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as our principal measure of skew because of the high degree of queen turnover in the study population. Queens within colonies did not make significantly unequal contributions to queen and worker adult or pupal offspring, indicating that skew among female eggs reflected skew among daughter queens. On average, both skew among female eggs (measured by the *B* index) and queen–queen relatedness proved to be low (means±SE=0.06±0.02 and 0.28±0.08, respectively). However, contrary to current skew models, there was no significant association of skew with either relatedness or worker number (used as a measure of productivity). In *L. acervorum*, predictions of the concession model of skew may hold between but not within populations because queens are unable to assess their relatedness to other queens within colonies. Additional phenomena that may help maintain low skew in the study population include indiscriminate infanticide in the form of egg cannibalism and split sex ratios that penalize reproductive monopoly by single queens within polygynous colonies.

34	Keywords separated by ' - '	Kin selection - Polygyny - Reproductive skew - Social evolution - Social insect
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4 **A test of reproductive skew models in a field population**
5 **of a multiple-queen ant**6 **R. L. Hammond · M. W. Bruford · A. F. G. Bourke**7 Received: 7 April 2006 / Revised: 16 June 2006 / Accepted: 6 July 2006
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queens within polygynous colonies.

Keywords Kin selection · Polygyny · Reproductive skew ·
Social evolution · Social insect

Introduction

The extent to which coexisting breeding individuals share
reproduction varies greatly across animal societies. Societies
with high reproductive skew are those in which one or a few
individuals monopolize reproduction; societies with low
reproductive skew occur when breeders share reproduction
more evenly. The extension by Reeve (1991) and Reeve and
Ratnieks (1993) of the original skew models of Vohrenkamp
(1979, 1983) and Emlen (1982a,b) has led to a wealth of
new models aimed at explaining skew variation within and
between species, along with a growing number of empirical
tests of these models. The importance of these studies arises
because skew models offer a potential explanation for the
wide variation in skew observed across animal societies. In
principle, skew models also provide a means of testing kin
selection theory (Hamilton 1964), on which they are based.

The many skew models now present in the literature
differ in both their assumptions and in the predictions they
make regarding the expected genetic, ecological, demo-
graphic and social correlates of skew (Table 1). Empirical

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t1.1 **Table 1** Assumptions of models of reproductive skew and the models' predicted correlations

	Transactional models			Compromise models	Synthetic model	Results of present study
t1.2	Concession models	Resource inheritance models	Restraint models	Tug-of-war models		
t1.4	Main assumptions:	1. Dominant controls group membership	1. Dominant controls group membership	1. Dominant controls group membership	1. Limited control by both parties	1. Synthesized assumptions of transactional and compromise models
t1.5		2. Dominant controls skew	2. Dominant controls skew	2. Subordinate controls skew	2. Gaining share of reproduction is costly	
t1.6			3. Subordinate inherits dominant's resource			
t1.7	Predictions:					
t1.8	1. Skew vs relatedness	Positive ^{a,b,c} or Negative ^{b,c}	Positive or Negative	Negative	Negative or no correlation	Positive or negative
t1.9	2. Skew vs degree of ecological constraint	Positive ^{a,b}	–	Negative	No correlation	Positive or negative
t1.10	3. Skew vs per capita productivity	Positive ^a	–	Negative	No correlation	Positive or negative
t1.11	4. Relatedness vs group productivity	No correlation ^a	–	No correlation	Positive	–
t1.12	Selected references	Reeve and Ratnieks (1993) ^a ; Cant and Johnstone (1999) ^b ; Johnstone et al. (1999) ^c	Kokko and Johnstone (1999); Ragsdale (1999)	Johnstone and Cant (1999b)	Reeve et al. (1998)	Johnstone (2000)

t1.13 Superscripts indicate predictions varying depending on detailed assumptions. –, no prediction made or not considered in this study. See also Cant (1998, 2006), Johnstone and Cant (1999a), Cant and Johnstone (2000), Reeve (2000), Reeve and Emlen (2000), Kokko (2003) and Zink and Reeve (2005).

63 studies of skew in both invertebrates and vertebrates
 64 (reviews in: Keller and Reeve 1994; Emlen 1997; Reeve
 65 and Keller 2001) have tended to lag behind the develop-
 66 ment of new models. This is because the assumptions of
 67 skew models are either not met or are difficult to verify,
 68 skew and its predicted correlates are not always simple to
 69 measure and different skew models make overlapping
 70 predictions (Clutton-Brock 1998; Magrath and Heinsohn
 71 2000; Table 1). The social Hymenoptera have been
 72 recognized as a particularly apt group for empirical tests
 73 of skew models because skew varies widely even among
 74 closely related species, a relatively large number of social
 75 groups can be sampled and insects lend themselves to
 76 experimental manipulation. However, conclusions from
 77 empirical studies have been mixed. Some studies have
 78 found support for concession models of reproductive skew
 79 (e.g., social wasps: Reeve et al. 2000; Sumner et al. 2002;
 80 see also Nonacs et al. 2004), some for tug-of-war models

(e.g., social wasps: Seppä et al. 2002; social bees: Langer et al. 2004, 2006) and others have found no clear support for any current model (e.g., social wasps: Field et al. 1998; Fanelli et al. 2005; Liebert and Starks 2006; Nonacs et al. 2006; ants: Fournier and Keller 2001; Ruppell et al. 2002; Hannonen and Sundström 2003a; Fournier et al. 2004). One reason for these mixed results could be that not all tested species share the same model assumptions (Table 1). Whatever its causes, this situation creates a clear need for additional empirical studies so that the balance of evidence can be properly assessed.

The leptothoracine ants represent a group in which an understanding of the factors underlying variation in skew would be especially valuable because some species exhibit multiple-queen societies in which a single queen monopolizes reproduction (i.e., functional monogyny), whereas in other multiple-queen (polygynous) species, reproduction is more evenly distributed among queens (Buschinger 1974;

99 Bourke and Heinze 1994). Leptothoracines most closely
 100 match the assumptions of concession models of skew
 101 (Bourke and Heinze 1994; Ruppell et al. 2002). For
 102 example, the maintenance of functional monogyny by
 103 aggressive dominance (Heinze and Lipski 1990; Heinze
 104 and Smith 1990) suggests that complete control of skew by
 105 dominants is possible (Table 1). In addition, the presence of
 106 subordinates increases the productivity of dominant queens,
 107 although the mechanism underlying this effect is unclear
 108 (Heinze and Oberstadt 2003). Consistent with concession
 109 models, broad-scale comparisons in leptothoracines (i.e., at
 110 the between-population and between-species level) suggest
 111 positive correlations of skew with relatedness (Heinze
 112 1995; Heinze et al. 1995b; Bourke et al. 1997) and inferred
 113 levels of ecological constraint (Bourke and Heinze 1994;
 114 Felke and Buschinger 1999). In contrast, a comprehensive
 115 study of *L. rugatulus* on skew variation among colonies
 116 (which either had been kept in the laboratory for 11 months
 117 or were artificially composed) found no support for
 118 concession models (Ruppell et al. 2002). However, to date,
 119 no study has examined skew as a function of predicted
 120 correlates among colonies within a field population of
 121 leptothoracines.

122 We investigated the covariation of skew, relatedness and
 123 productivity within a field population of the facultatively
 124 polygynous *Leptothorax acervorum*. We did not include
 125 ecological constraint (Table 1) in our study. This is because it
 126 is unlikely that *L. acervorum* queens are able to assess
 127 within-population levels of ecological constraint since
 128 readopted queens in polygynous colonies almost certainly
 129 mate near the nest and, if they disperse following the
 130 initiation of reproduction, do so on foot (Douwes et al.
 131 1987; Bourke and Heinze 1994; Felke and Buschinger 1999;
 132 Hammond et al. 2001). Therefore, queens are most likely to
 133 have evolved to adjust their reproductive output in response
 134 to the average, population-level degree of ecological con-
 135 straint, which is invariant for queens within a population.

136 Methods

137 Field collection and colony sampling

138 We studied *L. acervorum* in Thetford Forest, Norfolk, UK.
 139 In this population, approximately 20–50% of colonies are
 140 polygynous with a mean of two to five related queens per
 141 colony, 95% of which are singly mated (Chan and Bourke
 142 1994; Heinze et al. 1995a; Bourke et al. 1997; Hammond et
 143 al. 2001–2003). Sex ratios are split, with monogynous
 144 colonies producing mainly females and polygynous
 145 colonies producing mainly males (Chan and Bourke
 146 1994; Chan et al. 1999; Hammond et al. 2002). Collections
 147 of colonies were made in 1999 ('SD99' colonies) and 2000

(‘SD00’ colonies). The SD99 colonies ($n=46$, collected on 148
 June 3 and June 10) are the same as those whose collection 149
 is described by Hammond et al. (2001) and for which we 150
 have previously presented genetic analyses of traits other 151
 than reproductive skew (Hammond et al. 2001–2003). The 152
 SD00 colonies ($n=100$, collected between July 27 and 153
 August 24) came from a site approximately 1 km away. We 154
 have not previously presented data on the SD00 colonies. 155
 All SD99 colonies and 39 SD00 colonies were located by 156
 random searching (the remaining 61 SD00 colonies were 157
 located by searching in the area defined by a circle of 2-m 158
 radius centred on each of the focal 39 colonies). Only data 159
 from the 39 SD00 colonies located by random searching are 160
 presented in the current paper. After discovery, all colonies 161
 in both samples were collected using methods described in 162
 Chan and Bourke (1994). All adults and brood were 163
 extracted from their twigs within a few days of collection 164
 and frozen for later genetic analysis. Colony composition 165
 therefore reflected that found in the field at the time of 166
 collection. 167

168 We investigated reproductive skew in a subset of 17
 polygynous colonies (9 SD99 colonies and 8 SD00 169
 colonies). Polygynous colonies were defined as those 170
 containing more than one dealate, mated queen (henceforth, 171
 ‘queens’; dealate queens are those that have shed their 172
 wings). We determined the insemination status of queens by 173
 noting the presence of a full or empty sperm receptacle 174
 upon ovarian dissection (Bourke 1991; Hammond et al. 175
 2001). We selected 9 polygynous colonies with 2–8 queens 176
 per colony (mean \pm SD=3.6 \pm 1.8 queens) from the SD99 177
 sample (i.e., the 9 polygynous colonies in Table 1 of 178
 Hammond et al. 2001). In the SD00 sample, 11 of the 39 179
 focal colonies proved to be polygynous, but we omitted 3 180
 of these 11 colonies from our skew analysis. In two of the 181
 omitted colonies, parentage analyses could not be con- 182
 ducted because both colonies contained high numbers (16 183
 and 17) of closely related queens, which therefore shared 184
 many alleles. Omitting these colonies is unlikely to have 185
 biased our results since, in the remaining colonies, 186
 relatedness varied across the whole spectrum of likely 187
 values (−0.01–0.89), indicating that the exclusion of these 188
 two colonies did not truncate variability in relatedness. 189
 The third SD00 colony was omitted because it contained 190
 no eggs. In the eight SD00 colonies in which we 191
 measured skew, there were 2–7 queens per colony 192
 (mean \pm SD=3.4 \pm 2.0 queens). 193

Molecular methods 194

195 We genotyped individuals using the microsatellite loci 195
 LXAGT1, LXAGA1, LXAGA2 (Bourke et al. 1997), 196
 MYRT3 (Evans 1993), LXGT223 (Hamaguchi et al. 197
 1993) and L18 (Foitzik et al. 1997), using methods 198

199	described by Hammond et al. (2001). In the Thetford Forest	248
200	population, these loci have a mean expected heterozygosity	249
201	of 0.88 and a mean of 23 alleles per locus (Hammond et al.	250
202	2001). In the SD99 colonies, a total of 32 queens and the	251
203	contents of 29 corresponding sperm receptacles (3 were lost	252
204	during dissection) were genotyped at a mean of 6.0 loci	253
205	(range=4–6), as described in Hammond et al. (2001). In the	
206	SD00 colonies, a total of 27 queens and the contents of 27	
207	corresponding sperm receptacles were genotyped at a mean	
208	of 3.6 loci (range=2–4). Genotyping of the contents of	
209	sperm receptacles had a high failure rate (38% in SD99	
210	samples and 30% in SD00 samples). In SD99 colonies, as	
211	described in Hammond et al. (2001), we also typed a per	
212	colony mean of 12.8 adult workers ('old workers',	
213	range=0–15), 13.9 callow workers or worker pupae ('new	
214	workers', range=0–19), 10.3 adult males (range=0–19) and	
215	6.7 alate (winged) queens or queen pupae ('new queens',	
216	range=0–21) at a mean of 6.0 loci. Finally, across both sets	
217	of colonies, we genotyped a mean of 42.6 eggs per colony	
218	at a mean of 2.0 loci (range=1–4). These consisted of a	
219	mean (range) of 54.9 (36–89) eggs from the SD99 colonies	
220	(the samples described in Hammond et al. (2003) plus a	
221	few additional SD99 eggs) and a mean (range) of 28.8	
222	(20–38) eggs from the SD00 colonies. Eggs were genotyped	
223	at loci found to be diagnostic for parentage analyses on the	
224	basis of the genotypes of queens and the queens' mates	
225	(the genotypes of the queens' mates being deduced from	
226	those of the contents of the sperm receptacles or those of	
227	female progeny). Within colonies, we attributed female	
228	(diploid) eggs to one of the queens using exclusion criteria.	
229	The high degree of genetic variation per locus, together with	
230	the absence of relatedness between <i>L. acervorum</i> queens	
231	and their mates and between mates of coexisting queens	
232	(Hammond et al. 2001), meant that almost all eggs could be	
233	assigned to individual queens (see 'Parentage analysis'	
234	under 'Results').	
235	Relatedness	
236	We estimated regression relatedness among coexisting	
237	queens in the SD00 colonies and, for the SD99 colonies,	
238	used relatedness values calculated previously (Hammond	
239	et al. 2001–2003). In the SD00 colonies, we calculated	
240	Queller and Goodnight's (1989) regression relatedness	
241	from genotype data with the program RELATEDNESS	
242	5.07 (Goodnight Software: http://www.gsoft.smu.edu/Gsoft.html).	
243	Colony productivity	
244	Colony productivity	
245	In both the SD99 and SD00 colonies, we used the number	
246	of adult workers as a surrogate measure of colony	
247	productivity. This was justified because, based on previous	
	data from polygynous colonies in the study population in	248
	Chan et al. (1999), we found colony sexual production	249
	(measured as biomass of either new queens, or males or	250
	new queens and males combined) to be highly correlated	251
	with number of adult workers (all Pearson's $r > 0.47$, all	252
	$n = 30$, all $P < 0.009$).	253
	Queen turnover	254
	Previous work has shown that polygynous colonies of	255
	<i>L. acervorum</i> in the study population have a high rate of	256
	queen turnover, with large proportions of old workers, new	257
	queens and males being unattributable to resident queens	258
	(Bourke et al. 1997; Hammond et al. 2001). In the present	259
	study, we estimated the degree of queen turnover in SD99	260
	colonies only since no adults or pupae were genotyped in	261
	SD00 colonies. We estimated the genetically effective	262
	turnover of queens (t) across pairs of female age cohorts	263
	using Eq. 4 in Pedersen and Boomsma (1999). This defines	264
	100% turnover as occurring when all queens contribute to	265
	one cohort only and 0% turnover as occurring when all	266
	queens contribute to both cohorts. The variables used in the	267
	estimation of t are the relatednesses within and between the	268
	two age cohorts being compared. We measured related-	269
	nesses within and between female eggs, new workers, old	270
	workers and new queens. Relatednesses were averaged	271
	across colonies for the estimation of population-level	272
	turnover. Since <i>L. acervorum</i> workers overwinter once as	273
	larvae, whereas queens usually overwinter twice	274
	(Buschinger 1973), we assumed that, relative to eggs, new	275
	workers were 0–1 years older, old workers were >1 year	276
	older and new queens were 2 years older. These relative	277
	ages are approximate because some workers may be close	278
	in the year that they were laid as eggs, the longevity of	279
	adult workers is unknown, and some queens may overwin-	280
	ter as larvae only once. Nonetheless, comparing relatedness	281
	within and between female eggs and these cohorts allowed	282
	us to estimate queen turnover across an ever-increasing age	283
	interval.	284
	Reproductive skew	285
	The likely occurrence of high queen turnover meant that	286
	reproductive skew could not easily be calculated from the	287
	genotypes of adult or pupal progeny. We therefore	288
	measured skew in samples of female eggs (SD99 colonies:	289
	mean=44.8 female eggs per colony, range=28–77; SD00	290
	colonies: mean=25.0 female eggs per colony, range=20–33).	291
	This assumed that individual queens within colonies did	292
	not differ in the queen-to-worker ratio among their	293
	progeny (we consider other assumptions in 'Discussion').	294
	We were able to test this assumption by comparing the	295
	proportion of either caste attributable to each queen in four	296

SD99 colonies with sufficient numbers of new workers and new queens. In one of these colonies (SD99.54), we included as a maternal queen an individual that was not present at collection but whose existence could be inferred from the genotypes of her daughters, i.e., a ‘lost’ queen (Hammond et al. 2003). In each colony, a minority of new workers and new queens could be not be assigned to either resident or lost queens. We therefore grouped these progeny into a ‘queen unknown’ parentage class.

We did not investigate reproductive skew among male eggs for two reasons. First, the sample sizes for male eggs in each colony were small because in *L. acervorum*, only a small minority of eggs laid by queens (16%) are male and workers lay very few male eggs (Hammond et al. 2002, 2003). Second, parentage assignment of males, being haploid, was much more difficult than for females because queens often shared a high proportion of alleles (frequently, it was the paternal alleles in females that allowed parentage assignment). However, in five SD99 colonies, the sample size of adult, queen-produced males was large enough and parentage assignment was possible. In these colonies, we investigated whether reproductive skew differed between sexes of progeny by comparing the proportion of adult males and new workers attributable to each queen within the colonies. We did not compare adult males and new queens because such a comparison would have been confounded by year since usually queens take 2 years to develop, whereas workers and males take only 1 year (Buschinger 1973). As in our comparison of skew between castes, progeny that could not be assigned to either resident or lost queens were grouped into a ‘queen unknown’ parentage class.

We used Nonacs’s B index (Nonacs 2000, 2003) to quantify skew in female eggs. Using the program SKEW CALCULATOR 2003 (Nonacs 2003), we calculated B , the 95% confidence limits of B (using 10,000 randomizations) and, given the queen number in each colony, the maximum (where only one queen reproduces in each colony) and minimum (where all queens reproduce equally) possible values of B . To control for the maximum and minimum values of B varying across colonies (P. Nonacs, personal communication), we also calculated an adjusted B index (B_{adj}). We calculated this as the absolute difference between the observed and minimum B values divided by the absolute difference between the maximum and minimum B values.

343 Statistical methods

344 Queen–queen relatedness (‘relatedness’), colony size
345 (‘worker number’, i.e., number of old workers), reproduc-
346 tive skew (as measured by B or B_{adj}) and the number of
347 queens per colony (‘queen number’) were all normally

distributed (Kolmogorov–Smirnov tests, all $P > 0.05$). There
was no significance difference in any variable across
sampling years (SD99 vs SD00: all $t_{15} < 1.07$, all $P > 0.30$),
so data were pooled across years for further analyses. We
tested relationships predicted by the skew models (Table 1)
in two general linear models (GLM). First, in ‘skew GLM’,
we tested whether skew (B or B_{adj}) varied with relatedness,
queen number and worker number (as a measure of
productivity). We also tested whether skew varied with
productivity per queen by testing in these analyses for an
interaction between queen and worker number. Second, in
‘productivity GLM’, we tested whether worker number
varied with relatedness. In addition, in ‘queen number
GLM’, we tested whether relatedness varied with queen
number. All GLM analyses were carried out with SPSS
(version 12.0.0). To compare skew between castes (new
queens vs new workers) and sexes (males vs new workers),
we used exact tests calculated by the program R×C [Miller
MP (1997) R×C: a program for the analysis of contingency
tables, 1.0 edn. Department of Biological Sciences, North-
ern Arizona University, Flagstaff]. Where multiple tests
were performed on the same data, we applied sequential
Bonferroni correction (Rice 1989).

371 Results

372 Relatedness and queen turnover

Average queen–queen relatedness (mean±SE) was
0.28±0.08 ($n=59$ queens from 17 colonies). The genetical
effective turnover of queens (t) was 50.3% (comparing
eggs vs new workers, $n=8$ colonies), 43% (comparing eggs
vs old workers, $n=8$ colonies) and 67.2% (comparing eggs
vs new queens, $n=5$ colonies). Therefore, queen turnover
was substantial and, as expected, showed evidence of rising
as the age interval between cohorts increased (with the
reversal of values between eggs vs new workers and eggs
vs old workers, relative to those expected, presumably
stemming from high overlap between the ages of new and
old workers and from sampling error in the underlying
relatedness estimates). These results, coupled with the
complementary finding that a mean of 27% of new
workers, new queens and old workers were not assignable
to resident queens (see below) and with previous findings
from the same population (Bourke et al. 1997), provided
support for measuring skew among eggs in this study.

391 Parentage analysis

We could successfully attribute 91% (550 out of a total
 $n=603$) of all female eggs to individual resident queens.
The remaining 9% were either not attributable to any

395 resident collected queen (8%) or were equally likely to be
 396 the offspring of two or more resident queens (1%). Almost
 397 half of the eggs that were unattributable to resident queens
 398 were found in two colonies (SD99.74 and SD99.96);
 399 omitting these raised the proportion of successfully
 400 assigned eggs to 95%. In our analysis of skew (see below),
 401 we ignored the small fraction of unattributed eggs and
 402 analyzed skew in the large majority of eggs whose
 403 maternity we could deduce. Furthermore, we included all
 404 colonies since the omission of the two colonies with the
 405 highest proportions of unattributable eggs did not alter the
 406 results. Compared to female eggs, a lower proportion of
 407 adult males (82%), new queens (64%), new workers (69%)
 408 and old workers (85%) could be attributed to resident
 409 queens.

410 Variation in skew as measured across castes and sexes

411 There were no significant differences between the propor-
 412 tion of new queens and new workers attributable to each
 413 resident queen in all four SD99 colonies where compar-
 414 isons were possible (Table 2), supporting our assumption
 415 that skew in female eggs provides an accurate estimate of
 416 reproductive skew in new queens. However, there were
 417 significant differences between the proportion of males and
 418 new workers attributable to each resident queen in all five
 419 SD99 colonies where comparisons were possible (Table 3).
 420 Queens coexisting within the same colony therefore
 421 differed in their relative success at producing male and
 422 female offspring, with some concentrating on male produc-
 423 tion and others on female production.

424 Average reproductive skew

425 Reproduction was relatively equitably distributed among
 426 queens, with only 4 of 59 resident queens (6.8%) failing to
 427 contribute any female eggs (Fig. 1). The highest proportion

of eggs contributed by a single queen was 69.2% in a 428
 colony with 3 queens (colony SD00.129; Fig. 1). Average 429
 skew across colonies was low, with the overall mean (\pm SE) 430
 of B equalling 0.06 ± 0.02 and of B_{adj} equalling 0.12 ± 0.03 431
 (Fig. 2). The mean level of B (randomization test, 432
 $P < 0.0001$) and skew in 5 of 17 colonies (randomization 433
 test, $P < 0.004$, corresponding to an overall alpha of 0.05) 434
 was significantly greater than that expected by chance 435
 (Fig. 2). However, even in the 5 colonies with significant 436
 skew, skew estimates were nearer their minimum than their 437
 maximum level (Fig. 2). 438

Relationship of reproductive skew with relatedness, worker 439
 number and queen number 440

We found no significant relationship of skew with 441
 relatedness, queen number or worker number (skew GLM, 442
 $B: F_{4,12} = 0.99, P = 0.45; B_{adj}: F_{4,12} = 0.73, P = 0.59$; Fig. 3). 443
 There was also no significant interaction between queen 444
 number and worker number ($B: F_{1,12} = 2.91, P = 0.11; B_{adj}: F_{1,12} = 2.52, P = 0.14$). Bivariate linear regressions showed 445
 that our analyses had relatively high power because the 446
 standard deviations of the relevant regression coefficients 447
 were small (B vs relatedness: $b \pm SD = -0.03 \pm 0.06$, 448
 $F_{1,15} = 0.18, r^2 = 0\%, P = 0.67$; B vs queen number: 449
 $b \pm SD = 0.01 \pm 0.01, F_{1,15} = 0.96, r^2 = 0\%, P = 0.34$; B vs worker 450
 number: $b \pm SD = 0.00 \pm 0.00, F_{1,15} = 0.08, r^2 = 0\%, P = 0.79$; B 451
 vs worker number per queen: $b \pm SD = 0.00 \pm 0.00, F_{1,15} = 0.21,$ 452
 $r^2 = 0\%, P = 0.65$; B_{adj} vs relatedness: $b \pm SD = -0.03 \pm 0.09,$ 453
 $F_{1,15} = 0.12, r^2 = 1\%, P = 0.74$; B_{adj} vs queen number: 454
 $b \pm SD = 0.00 \pm 0.02, F_{1,15} = 0.68, r^2 = 1\%, P = 0.80$; B_{adj} vs 455
 worker number: $b \pm SD = 0.00 \pm 0.00, F_{1,15} = 0.01, r^2 = 0\%,$ 456
 $P = 0.95$; B_{adj} vs worker number per queen: $b \pm SD =$ 457
 $0.00 \pm 0.00, F_{1,15} = 0.09, r^2 = 1\%, P = 0.77$). We also found that 458
 relatedness did not vary significantly with worker number 459
 (productivity GLM: $F_{1,15} = 0.04, P = 0.84$) or queen number 460
 (queen number GLM: $F_{1,15} = 0.01, P = 0.91$). 461
 462

t2.1 **Table 2** Number of new queens and new workers attributable to individual queens in four polygynous *L. acervorum* colonies

t2.2 Colony		A	B	C	D	E	F	G	H	U	Totals	P value
t2.3 SD99.53	New queens	0	2	7	2	-	-	-	-	4	15	0.630
t2.4	New workers	0	1	4	3	-	-	-	-	7	15	
t2.5 SD99.54	New queens	0	2	0	10	-	-	-	-	9	21	0.247
t2.6	New workers	1	3	0	4	-	-	-	-	11	19	
t2.7 SD99.55	New queens	2	4	4	-	-	-	-	-	5	15	0.681
t2.8	New workers	3	5	5	-	-	-	-	-	2	15	
t2.9 SD99.94	New queens	1	0	0	0	0	4	0	0	0	5	0.196
t2.10	New workers	1	2	2	3	1	2	0	1	3	15	

t2.11 Individual queens (differing across colonies) are labelled A, B, C, etc. The final column (U) in each sequence per colony includes progeny of unknown parentage (i.e., progeny that could not be attributed to any queen within the colony). The queens in SD99.54 also include one 'lost' queen whose presence was inferred from progeny genotypes (see 'Reproductive skew' under 'Methods'). P value is from exact probability tests of the null hypothesis that, within colonies, individual queens do not differ in the ratio of new workers and new queens produced.

t3.1 **Table 3** Number of males and new workers attributable to individual queens in five polygynous *L. acervorum* colonies

t3.2	Colony		A	B	C	D	E	U	Totals	P value
t3.3	SD99.55	Males	0	9	0	–	–	6	15	0.008
t3.4		New workers	3	5	5	–	–	2	15	
t3.5	SD99.61	Males	0	7	–	–	–	9	16	0.005
t3.6		New workers	0	14	–	–	–	1	15	
t3.7	SD99.64	Males	10	0	2	–	–	2	14	<0.0001
t3.8		New workers	0	7	8	–	–	8	23	
t3.9	SD99.74	Males	0	0	0	1	6	0	7	<0.0001
t3.10		New workers	1	1	1	4	0	8	15	
t3.11	SD99.78	Males	0	0	17	–	–	0	17	<0.0001
t3.12		New workers	2	8	4	–	–	1	15	

t3.13 Individual queens (differing across colonies) are labelled A, B, C, etc. The final column (U) in each sequence per colony includes progeny of unknown parentage (i.e., progeny that could not be attributed to any queen within the colony). The queens in SD99.64 and SD99.74 also each include one ‘lost’ queen whose presence was inferred from progeny genotypes (see ‘Reproductive skew’ under ‘Methods’). P value is from exact probability tests of the null hypothesis that, within colonies, individual queens do not differ in the ratio of males and new workers produced. All P values are also significant after sequential Bonferroni correction.

463 **Discussion**

464 Using parentage analyses based on microsatellite markers,
 465 we measured skew among female eggs in a sample of 17
 466 polygynous colonies taken from a field population of the
 467 ant *L. acervorum*. Skew tended to be low, consistent with
 468 previous data showing that nearly all queens participate in
 469 egg laying (Bourke 1991) and that the maternity of new
 470 queens is shared (Bourke et al. 1997). However, despite

wide variation in queen–queen relatedness, we found no 471
 significant association of skew with relatedness. We also 472
 found no significant association of skew with productivity 473
 (as measured by worker number) or per capita productivity. 474

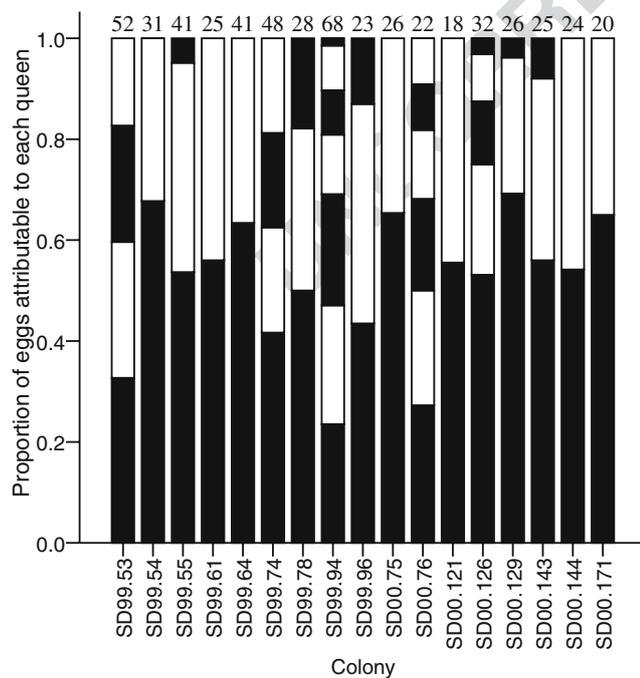


Fig. 1 Relative proportions of female eggs produced by queens within 17 polygynous *Leptothorax acervorum* colonies. Alternating black and white segments of each bar represent the proportion of female eggs attributable to different queens within a given colony. Numbers above bars equal the number of female eggs per colony that were successfully attributed to resident queens (total n=550)

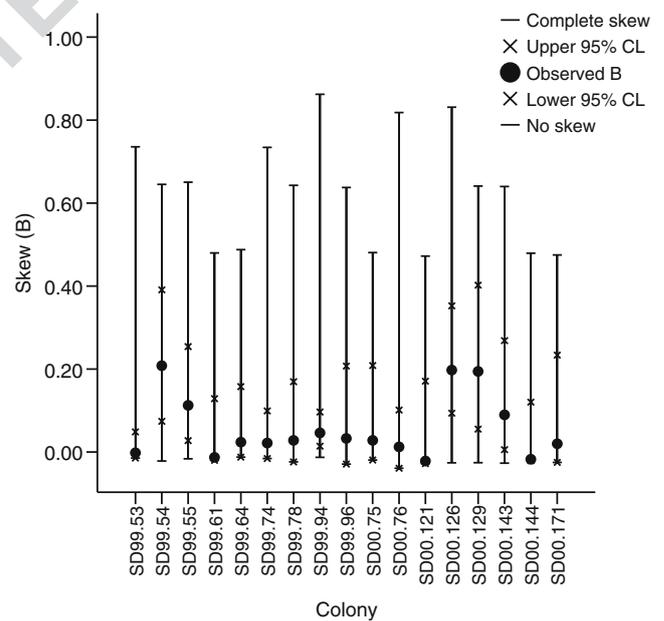


Fig. 2 Reproductive skew, as estimated by the B index among female eggs, in 17 polygynous *L. acervorum* colonies. For each colony, upper horizontal bar (‘—’) denotes the maximum value of B (i.e., value if one queen monopolizes all reproduction), given the observed number of queens in the colony; upper ‘x’ denotes the upper 95% confidence limit of B, based on 10,000 randomizations; filled circle denotes observed B; lower ‘x’ denotes lower 95% confidence limit of B, based on 10,000 randomizations; lower horizontal bar (‘—’) denotes the minimum value of B (i.e., value if all queens share reproduction equally), given the observed number of queens in the colony. Following Bonferroni correction, skew was significantly greater than expected by chance in five colonies (SD99.54, SD99.55, SD99.94, SD00.126 and SD00.129) and marginally greater than expected by chance in a sixth colony (SD00.143)

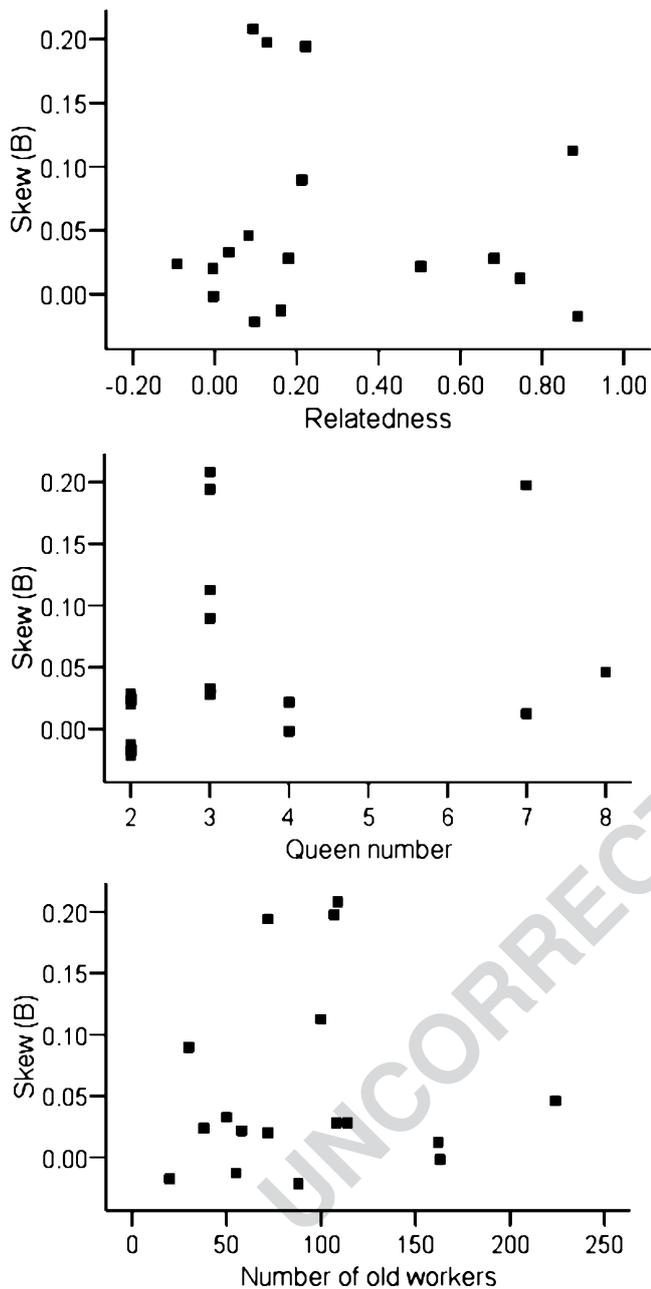


Fig. 3 Variation in reproductive skew, as estimated by the B index among female eggs, in 17 polygynous *L. acervorum* colonies as a function of queen–queen relatedness within colonies (*upper figure*), queen number (*middle figure*) and number of old (adult) workers (representing a measure of productivity; *lower figure*)

475 These findings were contrary to the predictions of the
 476 concession model of reproductive skew (Table 1). Further-
 477 more, contrary to the prediction of the tug-of-war model
 478 (Table 1), we found no significant association of relatedness
 479 and productivity (as measured by worker number). The
 480 absence of a significant association between relatedness and
 481 queen number was consistent with our previous findings
 482 from an overlapping data set (Hammond et al. 2001).
 483 Overall, our results failed to match any single current skew

484 model predicting an association of skew with the variables
 485 that we investigated (Table 1). In this, our results are
 486 consistent with the majority of similar, within-population
 487 studies of the expected correlates of skew in other social
 488 Hymenoptera, especially ants (see ‘Introduction’).

489 Our principal measure of reproductive skew was the
 490 degree to which coexisting queens shared the parentage of
 491 female (diploid) eggs. We selected this measure because of
 492 the high turnover among *L. acervorum* queens in the study
 493 population (Bourke et al. 1997; present study), which
 494 meant that offspring sampled as adults would no longer
 495 have been assignable to resident queens. This measure of
 496 skew assumed that egg-to-adult survival of female eggs
 497 does not vary with parentage, that queens do not differ in
 498 the chances of their female eggs developing into adult
 499 queens or workers and that skew among female progeny
 500 matches skew among male progeny. The first of these
 501 assumptions is plausible because, although differential
 502 mortality stemming from nepotism has been found in the
 503 polygynous ant *Formica fusca* (Hannonen and Sundström
 504 2003b), *L. acervorum* queens, although known to eat eggs,
 505 do not discriminate eggs by their maternal origin (Bourke
 506 1994). Likewise, as regards the second assumption,
 507 although coexisting queens have been shown to differ in
 508 their relative contributions to worker and queen progeny in
 509 some polygynous ant species (Ross 1988; Pamilo and
 510 Seppä 1994), in the present study, we found that *L.*
 511 *acervorum* queens contributed similar shares to worker
 512 and queen progeny (see also Rüppele et al. 2002). This
 513 finding is consistent with queen–worker caste fate being
 514 environmentally determined in *Leptothorax* (Wesson 1940).
 515 It also suggests that the workers’ biasing of caste fate that
 516 we have previously described in *L. acervorum* (Hammond
 517 et al. 2002) is exercised randomly with respect to female
 518 parentage. Contrary to our third assumption, we found that
 519 coexisting *L. acervorum* queens exhibited significant
 520 variation in their relative contributions to female and male
 521 progeny (cf. Fournier and Keller 2001). In general, skew
 522 among male progeny was higher than among female
 523 progeny ($B=0.56$ and 0.15 among males and new workers,
 524 respectively, and $B_{\text{adj}}=0.67$ and 0.28 among males and new
 525 workers, respectively; data from five colonies in Table 3),
 526 from which it follows that skew among sexual progeny as a
 527 whole would be higher than skew estimated among females
 528 only. However, this does not necessarily affect our main
 529 conclusions regarding the lack of association between skew
 530 and its predicted correlates across colonies. This is because
 531 it seems unlikely that skew in males would vary as a
 532 function of variables with which we found skew among
 533 females to be uncorrelated.

534 Previous evidence suggests that leptothoracine ants
 535 exhibit a positive relationship of skew with relatedness at
 536 the between-population and between-species level, as the

537 concession model of skew evolution predicts (see
538 'Introduction'). However, within-population studies reveal
539 either no relationship (present study) or a negative
540 relationship (Rüppell et al. 2002). Applied within popula-
541 tions, skew models assume that coexisting breeders are
542 capable of assessing within-group relatedness and adjusting
543 their share of reproduction accordingly. At first sight, two
544 pieces of evidence suggest that *L. acervorum* queens in
545 polygynous colonies could be capable of assessing queen-
546 queen relatedness. The first is the negative relationship of
547 skew and relatedness in *L. rugatulus* (Rüppell et al. 2002).
548 The second is the existence of worker-controlled sex ratios
549 associated with variation in relative colony-level related-
550 ness asymmetry (relative relatedness to the sexes) in *L.*
551 *acervorum* and other ant species (Chan and Bourke 1994;
552 Sundström 1994; Evans 1995; Sundström et al. 1996), a
553 precondition for which is workers' assessment of related-
554 ness asymmetry. However, in *L. rugatulus* (but not *L.*
555 *acervorum*), queens are dimorphic, with small-bodied
556 queens (microgynes) producing relatively more sexuals
557 than large-bodied queens (macrogynes) (Rüppell et al.
558 2002). Furthermore, microgynes tend to be less related
559 than macrogynes (Rüppell et al. 2001). Therefore, unlike
560 *L. acervorum* queens, *L. rugatulus* queens may have a
561 physical cue (frequency of nestmate microgynes) that
562 covaries with relatedness and, at least partly, predicts
563 nestmates' share of reproduction. As regards workers'
564 assessment of relatedness asymmetry, it is likely that such
565 assessment, which occurs on the basis of chemical cues
566 (Boomsma et al. 2003), is an easier chemosensory task than
567 queens' assessment of queen-queen relatedness since it
568 almost certainly requires discriminations on a coarser scale.
569 Therefore, it remains possible that *L. acervorum* queens in
570 polygynous colonies are unable to assess within-colony
571 relatedness and that this is why they fail to adjust their
572 levels of skew as a function of relatedness varying within
573 populations.

574 Not only processes in the concession models operating at
575 the population level, other factors may also contribute to
576 the maintenance of low skew in the study population of
577 *L. acervorum* (and other polygynous ants sharing its
578 biology). One is indiscriminate infanticide in the form of
579 indiscriminate egg cannibalism (Bourke 1991, 1994).
580 Coupled with low costs of offspring (egg) production, this
581 is predicted to promote low skew by a model of Johnstone
582 and Cant (1999a). Another is split sex ratios (Chan and
583 Bourke 1994; Chan et al. 1999; Hammond et al. 2002).
584 These could interact with skew evolution to reward the
585 maintenance of low skew in polygynous colonies, given
586 that queens achieving reproductive monopoly within
587 polygynous colonies should lose fitness through their
588 workers rearing less-valuable daughters from the sexual
589 brood (Bourke 2001; Nonacs 2002). Future work in *L.*

acervorum and other species should therefore concentrate
590 on (a) further testing of which assumptions of the differing
591 skew models are applicable, (b) greater integration of the
592 differing skew models into a single comprehensive frame-
593 work (e.g., Johnstone 2000) and (c) the experimental
594 testing of the models' predictions (e.g., Langer et al. 2004).
595

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