

Many ant species have winged queens that fly out from natal colonies and perform ICF, but numerous other species behave differently (Heinze 2008). More atypical life histories await discovery because a majority of ant species have never been studied. Since field observations give only limited information about reproductive biology (e.g., mating flight, founding behaviour), whole colonies need to be sampled at different times of the year. Unlike social wasps with open nests, the demography of individual ant colonies cannot be monitored over time, and researchers must rely on an adequate sample of colonies (Tschinkel 2011). While one colony is only one data point in time, ovarian dissections can add valuable information about the events that preceded excavation. Indeed, the presence of sperm in queens' spermathecae provides unambiguous data about mating. Furthermore, examination of ovaries gives information about egg-laying activity, past and present.

Ovarian dissections in *Monomorium algiricum* revealed three key aspects of its life history: (I) both monogynous and polygynous colonies are found throughout the year. When there is polygyny, individual queens are less fecund than in monogynous colonies, and this needs to be distinguished from seasonal decline; (II) new gynes mate promptly after emergence. They can coexist with the previous cohort of queens, from which they can only be distinguished by examining ovaries: newly mated queens have developing oocytes but no dark yellow bodies because many eggs have not been laid; (III) egg-laying stops from autumn until spring.

Sexual activity: Sexuals had been produced in 16 of 22 colonies collected at the end of summer-autumn, although three of these colonies had males only. Our data suggest that new gynes are not reared in colonies with many "old" queens (mated the previous year), hence many queens showing oogenesis may inhibit the rearing of diploid larvae as queens. In contrast, gynes and males were produced in colonies having one or a few "old" queens with active ovaries. In *Monomorium pharaonis*, the production of gynes was inhibited by the presence of fertile queens (Edwards 1987), through cannibalism of the sexual brood by the workers (Edwards 1991). In *Aphaenogaster senilis*, where colonies also reproduce by fission, inhibition of gyne production was shown to be mediated by volatile pheromones coming from the Dufour's and postpharyngeal glands (Boulay & al. 2007, Ruel & al. 2013). In *Linepithema humile* (Mayr, 1868), Vargo & Passera (1991) demonstrated that active queens exert pheromonal control over the production of gynes; gyne larvae are executed by workers. In *M. algiricum*, the presence of one or few "old" queens with active ovaries seems insufficient to inhibit rearing of new gynes, although this mechanism of regulation (pheromones or cannibalism by workers) needs to be studied with more colonies in the future. We did not detect any correlation between sexual investment and colony size, but such analysis is weakened by inter-annual variation and a low number of samples per year. Moreover, events of colony fission (DCF) cause a drastic reduction in worker number (SCHMIDT & al. 2011).

Except for two colonies collected in September, all *Monomorium algiricum* queens dissected were mated (N = 274). This striking result gives a reliable picture of mating biology in nature because the queens were dissected soon after excavation. We did not observe mating in the field but we can assume that ergatoid queens meet foreign males on the ground, close to their nests as in *M. pharaonis* (see PETERSEN & BUSCHINGER 1971) and Formicinae species like *Proformica longiseta* COLLINGWOOD, 1978 (FERNÁNDEZ-ESCUDERO & al. 2002). Mating could even occur underground following entry of foreign males inside the nests. Males fly and probably use their large bulging eyes to locate single queens on the ground, or even nest entrances. At a shorter scale, virgin queens then release sex attractants, "calling" the males as known in *M. pharaonis* (see ALLARD & al. 2006). This female-calling strategy eliminates the dangers associated with aerial dispersal during mating, such as in species of *Monomorium* with winged queens. In *M. algiricum* the newly mated queens remain in their natal nest for the rest of their lives, unless they leave with workers and brood to form a new colony by DCF.

Regulation of queen number: Since dissections occurred over several years, photographs of ovaries were useful to compare and standardize our descriptions. Visual assessment of ovarian activity was not always straightforward, especially because there are dozens of ovarioles. Since yellow bodies do not disappear but oogenesis can vary over time, these features can give apparently discordant information. For instance, several *Monomorium algiricum* queens had dark yellow bodies even though they lacked developing yolky oocytes (Fig. 4). Others had undeveloped ovaries together with one or more large yolky oocytes and this is also evidence of past oogenesis (Fig. 6).

Ovarian activity varied considerably depending on the number of co-existing queens as well as time of year. It is possible that higher foraging success in some colonies affects the ovarian activity of resident queens; if little food is available, several queens may not all be able to have very developed ovaries. Queen number affected the estimated fecundity of individuals. In ten of 11 monogynous colonies examined, ovaries of the single queen were more developed than in polygynous colonies. This suggests mutual inhibition among multiple coexisting queens, as shown in other species, e.g., *Cardiocondyla obscurior* WHEELER, 1929 (SCHREMPF & al. 2011). Mutual inhibition may be regulated by fertility signals encoded in the cuticular hydrocarbons (PEETERS & LIEBIG 2009). In *Monomorium algiricum*, although we could distinguish mutually-inhibited queens from seasonally-inactive queens, we did not study the mechanism of inhibition in detail. Multiple data suggest that oogenesis is seasonal, and queens (both young and "old") stop ovipositing during the long winter. Some "old" queens can survive until the following year, but it is likely that others die during winter.

Colony B was observed in the laboratory for several weeks. Queens and brood always grouped very closely together, surrounded by many workers who fed them by trophallaxis. Even though the queens were not marked individually, we did not detect aggression. Queen number appears not regulated by dominance interactions but may result instead from contingent events: (1) highly seasonal production of new gynes that do not disperse individually; (2) fission of polygynous colonies that sometimes results in monogyny, especially if workers and queens distribute themselves erratically across parent and daughter colonies.

Monomorium is generally known to be polygynous, including species with winged queens, e.g., *M. pharaonis* (see SCHMIDT & al. 2011), *M. subopacum* (SMITH, 1858) (C. Peeters, unpubl.); species with ergatoid queens, e.g., *M. creticum* EMERY, 1895 (A. Buschinger, pers. comm.), *M. medinae* FOREL, 1892 (ESPADALER 1982), *M. hesperium* EMERY, 1895 (ESPADALER & AGOSTI 1985); species with both types of queens, e.g., *M. ergatogyna* WHEELER, 1904 (WARD 2005), *M.* cf. *rubriceps* MAYR, 1876 (BUSCHINGER 2011), *M. subapterum* WHEELER, 1917 (FERSCH & al. 2000). *Monomorium algiricum* has ergatoid queens only, and our data reveal both monogynous and polygynous colonies. It is thus different from other species having ergatoid queens, a proportion of which are strictly monogynous while others are always polygynous (PEETERS 2012).

Annual cycle and timing of colony fission: *Monomorium algiricum* inhabits mountainous regions that are very cold in winter, and extremely hot and dry during summer. Accordingly, workers forage during six to seven months of the year only, roughly in spring (March - April to June) and autumn (late August - middle of October) (A. Tinaut, unpubl.). A similar decrease in foraging activity is seen in other Mediterranean species (TINAUT 1982, CERDÁ & al. 1988, CROS & al. 1997). Evidence of strong seasonality was also obtained for *Monomorium* sp. (*minimum* (BUCKLEY, 1866) group) at high elevation in the Pinal Mountains, Arizona, USA; colony RAJ4208 was collected at end of winter (March 2009) with at least 15 ergatoid queens, all mated and with moderately active ovaries (mature oocytes) but no dark yellow bodies (C. Peeters, unpubl.). These dissection data together with the absence of eggs in the nest indicate that queens are inactive during winter, as in *M. algiricum*.

We did not obtain direct data about colony foundation in *Monomorium algiricum*. Our fieldwork was done throughout the year but nest emigration was never observed, and no ergatoid queens were found walking above ground, either alone or accompanied by workers. We did not find small incipient colonies (single queen with few workers and brood) that could be construed as recently started by one queen. We surmise that colonies reproduce exclusively by DCF because ergatoid queens lack wing muscles that can be used to feed the first brood (see PEETERS 2012). In species that shifted from ICF to DCF, winged reproductives are selected against because the expensive wing muscles are not needed (PEETERS & MOLET 2010).

Figure 8 summarizes indirect data for our hypothesized life history for *Monomorium algiricum.* New workers emerge in spring, and summer colonies are bigger than in spring

(2174 vs. 1328 workers on average). At the end of summer, sexuals are produced in a majority of colonies. Gynes mate and remain in their natal colonies, and they start oogenesis although few eggs seem to be laid before winter. We suggest that colonies fission either at the end of spring following the emergence of many young workers, or in autumn after newly mated ergatoid queens begin ovarian activity. The factors triggering DCF vary across ant lineages, although they are generally poorly known (CRONIN & al. 2013). In the monogynous *Cataglyphis cursor* (FONSCOLOMBE, 1846), (I) colony fission is seasonal and always follows the production of new sexuals, at the end of winter hibernation; (II) fissioning and non-fissioning colonies overlap in size; (III) colonies divided in 4.0 ± 1.3 propagules, with larger colonies producing larger propagules but not more propagules; (IV) the mother queen was replaced in half of the fissioning colonies (CHÉRON & al. 2011).

Colony foundation is little studied in the genus *Monomorium*, but the ergatoid morphology of queens in many species allows a reliable prediction of widespread DCF. Indeed, DCF occurs even in species with winged queens, such as *M. pharaonis* in which there is no aerial dispersal (PETERSEN & BUSCHINGER 1971). The absence of a link between polygyny and queen morphology (winged or ergatoid) means that DCF is not necessarily coupled with polygyny, as often claimed in the literature (see CRONIN & al. 2013).

Why evolve ergatoid queens? Most species in the *Monomorium salomonis* (LINNAEUS, 1758) group have winged queens, and these are much bigger than workers (BOLTON 1987). Historically, in some *Monomorium* having both winged and ergatoid queens, the latter were described as parasitic species just because they were wingless, with conspecific workers assumed not to exist (e.g., BERNARD 1955). BOLTON (1986) already pointed out that ergatoid queens are associated with a shift in dispersal strategy, and in a proportion of species they completely replace winged queens. Compared to the winged queens of *M. subopacum* (collected near Algeciras, Spain), ergatoid queens of *M. algiricum* have a decreased thorax volume, and they weigh half as much (0.004 ± 0.0006 g (n = 11) vs. 0.002 ± 0.001g (n = 11); C. Peeters, unpubl.). Ergatoid queens are often reduced in size and are thus less costly for the colony to produce (PEETERS 2012).

Many DCF species show a dramatic decrease in the number of new gynes reared annually, although this is balanced by increased numbers of workers that are essential for the success of newly divided colonies (CRONIN & al. 2013). In *Monomorium algiricum*, many workers were produced in spring, a part of which is to be considered as reproductive investment. However many gynes were produced compared to other species with ergatoids (PEETERS 2012).

Since ergatoid queens are restricted to disperse on foot, they cannot colonize disjunct habitats (PEETERS 2012). *Monomorium algiricum* currently occurs on both sides of the Mediterranean Sea, and we may speculate that winged queens were lost before the end of a land connection. About six million years ago the Mediterranean evaporated partly or completely (BRAGA & al. 2002), and exchanges of fauna occurred between Africa and southern Spain.

Acknowledgements

We thank Paqui Ruano for statistical and logistic help, Pedro Sandoval, Keith Bensusan, Jonathan Avilés and José Vidal Cordero for field and laboratory assistance, Thibaud Monnin for useful comments on the manuscript. CP was supported by the French National Research Agency (ANR-06-BLAN-0268).

References

ALLARD, D., BØRGESEN, L., VAN HULLE, M., BOBBAERS, A., BILLEN, J. & GOBIN, B. 2006: Sperm transfer during mating in the pharaoh's ant, *Monomorium pharaonis*. – Physiological Entomology 31: 294-298.

BILLEN, J. 1982: Ovariole development in workers of *Formica sanguinea* LATR. (Hymenoptera: Formicidae). – Insectes Sociaux 29: 86-94.

BERNARD, F. 1955: Morphologie et comportement des fourmis lestobiotiques du genre *Epixenus* EMERY. – Insectes Sociaux 2: 273-283.

BOLTON, B. 1986: Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae). – Journal of Natural History 20: 267-272.

BOLTON, B. 1987: A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* MAYR. – Bulletin of the British Museum of Natural History (Entomology) 54: 263-452.

BOULAY, R., HEFETZ, A., CERDÁ, X., DEVERS, S., FRANCKE, W., TWELE, R. & LENOIR, A. 2007: Production of sexuals in a fission-performing ant: dual effects of queen pheromones and colony size. – Behavioural Ecology and Sociobiology 61: 1531-1541.

BRAGA, J.C., MARTÍN, J.M. & QUESADA, C. 2002: Patterns and average rates of late Neogene-recent uplift of the Betic Cordillera, SE Spain. – Geomorphology 50: 3-26.

BUSCHINGER, A. 2011: Queen polymorphism in an Australian ant, *Monomorium* cf. *rubriceps* MAYR, 1876 (Hymenoptera: Formicidae). – Myrmecological News 15: 63-66.

CERDÁ, X., BOSCH, J., ALSINA, A. & RETANA, J. 1988: Dietary spectrum and activity patterns of *Aphaenogaster senilis* (Hymenoptera: Formicidae). – Annales Société Entomologique de France (N.S.) 24: 69-75.

CHÉRON, B., CRONIN, A.L., 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: 1448-1458.

CRONIN, A., MOLET, M., DOUMS, C., MONNIN, T. & PEETERS, C. 2013: Recurrent evolution of dependent colony foundation across eusocial insects. – Annual Review of Entomology 58: 37-55.

CROS, S., CERDÁ, X. & RETANA, J. 1997: Spatial and temporal variations in the activity patterns of Mediterranean ant communities. – Ecoscience 4: 269-278.

EDWARDS, J. 1987: Caste regulation in the pharaoh's ant *Monomorium pharaonis*: the influence of queens on the production of new sexuals forms. – Physiological Entomology 12: 31-39.

EDWARDS, J. 1991: Caste regulation in the pharaoh's ant *Monomorium pharaonis*: recognition and cannibalism of sexual brood by workers. – Physiological Entomology 16: 263-271.

ESPADALER, X. 1982: *Xenhyboma mystes* SANTSCHI, 1919 = *Monomorium medinae* FOREL, 1892. Évidence biologique de la synonymie (Hymenoptera: Formicidae). – Nouvelle Revue d'Entomologie 12: 111-113.

ESPADALER, X. & AGOSTI, D. 1985: *Monomorium hesperium* EMERY: description de la femelle (Hymenoptera, Formicidae).

– Mitteilungen der Schweizerischen entomologischen Gesellschaft 58: 295-297.

FERNÁNDEZ-ESCUDERO, I., PAMILO, P. & SEPPÄ, P. 2002: Biased sperm use by polyandrous queens of the ant *Proformica longiseta*. – Behavioral Ecology and Sociobiology 5: 207-213.

FERSCH R., BUSCHINGER A. & HEINZE, J. 2000: Queen polymorphism in the Australian ant *Monomorium* sp.10 (= *subapterum*). – Insectes Sociaux 47: 280-284.

GOBIN, B., PEETERS, C. & BILLEN, J. 1998: Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*. – Physiological Entomology 23: 329-336.

HEINZE, J. 2008: The demise of the standard ant (Hymenoptera: Formicidae). – Myrmecological News 11: 9-20.

PEETERS, C. 2012: Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). – Myrmecological News 16: 75-91.

PEETERS, C. & LIEBIG, J. 2009: Fertility signaling as a general mechanism of regulating reproductive division of labor in ants. In: GADAU, J. & FEWELL, J. (Eds.): Organization of insect societies: from genome to socio-complexity. – Harvard University Press, Cambridge, MA, pp. 220-242.

PEETERS, C. & MOLET, M. 2009 [2010]: Colonial reproduction and life histories. In*:* LACH, L., PARR, C. & ABBOTT, K. (Eds.): Ant ecology. – Oxford University Press, Oxford, UK, pp. 159-176.

PETERSEN, M. & BUSCHINGER, A. 1971: Das Begattungsverhalten der Pharaoameise, *Monomorium pharaonis* (L.). – Zeitschrift für Angewandte Entomologie 68: 168-175.

RUEL, C., LENOIR, A., CERDÁ, X. & BOULAY, R. 2013: Surface lipids of queen-laid eggs do not regulate queen production in a fission-performing ant. – Naturwissenschaften 100: 91-100.

SCHMIDT, A.M., LINKSVAYER, T.A., BOOMSMA, J.J. & PEDERSEN, J.S. 2011: Queen-worker caste ratio depends on colony size in the pharaoh ant (*Monomorium pharaonis*). – Insectes Sociaux 58: 139-144.

SCHREMPF, A., CREMER, S. & HEINZE, J. 2011: Social influence on age and reproduction: reduced lifespan and fecundity in multi-queen ant colonies. – Journal of Evolutionary Biology 24: 1455-1461.

TINAUT, A. 1982: Evolución annual de la mirmecocenosis de un encinar. – Boletín Estación Central de Ecología 11: 49-56.

TINAUT, A. & ORTIZ, F. 1988: Descripción del macho de *Monomorium algiricum* (BERNARD, 1955) y consideraciones sobre el valor taxonómico del género *Epixenus* EMERY, 1908 (Hymenoptera: Formicidae). – Boletin Asociación española Entomología 12: 165-174.

TINAUT, A. & RUANO, F. 1992: Braquipterismo y apterismo en formícidos. Morfología y biometría en las hembras de especies ibéricas de vida libre (Hymenoptera: Formicidae). – Graellsia 48: 121-131.

TSCHINKEL, W.R. 2011: Back to basics: sociometry and sociogenesis of ant societies (Hymenoptera: Formicidae). – Myrmecological News 14: 49-54.

VARGO, E.L. & PASSERA, L. 1991: Pheromonal and behavioral queen control over the production of gynes in the Argentine ant *Iridomyrmex humilis* (MAYR). – Behavioral Ecology and Sociobiology 28: 161-169.

WARD, P.S. 2005: A synoptic review of the ants of California (Hymenoptera: Formicidae). – Zootaxa 936: 1-68.