

Oecologia (2003) 136:558–564
DOI 10.1007/s00442-003-1300-x

POPULATION ECOLOGY

Cathy Liautard · William D. Brown · Ken R. Helms ·
Laurent Keller

Temporal and spatial variations of gyne production in the ant *Formica exsecta*

Received: 14 November 2002 / Accepted: 27 April 2003 / Published online: 29 May 2003
© Springer-Verlag 2003

Abstract Social insects have become a general model for tests of sex allocation theory. However, despite tremendous interest in the topic, we still know remarkably little about the factors that cause dramatic differences in sex allocation among local populations. A number of studies have suggested that environmental factors may influence sex allocation in ant populations. In polygynous (multiple queens per nest) populations of the ant *Formica exsecta*, sex allocation is extremely male biased at the population level, with only a small proportion of nests producing any gynes (female reproductive brood). We analysed the proportion of gyne-producing nests in 12 *F. exsecta* populations during three successive breeding seasons and found considerable temporal and spatial variability in the proportion of gyne-producing nests. The populations differed in a number of characteristics, including elevation, nest density, size of the nest mound, and number of nests per population. However, the proportion of gyne-producing nests was not associated with any of these geographic and demographic variables. Moreover, differences between populations in the production of gynes were not consistent between years. Thus, the proportion

of gyne-producing nests appears to vary stochastically, perhaps because of stochastic variations in environmental factors. For example, year-to-year variations in the proportion of gyne-producing nests were associated with differences in spring weather conditions between years. The finding that gyne production varies greatly between years suggests that it may not always be adaptive at a local scale.

Keywords Non-adaptive behaviour · Resources · Sex allocation · Spring temperature · Stochasticity

Introduction

Population sex ratio has a major influence on individual fitness. At equilibrium, parental expenditure should be partitioned between sexes in order to have identical fitness payoff from each sex (Fisher 1930). Some of the most important tests of this theory have been conducted on social Hymenoptera (ants, bees and wasps) (e.g., Trivers and Hare 1976). In social Hymenoptera, asymmetries in relatedness arise from the haplodiploid sex determining system, resulting in females being more related to sisters ($r=0.75$) than to daughters ($r=0.5$), sons ($r=0.5$) or brothers ($r=0.25$). Kin selection, combined with Fisher's sex ratio theory, provides quantitative predictions linking sex investment ratios to genetic relatedness asymmetry at both the population and nest levels (Trivers and Hare 1976; Boomsma and Grafen 1991). If workers control sex allocation (the relative investment in female and male reproductives), female bias is predicted to be 3:1 at the population level when all nest members are the offspring of a single, once-mated queen. This ratio is predicted as workers are three times more related to their sisters than to their brothers. An increase in the number of queens per nest and/or their mating frequency will lead to a decrease in relatedness asymmetry and thus a lower female bias, both at the population and nest levels (Trivers and Hare 1976; Boomsma and Grafen 1991; for reviews see Bourke and Franks 1995; Crozier and Pamilo

C. Liautard (✉) · K. R. Helms · L. Keller
Institute of Ecology,
University of Lausanne,
Bâtiment de Biologie, Lausanne, Switzerland
e-mail: Cathy.Liautard@helsinki.fi
Fax: +358-9-19157694

W. D. Brown
Department of Biology,
SUNY Fredonia,
Fredonia, NY 14063, USA

Present address:

C. Liautard, Department of Ecology and Systematics,
University of Helsinki,
P.O. Box 65, 00014 Helsinki, Finland

Present address:

K. R. Helms, Department of Entomology,
Texas A&M University,
College Station, TX 77843-2475, USA

1996; Chapuisat and Keller 1999). By contrast, if queens control sex ratios, population investment in reproductive females and males should be equal because queens are equally related to their sons and daughters.

Sex allocation has been analysed across a large range of eusocial Hymenoptera. Several studies have revealed that factors in addition to relatedness asymmetry also influence population- and colony-level sex investment. Sex allocation is sometimes correlated with colony size, colony productivity, nest density, or nest temperature (Nonacs 1986b; Rosengren and Pamilo 1986; Aron et al. 1994; Deslippe and Savolainen 1995; Rosenheim et al. 1996; Foitzik and Heinze 2000). These correlations may reflect the importance of resources relative to brood availability (e.g., Nonacs 1986b; Rosenheim et al. 1996; Brown and Keller 2000). For instance, when sex allocation appears to co-vary with nest productivity and colony size, larger, more productive nests tend to invest proportionally more in queen production while smaller, less productive nests tend to produce only or mostly males. Large nests having more resources would still raise male brood but direct most female larvae to the queen developmental pathway (Nonacs 1986a). The association between nest productivity or colony size with investment ratios may also stem from a shortage of brood, if, for example, large productive nests headed by a single queen are egg-limited (Rosenheim et al. 1996). As a result, workers in large productive colonies would benefit by producing the more expensive sex, typically gynes (female reproductive brood). The direct effects of abiotic conditions on sex allocation are less clear, but could result from the way in which the physical environment affects female caste determination. For example, some studies suggest that the production of gynes is increased under warm conditions (Rosengren and Pamilo 1986; Aron et al. 1994). Rosengren and Pamilo (1986) found that *Formica aquilonia* nests producing sexuals (mainly gynes) had higher temperatures than those failing to produce sexuals.

Environmental factors affecting sex allocation may vary spatially or temporally, which in turn may induce spatial and temporal variations in sex allocation. However, little is known about the magnitude of such variations and the factors responsible. Spatial and temporal variation in sex allocation patterns appear common in ant populations. Spatial variation has often been attributed to changes in relatedness asymmetry within colonies (Herbers 1990; Chan et al. 1999; Walin and Seppä 2001) and temporal variations to exceptional climatic variation between years (Herbers 1990; Buschinger and Heinze 2001). In our study we investigated the magnitude of variations in sex allocation in the ant *F. exsecta*, where relatedness asymmetry appears to have little impact on sex allocation.

Sex allocation has been extensively studied in *F. exsecta*. Polygynous (multiple queens per nest) populations of this species are characterized by a highly male-biased sex ratio with only a very low proportion of nests producing any gynes (Pamilo and Rosengren 1983; Brown and Keller 2000). A comparison of the genetic

structure of male- and gyne-producing nests showed no evidence of an association between relatedness asymmetry and nest sex ratios (Brown and Keller 2000). Instead, nest sex ratios were associated with the effective number of queens per nest. Nests producing gynes had a lower effective queen number than nests producing only males. This led Brown and Keller (2000) to propose the queen replenishment hypothesis to account for the observed pattern of sex ratio in *F. exsecta* and other highly polygynous ants. In *F. exsecta*, and other highly polygynous ants, queens frequently remain in their natal nest after mating and eventually disperse on foot with workers to initiate new nests nearby (Bourke and Franks 1995; Keller 1995; Liautard and Keller 2001). This mode of reproduction may lead to intense local resource competition (Clark 1978) between queens within nests and is often associated with dramatically male-biased sex ratios (reviewed in Bourke and Franks 1995; Crozier and Pamilo 1996). The queen replenishment hypothesis predicts that the production of new queens occurs preferentially or only in nests that contain relatively few queens because these are the nests that benefit most from recruiting new queens (Brown and Keller 2000). In polygynous ants, low queen number may cause egg and brood limitation in nests with abundant resources (Elmes and Keller 1993). Thus, as queen number decreases, local resource competition between queens is reduced, and below a certain threshold there is a premium on recruiting new queens to enhance nest survival and productivity. This threshold and the value of new queens will depend on resource availability relative to the current number of queens. Thus, environmental factors influencing the level of resources available should have important effects on gyne production. Nests with more limited resource levels and thus greater local resource competition should not produce queens. This, indeed, seems to be the case, as nests that fail to produce gynes have smaller workers and smaller males (Brown and Keller 2000) suggesting that such nests have relatively limited resources available per offspring, and lower productivity per queen (Brown et al. 2002). We therefore expect spatial and temporal variability in gyne production to be correlated with environmental factors.

The aim of this study was to investigate both spatial and temporal variations in gyne production in *F. exsecta*, and relate this to variations in environmental factors known to be correlated with sex allocation in other species. Spatial variation was assessed in 12 populations where elevation, number of nests, nest density, and nest size have been recorded. To assess temporal variations in sex ratio, we estimated the proportion of gyne-producing nests in those 12 populations for 3 years. Because temperature could affect sex allocation (Rosengren and Pamilo 1986; Aron et al. 1994), we also compared daily radiation (W/m^2 per day) for each of the 3 years of this study.

Materials and methods

Study area

We compared spatial and temporal variations in the proportion of gyne-producing nests from 12 populations of *F. exsecta* in the Jura Mountains of Switzerland, including the population studied by Brown and Keller (2000, 2002) and Brown et al. (2002). These populations represent all the known populations in the area. They were located in open pastures at the following sites within the Canton of Vaud: Le Bugnonet (BA and BB), Le Bois de Gaye (BG), Les Chenevières (CHEN), La Dunanche (DU), Les Agoxats (LA), La Conriéry (LC), Les Orgères (LO), Le Mollendruz (MO), Le Pré de Joux (PJ), Le Pré Nouveau (PN), and La Combe aux Rocs (ROC). At Le Bugnonet there were two genetically and spatially distinct groups of nests approximately 500 m apart (Liautard and Keller 2001), which we considered to be distinct populations (Bugnonet A, denoted BA, and Bugnonet B, denoted BB). All populations were situated within 6 km of each other, except for MO, which was approximately 20 km from the nearest population. Nests comprising these populations are almost entirely polygynous as indicated by the genetic structure of nests from CHEN, LO, PJ and PN (Brown and Keller 2000; Liautard and Keller 2001). The high density of nests within all 12 populations is also indicative of polygyny. Monogynous nests are typically more than 10 m apart (L. Sundström, personal communication), whereas polygynous nests occur at much greater densities. To assess temporal variability, population- and nest-level sex ratios were measured over three breeding seasons, from 1999 to 2001.

Sex ratios

We estimated nest-level production of males, gynes, and workers by gently opening nests and removing approximately 50 pupae. Field observations of larvae development suggest that the vast majority of sexuals are produced from the first eggs laid during the season (C. Liautard, personal observation). Samples were taken between late June and mid-July, once most of this first cohort had entered the pupal stage but before any had emerged as adults (early July in 1999 and 2001, mid-June in 2000). In 1999, we sampled pupae from up to 20 randomly selected nests in each population for a total of 221 nests overall. Four populations contained fewer than 20 nests, in which case all nests were sampled. Because of an extremely low frequency of gyne-producing nests in 1999, we increased our sample to up to 30 nests per population in the following years, totalling 273 and 296 nests in 2000 and 2001, respectively. We define a nest as an individual dome, the surface of which has been denuded of living vegetation by the ants and maintained with a cover of shredded dead grass and conifer needles. Workers occasionally move between nests (W. D. Brown, personal observation), which suggests that populations may be polydomous, but previous results suggest that sex allocation is decided at the level of the nest (Brown and Keller 2000, 2002; Brown et al. 2002). Pupae were held at 28°C and high humidity for approximately 7 days to allow them to develop sufficiently for identification of sex. Pupal sex was determined by moistening pupae in ethanol and observing size, eye shape, and genitalia. Furthermore, in 2001 we examined up to 70 additional nests per population (609 overall) simply to assess the presence of gyne pupae without collecting any individuals. This sample was combined with our previous 296 nests from 2001 to increase the total sample size and increase the power to detect differences in sex ratios between populations.

Because, as in previous studies (Brown and Keller 2000, 2002; Brown et al. 2002), we were primarily interested in the causes underlying the decision to produce gynes or not, we classified nests as male-producing if they produced males but no gynes, and gyne-producing, if they produced gynes (usually along with males). We also observed nests that produced workers but no sexual offspring; these were included in male-producing nests for analyses, as we were only interested in the factors leading to gyne production. On

average, the proportion of those worker-producing nests ranges between 7.1% and 20.0% per year, over all the populations. We then compared the proportion of gyne-producing nests between populations and between years.

Nest characteristics

We measured the surface area of the mound of the nest as an estimate of nest size and productivity. In 2000 and 2001, we estimated the surface area of all nests from which we collected pupae by taking two measurements of the diameter of the nest dome, roughly at right angles to each other. The edge of the nest was defined as the limit of the area denuded of vegetation by the ants. Following Deslippe and Savolainen (1994), we converted these into a single measure of nest surface area using the equation of an ellipse ($\pi ab/4$, where a and b are the two measures of nest diameter).

The relationship between nest surface area and the size of the worker force was estimated using mark-recapture methods presented in Brown et al. (2002). Prior to the emergence of brood, we marked between 200 and 2,432 adult workers from 59 nests with a leather and wood spray paint (Super magic colour spray, Magid, Central Islip, N.Y.). Approximately 24 h later, we recaptured workers on the nest and estimated worker number from the proportion of marked to unmarked ants. We used a similar mark-recapture technique to estimate the relationship between nest surface area and nest total productivity (workers and pupae of sexuals). We marked brood by gently opening nests, collecting between 20 and 3,980 pupae per nest, and marking each of these pupae with a dot of ink from a non-toxic, permanent red marker (Sharpie). We then released pupae back into their nest and recaptured a sample two days later. Again, the proportion of marked to unmarked individuals was used to estimate total pupal production.

Our mark-recapture study revealed that nest surface area was a good estimate of the number of workers and productivity of the nest. Nest surface area was significantly positively correlated with worker number (Fig. 1a; $r=0.77$, $n=59$, $P<0.0001$) and the number of brood produced (Fig. 1b; $r=0.74$, $n=59$, $P<0.0001$). When the most extreme estimate of brood production was excluded (upper right of Fig. 1b) the relationship between nest surface area and productivity remained significantly positive ($r=0.62$, $n=58$, $P<0.0001$). Thus, nest surface area is a reasonable estimate of the size and productivity of the nest.

Population characteristics

We assessed population characteristics by estimating population density, population size and population elevation. In 2000, we counted the number of nests per population by traversing the population along transects approximately 10 m apart, marking each nest with a luminescent coloured stake and recording nest location with a GPS12XL (Geographic Position System, Garmin, Romsey, UK). The elevation of each population was determined using local topographical maps (1:25,000, Carte nationale Suisse, no. 1241). Nest density was measured by counting the number of nests within 10 m of each nest, which is approximately equal to the maximal foraging distance of worker ants (Pisarski 1982). The average nest density was taken as a measure of density for the population as a whole.

Temporal variations

Because temporal variations in the occurrence of gyne-producing nests could be influenced by climatic conditions, we compared annual variations in climate during the period of larvae growth. We calculated the average daily radiation (W/m^2 per day) for each 7-day period. This yielded 13 measures per year of average radiation, ranging from the first week of April (i.e., the approximate time of

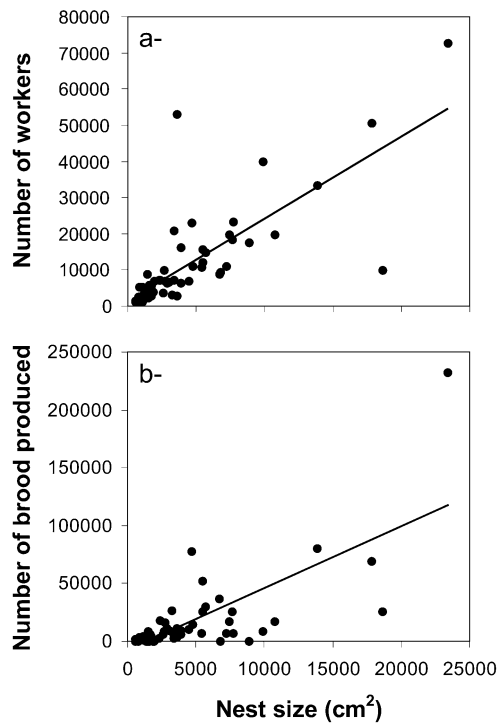


Fig. 1a, b Nest size (the surface area of the dome of the nest) significantly predicted both worker number and nest productivity. **a** Worker number. **b** Nest productivity

snow melt) and ending in late June (when the first larvae pupate). These values of radiation were taken from two weather stations: the first was 10 km from the nearest population of *F. exsecta* but was at a much lower elevation (Changins, at 430 m) and the other was at a similar elevation but about 45 km away (La Frétaz, at 1,202 m).

Statistical analyses

Data analyses were performed using S-PLUS 2000 (Software MathSoft). Non-normally distributed variables (Kolmogorov-Smirnov test, Lilliefors $P < 0.05$) were transformed prior to parametric testing. We first analysed the correlations between our environmental variables and how these variables differed between populations and between years. We tested for differences among populations in nest density (transformed via a $\sqrt{(x+0.5)}$ function) in

2000 using one-way analysis of variance (ANOVA) with population as the independent variable. We tested for differences in nest surface area (transformed via the \ln function) between populations and between 2000 and 2001 using two-factor ANOVA with population and year as the independent variables. We also analysed the correlation between nest surface area, number of nests, nest density, and elevation using Spearman correlation analysis.

To compare climatic variations between years, we performed a repeated-measures ANOVA, in which the independent values were the weekly values of mean daily radiation repeated for 3 years and weather station. Our repeated measures lacked compound symmetry, and therefore we carried out a Huynh-Feldt adjustment of the degrees of freedom (Zar 1999).

The relationship between population-level proportion of gyne-producing nests and four features that differed between populations (elevation, number of nests, average nest density and year) was subjected to analysis of covariance. We entered the rank proportion of gyne-producing nests in each population as the dependent variable, year (1999, 2000 or 2001) as a factorial variable, and elevation, number of nests, and average nest density as covariates. None of the interaction effects was significant ($P > 0.05$) and they were therefore excluded from the model.

We next analysed the relationship between nest-level decision to produce gynes or not and nest surface area with a general linear model (GLM). Sex ratio category (male- or gyne-producing, transformed via the logit function) was the binomially distributed dependent variable, population and year (2000 or 2001, as nest surface area was not measured in 1999) were the factorial independent variables, and nest surface area a covariate. The significance of each parameter was assessed using a χ^2 test.

Finally, we performed a GLM analysis on the entire sample of 1,092 nests from 1999, 2000 and 2001 to test whether the proportion of gyne-producing nests differed between populations and between years with the maximum possible statistical power. Nest sex ratio was the binomial dependent variable and population and year were factorial independent variables.

Results

Spatial variations

Populations differed greatly in elevation, number of nests, nest density and nest surface area (Table 1). The number of nests per population had the greatest coefficient of variation (129%), followed by nest surface area (99% in 2000 and 112% in 2001). The number of nests per population ranged from 9 to 1,234 (average \pm SD = 315 ± 420). Nest density and population elevation had

Table 1 Comparison of populations

Population	Elevation (m)	Number of nests	Density (nests within 10 m)	Nest surface area (cm ²) in 2000	Nest surface area (cm ²) in 2001
BA	1,000	9	6.18 \pm 2.67	2,568 \pm 1,172	809 \pm 437
BB	970	17	5.23 \pm 3.21	1,287 \pm 844	556 \pm 218
BG	1,120	135	5.91 \pm 2.67	3,778 \pm 3,627	2,499 \pm 1,864
CHEN	1,250	1234	7.22 \pm 3.65	6,519 \pm 5,266	2,578 \pm 1,978
DU	1,120	1057	7.09 \pm 6.82	3,862 \pm 4,960	2,977 \pm 3,247
LA	1,090	21	7.77 \pm 3.43	2,406 \pm 1,801	1,280 \pm 1,078
LC	1,080	14	3.89 \pm 1.68	4,433 \pm 4,019	2,608 \pm 2,029
LO	1,050	260	4.96 \pm 3.84	4,371 \pm 3,362	2,593 \pm 3,253
MO	1,190	125	8.54 \pm 5.35	3,228 \pm 2,092	1,874 \pm 1,603
PJ	1,100	339	3.38 \pm 2.16	2,813 \pm 3,069	2,001 \pm 2,485
PN	1,100	516	4.46 \pm 2.76	2,300 \pm 1,450	1,542 \pm 1,656
ROC	1,120	49	4.56 \pm 2.24	3,268 \pm 2,822	1,643 \pm 2,649
Coefficient of variation	30%	129%	28%	99%	112%

Table 2 Correlation between independent variables of our linear model

	Elevation		Number of nests		Mean nest density		Mean nest surface area
	r_s	P	r_s	P	r_s	P	
Elevation	–	–	–	–	–	–	–
Number of nests	0.77	0.01	–	–	–	–	–
Mean nest density	0.36	0.36	0.08	0.8	–	–	–
Mean nest surface area	0.54	0.07	0.53	0.08	0.02	0.95	–

relatively low coefficients of variation. The elevation of populations ranged from 970 to 1,250 m (average \pm SD=1,097 \pm 75 m), which corresponds to a change of 1–2°C in average temperature. Nest density (number of nests within 10 m) ranged from 0 to 32 (average \pm SD=5.0 \pm 4.2).

Nest density differed significantly between populations ($F_{11,258}=5.56$, $P<0.001$). Nest surface area differed significantly between years ($F_{1,547}=93.8$, $P<0.001$) and between populations ($F_{11,547}=7.48$, $P<0.001$). At the population level, there was a tendency for each of the variables measured (elevation, number of nests, and nest surface area) to be positively correlated with each other (positive Z values, Table 2). However, only the correlation between elevation and number of nests was significant.

The proportion of gyne-producing nests differed significantly between populations (Fig. 2; $\chi^2=36.2$, $df=11$, $P<0.001$). However, none of elevation ($F_{1,32}=0.0002$, $P=0.99$), number of nests ($F_{1,31}=1.82$, $P=0.19$), or density ($F_{1,30}=0.24$, $P=0.63$) was associated with the proportion of gyne-producing nests in a population. Similarly, nest surface area was not significantly associated with gyne production ($\chi^2=0.015$, $df=1$, $P=0.90$). Another indication that the proportion of gyne-producing nests is independent of population characteristics is the highly variable rank of populations between years (Table 3). The Kendall rank correlation indicates that none of the 1999–2000 population rank ($Z=-0.36$, $P=0.7$), 1999–2001 population rank ($Z=1.4$, $P=0.14$), or 2000–2001 population rank ($Z=-0.07$, $P=0.94$) were correlated. This indicates that population-level proportion of gyne-producing nests was not consistent from one year to another and thus the proportion of gyne-producing nests is not a stable property of populations.

Temporal variations

Mean weekly radiation, a component of weather conditions that is likely to influence nest and environmental temperature, differed significantly between years ($F_{1,30}=7.63$, $P=0.009$). The average daily radiation between April and June was lowest in 1999 (4,679 W/m² per day at Changin and 4,277 W/m² per day at La Frétaz), highest in 2000 (5,359 W/m² per day at Changin and 5,039 W/m² per day at La Frétaz) and intermediate in 2001 (4,913 W/m² per day at Changin and 4,680 W/m² per day at La Frétaz).

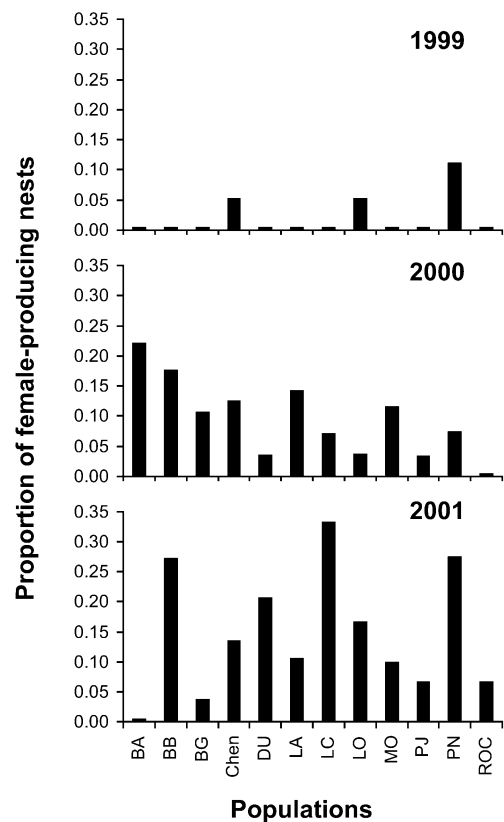


Fig. 2 Proportion of gyne-producing nests in each population for the three years. In 2001, proportions shown are the ones for the 30 nests for which pupae were collected. Populations for which no gyne-producing nests were found are represented with a bold bar

Table 3 Rank of each population according to its proportion of gyne-producing nests each year. The higher the rank, the greater the proportion of gyne-producing nests

Population	Ranks		
	1999	2000	2001
BA	1	12	1
BB	1	11	10
BG	1	7	2
CHEN	10	9	7
DU	1	3	9
LA	1	10	6
LC	1	5	12
LO	10	3	8
MO	1	8	5
PJ	1	2	3
PN	12	5	11
ROC	1	1	3

The proportion of gyne-producing nests was significantly different between years (Fig. 2; $\chi^2=45.8$, $df=2$, $P<0.001$). The average proportion of gyne-producing nests in 1999 was only 1.8%, 9.6% in 2000 and 14.9% in 2001. In 1999 only 3 of the 221 nests sampled produced gynes. As a result, we observed no gyne-producing nests in 75% (9 of 12) of the populations, including the four populations for which we sampled all nests. Therefore at least 33% of the populations did not produce any gynes in 1999, the year with least overall sunshine. Thus, climatic variations may have an influence on the proportion of gyne-producing nests.

Discussion

Our study shows that gyne production may vary greatly between years as well as between populations, yet such variations may be difficult to explain. Populations of polygynous *F. exsecta* differ significantly in a number of environmental characteristics that are known to influence sex allocation in other species of ants. First, we found that nest surface area, which was significantly positively associated with worker number and the productivity of nests, differed significantly among populations. We also found that nest density differed significantly among populations. In addition, our study populations were distributed over a considerable range of elevations (Table 1), which is likely to influence the average daily temperature of nests and eventually the resource level available for nests. Most of the environmental variables we analysed were not correlated with each other, except altitude and the number of nests. Despite this high variability in environmental factors and gyne production, we found no correlation between gyne production and any of the analysed variables.

A possible explanation for the lack of association between population characteristics and population proportion of gyne-producing nests is that differences among populations in resource availability co-vary with worker and nest densities. Thus, although populations most likely vary in the amount of resources available, those differences may not result in differences among populations in per capita resource availability. This is likely to be the case if differences in resource availability are relatively stable among sites and if habitats are saturated because differences among habitats should translate into different population sizes rather than into resource dependent effects on gyne production (see, for example, Fretwell 1972). Indeed, an important characteristic of highly polygynous ants such as *F. exsecta* is habitat saturation (Hölldobler and Wilson 1977; Sundström 1993; Ross et al. 1996; Pedersen and Boomsma 1999). The *F. exsecta* in our study populations certainly occur at high density, both in numbers of nests (Table 1) and in overall worker populations (C. Liautard and K. Helms, personal observations). Thus, on average, each queen, colony or nest, may be similarly resource limited. Consistent with this explanation, habitats of *F. exsecta* populations in the

Swiss Jura appear exceptionally stable. Other than changes in farming techniques, which would have simultaneously influenced all of the populations, the habitat has remained stable over a long time period. Based on maps from the beginning of the twentieth century, the meadows in which *F. exsecta* now occur were cut from the forest well over 100 years ago and have been used as summer pastures since that time (Swiss National Maps).

The hypothesis that populations are at equilibrium with regard to population density, coupled with local, stochastic variations in resource availability, could explain why there were both substantial spatial (between populations) and temporal (within populations) variations in gyne production. One factor promoting resource variability is likely to be climatic variations. Random variations in temperature or rainfall may differently affect populations, resulting in random temporal fluctuations in resource availability relative to the long-term average. Hence, even if populations are at density equilibrium, unpredictable climatic fluctuations may influence the relative amount of energy available per ant and thus have unpredictable effects on sex allocation at the colony and population levels.

A possible explanation for variations in gyne production across years is climatic differences. Regional spring solar radiation differed significantly between the 3 years of our study, 1999 being exceptionally cool with extremely low solar radiation. In 1999, exceptionally few nests produced gynes, and pupae were first observed in nests in early July, 3 weeks later than in 2000 (C. Liautard, unpublished data). As solar radiation is likely to be correlated to temperature, it is consistent with the importance of temperature in colony sex allocation. Other studies have also noted that temperature, or factors likely to be associated with temperature, affect sex allocation in social insects. For example, nest temperature influences the proportion of gynes produced in the ant *Linepithema humile* (Aron et al. 1994) and gyne production in *F. aquilonia* (Rosengren and Pamilo 1986). The reason why solar radiation may affect sex allocation is unclear; however, daily radiation influences nest and air temperature, which should influence resource availability via its effect on plant growth and insect development. Nest temperature could also directly affect caste determination (Aron et al. 1994). It seems that 1999 was an exceptional year for *F. exsecta*. Previous studies in the CHEN population showed that the proportion of gyne-producing nests during another 2-year period (1996 and 1997) was close to what we observed in 2000 and 2001 (Brown and Keller 2000, 2002). In other species, temporal variations in sex allocation are also attributed to exceptional years (Elmes 1987; Herbers 1990; Chan et al. 1999; Buschinger and Heinze 2001). However, it is difficult to draw a strong conclusion on the direct or indirect effects of solar radiation on gyne production in *F. exsecta*. Although extremely limited gyne production occurred during the year with exceptionally cool temperatures, the warmest year (2000) did not exhibit the highest proportion of gyne-producing colonies.

In conclusion, our study found considerable temporal and some spatial variability in gyne production in *F. exsecta*. Temporal variability in gyne production within populations suggests that stochastic variables may be important in determining sex allocation patterns in this species. Because gyne production seems to be a function of both resource level and queen number, any factor affecting either of these variables stochastically could result in the observed patterns. Our results show that environmental factors affecting gyne production in species such as *F. exsecta* may be complex and difficult to isolate. Moreover, the finding that gyne production varies greatly between years suggests that sex allocation is not always optimal especially in populations where no gynes are produced, but might simply be adaptive on average, while subject to substantial variations. For example, no gynes were produced in a significant proportion of the populations studied in 1999. A genetic study showed that dispersal by young queens is very rare among populations in the Jura mountains (Liautard and Keller 2001). Although male dispersal is more common than queen dispersal, it is still a relatively rare between populations (P. Seppä, unpublished data). Thus, the complete lack of queen production and exclusive production of males by several populations in some years is unlikely to be adaptive since the mating success of these males is expected to be close to zero.

Acknowledgements We thank Ludovic Aymon, Michelle Kuns, Martine Ehinger, Frédéric Guillaume, Laurent Hosseini, Carlo Ossola, Christian Parisod and Raoul Vega for help in the field; and Andrew Bourke, Michel Chapuisat, Christoph Haag, Rob Hammond for useful comments on the manuscript. This work was funded by several grants from the Swiss NSF and the Academy of Finland grant no. 42725.

References

- Aron S, Passera L, Keller L (1994) Queen-worker conflict over sex ratio: a comparison of primary and secondary sex ratios in the Argentine ant, *Iridomyrmex humilis*. *J Evol Biol* 7:403–418
- Boomsma JJ, Grafen A (1991) Colony-level sex ratio selection in the eusocial Hymenoptera. *J Evol Biol* 3:383–407
- Bourke AFG, Franks NR (1995) *Social evolution in ants*. Princeton University Press, Princeton
- Brown WD, Keller L (2000) Colony sex ratios vary with queen number but not relatedness asymmetry in the ant *Formica exsecta*. *Proc R Soc Lond B Biol Sci* 267:1751–1757
- Brown WDB, Keller L (2002) Queen recruitment and split sex ratios in polygynous colonies of the ant *Formica exsecta*. *Ecol Lett* 2:102–109
- Brown WD, Keller L, Sundström L (2002) Sex allocation in mound-building ants: the role of queen replenishment, resource abundance and local resource competition. *Ecology* 83:1945–1952
- Buschinger A, Heinze J (2001) *Stenammas debile* (Hymenoptera, Formicidae): productivity and sex allocation across three years. *Insectes Soc* 48:110–117
- Chan GL, Hingle A, Bourke AFG (1999) Sex allocation in a facultatively polygynous ant: between-population and between-colony variation. *Behav Ecol* 10:409–421
- Chapuisat M, Keller L (1999) Testing kin selection with sex allocation data in eusocial Hymenoptera. *Heredity* 82:473–478
- Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165
- Crozier RH, Pamilo P (1996) *Evolution of social insect colonies. Sex allocation and kin-selection*. Oxford University Press, Oxford
- Deslippe RJ, Savolainen R (1994) Role of food supply in structuring a population of *Formica* ants. *J Anim Ecol* 63:756–764
- Deslippe RJ, Savolainen R (1995) Sex investment in a social insect—the proximate role of food. *Ecology* 76:375–382
- Elmes GW (1987) Temporal variation in colony populations of the ant *Myrmica sulcinodis*. 1. Changes in queen number, worker number and spring production. *J Anim Ecol* 56:559–571
- Elmes GW, Keller L (1993) Distribution and ecology of queen number in ants of the genus *Myrmica*. In: Keller L (ed) *Queen number and sociality in insects*. Oxford University Press, Oxford, pp 294–307
- Fisher RA (1930) The genetical theory of natural selection. In: Bennett JH (ed) *The genetical theory of natural selection, a complete variorum edition*. Oxford University Press, Oxford
- Foitzik S, Heinze J (2000) Intraspecific parasitism and split sex ratios in a monogynous and monandrous ant (*Leptothorax nylanderii*). *Behav Ecol Sociobiol* 47:424–431
- Fretwell SD (1972) Seasonal environment. In: MacArthur RH (ed) *Monographs in population biology*, vol 5. Princeton University Press, Princeton, p 217
- Herbers JM (1990) Reproductive investment and allocation ratios for the ant *Leptothorax longispinosus*: sorting out the variation. *Am Nat* 136:178–208
- Hölldobler B, Wilson EO (1977) The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8–15
- Keller L (1995) Social life: the paradox of multiple-queen colonies. *Trends Ecol Evol* 10:355–360
- Liautard C, Keller L (2001) Restricted effective queen dispersal at a microgeographic scale in polygynous populations of the ant *Formica exsecta*. *Evolution* 55:2484–2492
- Nonacs P (1986a) Ant reproductive strategies and sex allocation theory. *Q Rev Biol* 61:1–21
- Nonacs P (1986b) Sex ratio determination within colonies of ants. *Evolution* 40:199–204
- Pamilo P, Rosengren R (1983) Sex ratio strategies in *Formica* ants. *Oikos* 40:24–35
- Pedersen JS, Boomsma JJ (1999) Effect of habitat saturation on the number and turnover of queens in the polygynous ant, *Myrmica sulcinodis*. *J Evol Biol* 12:903–917
- Pisarski B (1982) *Structure et organisation des sociétés de fourmis de l'espèce Formica (Coptoformica) exsecta Nyl. (Hymenoptera, Formicidae)*. Polish Academy of Sciences, Warsaw
- Rosengren R, Pamilo P (1986) Sex ratio strategy as related to queen number, dispersal behaviour and habitat quality in *Formica* ants. *Entomol Gen* 11:139–151
- Rosenheim JA, Nonacs P, Mangel M (1996) Sex ratios and multifaceted parental investment. *Am Nat* 148:501–535
- Ross KG, Vargo EL, Keller L (1996) Simple genetic basis for important social traits in the fire ant *Solenopsis invicta*. *Evolution* 50:2387–2399
- Sundström L (1993) Genetic population structure and sociogenetic organisation in *Formica truncorum* (Hymenoptera; Formicidae). *Behav Ecol Sociobiol* 33:345–354
- Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insects. *Science* 191:249–263
- Walín L, Seppä P (2001) Resource allocation in the red ant *Myrmica ruginodis*—an interplay of genetics and ecology. *J Evol Biol* 14:694–707
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River