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Reproductivity and relatedness in a communal halictine bee *Lasioglossum (Chilalictus) hemichalceum*

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Summary

The biology of communal species is not well known. Here we report the reproductivity (number of offspring per female) and genetic relatedness for *Lasioglossum (Chilalictus) hemichalceum**, a communal halictine bee. There is a positive Model II regression, with a slope indistinguishable from one, between natural logarithms of the number of offspring and the number of adult females in a colony; indicating that as colony size increases the reproductivity per female does not decrease. This pattern is like that found in one other communal species and unlike that found in a wide variety of eusocial species. Relatedness among adult nestmates, based on two variable loci, is low. For 52 colonies it is about 0.13, and for a subset of 25 reproductively active colonies it was not distinguishable from zero. This indicates that the role of kin selection is minor at best in this highly cooperative, communal species. A review of the relatedness data available for communal groups, both foundress associations and species that are communal throughout their colony cycle, indicates that communal sociality is often but not always associated with low intra colony relatedness.

Introduction

The social systems of many group-living hymenopteran species involve cooperation among reproductively active individuals. In ants, associations among foundresses occur (eg. Bartz and Hölldobler, 1982; Mintzer and Vinson, 1985; Rissing and Pollock, 1986; Ross and Fletcher, 1985; Tschinkel and Howard, 1983), and may involve unrelated females (Hagen et al., 1988; Pollock and Rissing, 1985, 1989; Rissing and Pollock, 1986, 1987; Rissing et al., 1989). There are also numerous species of communal wasps (see Eickwort, 1981a; Evans and Hook, 1982, 1986; Matthews, 1991; McCorquodale, 1988, 1989a, 1989b; McCorquodale and Naumann, 1988; West-Eberhard, 1978). Cohabitation of nests by two or more egg-laying

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* Called *L. erythrurum* in several of PK's previous publications.
Voucher specimens are deposited in the Museum of Victoria, Abbotsford, Victoria, Australia.

females is also a common feature in bees. It is found in the Nomiinae, Halictinae, Andreniinae, Panurginae, Oxaeidae, Collectidae, Megachilidae, and Anthophoridae (Abrams and Eickwort, 1980a, 1980b; Eickwort, 1981a, 1981b; Eickwort and Eickwort, 1969; Garófalo et al., 1992; Sakagami and Zucchi, 1978; Santos and Garófalo, 1994). Communality, by definition, is characterized by a lack of reproductive castes and a lack of overlap of generations. The latter criterion is not always rigorously applied (Abrams and Eickwort, 1980; Michener, 1974), but some authors term the simultaneous presence of a reproductively active mother and her reproductively active daughters "eosocial" (Plateaux-Quénu et al., 1989).

The evolutionary maintenance of cooperative societies is problematical (see Axelrod and Dion, 1988), especially if group members are not closely related. Strassmann (1989) compared the relatedness data on foundress associations of polistine wasps with that found in several species of ants and noted that higher genetic relatedness is associated with a reproductive division of labor in the wasps while hierarchy is absent in ant foundress groups made up of unrelated females (Strassmann, 1989). Because these two groups are quite different, this apparent association between relatedness and a reproductive division of labor may not be due to the differences in relatedness alone. However, this association is compatible with the optimization model proposed by Vehrencamp (1983a, 1983b) predicting that a dominant individual may be able to bias the fitness of group members in her favor if group members are relatives because of inclusive fitness effects. More recently, Gadagkar (1991) reviewed the relatedness values for eusocial Hymenoptera. The values reported for behaviorally eusocial bees are very similar to those for behaviorally eusocial wasps.

The optimization model of Vehrencamp (1983a, 1983b) suggestes that egalitarian cooperation among nonrelatives can occur if there is a small fitness benefit for group living and if there is little fitness cost for individuals leaving the group. If group members are relatives, then a dominant individual can bias the fitness of group members in her favor because of inclusive fitness effects. The amount of fitness disparity that can be imposed by a dominant increases with intracolony relatedness, but the magnitude of bias is still limited by the options available to subordinate group members (Vehrencamp, 1983a, 1983b). This theory was recently elaborated to look at the conditions under which "reproductive skew" occurs in associations among queens (Reeve and Ratnieks, 1993).

New data indicate that intracolony relatedness for cooperative foundress associations in the Hymenoptera ranges widely. In *Acromyrmex versicolor* and *Veromessor pergandei*, ant species in which colonies are founded by groups of queens, co-foundresses are no more closely related than randomly selected queens (Hagen et al., 1988; Rissing et al., 1989). In a species of social bee, *Exoneura bicolor*, colonies are initiated by a group of foundresses, all of which are reproductively active. In forming colonies, *E. bicolor* foundresses associate with kin to create colonies of related individuals and intracolony relatedness is about 0.6 (Schwarz, 1987; Schwarz and Blows, 1991). The intracolony relatedness among the female offspring of these foundresses is about 0.5. A similar study of *E. richardsoni* also indicates that foundress associations are made up of related females ($r = 0.497 \pm 0.152$, 41 nests, 94 females) and the female offspring of these foundresses are even more closely related ($r = 0.759 \pm 0.086$, 30 nests, 79 females) (Schwarz et al., in prep.). These data indicate that reproductive division of labor ("reproductive skew" *sensu* Reeve and Ratnieks, 1993) occurs among *E. richardsoni* and perhaps also among *E. bicolor* foundresses.

There is only one fully cooperative species for which relatedness values are available in the literature. *Cerceris antipodes*, an apparently communal, ground-nesting wasp in which cooperation among reproductively active females continues throughout the colony cycle, has rather high intracolony relatedness values. At one nest aggregation average relatedness exceeded 0.5 for two successive years, at a second it was about 0.3. At two additional sites, the average relatedness values were also about 0.3 but not significantly different from zero due to large standard errors (McCorquodale, 1988). Unfortunately, little is known about the within nest behavior of *C. antipodes*.

It is important to obtain relatedness values for communal species for which behavioral data are available to examine the association between intracolony relatedness and cooperative behavior. This will clarify the role of kin selection in the evolution of cooperative associations. For this reason we studied the intracolony relatedness of a communal halictine bee species, *Lasioglossum (Chilalictus) hemichalceum*.

L. hemichalceum is known to be a cooperative, communal bee with an annual, bivoltine, life history and an unusual mating system. Reproductive activity typically begins in the spring (November) when females that have overwintered as mated adults rear brood consisting of small males and females. Mating occurs and these first-generation females go on to rear a second brood consisting of small males, large, macrocephalic males, and females (Kukuk and Schwarz, 1988). Mating occurs and the second-generation females overwinter (March through October) to begin the cycle in the next year. During especially rainy summers (1990–1991 and 1992–1993) only one generation of brood is reared (Kukuk in prep). *L. hemichalceum* males occur in two morphs; a small, rather typical, male that leaves the nest and mates on flowers, and a morph nearly three times the size of small males that has a disproportionately large head and mandibles along with small wings. These latter males remain in their nests, fight to-the-death with one another, and mate with resident females (Kukuk, in prep; Kukuk and Schwarz, 1988).

Up to 20, but usually less than 10, females live in communal groups in which all individuals are reproductively active. During the inactive phases of the colony cycle, groups may be larger (Kukuk, unpub. data). Agonistic behavior between reproductively active females is very rare in the laboratory during staged, paired encounters between females, even if females are from different nests or nest aggregations (Kukuk, 1992). In addition, nectar is shared by oral trophallaxis between nestmates and nonnestmates alike (Kukuk and Crozier, 1990; Kukuk and Schwarz, 1987). Here we report reproductivity and intracolony relatedness for this communal, halictine bee.

Materials and methods

Samples were obtained by excavation of 52 colonies between 10 February and 16 February 1991, from a nest aggregation located in southwestern Victoria, Australia,

Table 1. List of enzyme, stain, and buffer systems used in the study of allozyme variation in *Lasioglossum (Chilalictus) hemichalceum*

Enzyme	Symbol	Enzyme Commission Number	Number of loci	Number of bees*	Buffer**	Stain***
Adenylate kinase	AK	2.7.4.3	1	52	AC	4
Creatine kinase	CK	2.7.3.2	1	52	AC	4
Enolase	ENOL	4.2.1.11	1	30	TC	2
Fructose-bisphosphatase	FBP	3.1.3.11	2	40	AC	3
Fumarate hydratase	FUM	4.2.1.2	1	30	AC	1
Glucokinase	GK	2.7.1.2	1	33	RW	1
Glucose-6-phosphate dehydrogenase	G6PDH	1.1.1.49	1	52	AC	1
Glucose-6-phosphate isomerase	GPI	5.3.1.9	1	52	TC	1
Glycerol-3-phosphate dehydrogenase	G3PDH	1.1.1.8	2	323	AC	4
3-Hydroxybutyrate dehydrogenase	HBDH	1.1.1.30	1	40	AC	1
Isocitrate dehydrogenase	IDH	1.1.1.42	1	52	TC	1
Malate dehydrogenase	MDH	1.1.1.37	2	323	AC	1
Malate dehydrogenase (NADP$^+$)	ME	1.1.1.40	1	33	RW	1
Peptidase with leucyl-alanine	PEP-LA	3.4.11.13	2	53	RW	1
Phosphoglucomutase	PGM	5.4.2.2	1	53	TC	1
Phosphogluconate dehydrogenase	PGD	1.1.1.43	1	53	AC	1
Pyruvate kinase	PK	2.7.1.40	1	30	TC	1
Superoxide dismutase	SOD	1.15.1.1	1	53	RW	2
Triose-phosphate isomerase	TPI	5.3.1.1	1	40	RW	1

* With the exception of G3PDH and MDH where 48 males were included, all bees were female.

** Gel & electrode buffers: RW from Ridgeway et al. (1970); AC (N-(3-aminopropyl)-morpholine & citric acid) from Clayton and Tretiak (1972); TC = gel type 4 from Selander et al. (1971).

*** Stain recipes: 1, May et al. (1989); 2, Harris & Hopkinson (1976); 3, Nash & Challinor (1985); 4, Allendorf et al. (1977).

at a 5-way intersection including Jackie's Swamp Road and Fish Holes Road in Cabboboonee State Forest using the methods described by Abrams and Eickwort (1980). Of these, 35 were excavated in their entirety.

Horizontal, starch-gel, electrophoretic methods followed those described by May et al. (1989) and Leary and Booke (1990), and were carried out using the gel, electrode buffer, and histochemical staining systems indicated in Table 1. Gels were made with 12 grams of Sigma starch per 100 ml of gel buffer and were run between three and four hours. The enzyme nomenclature and commission numbers given in Table 1 follow the recommendations of Webb (1984).

Data for two polymorphic loci, *G3PDH-2* and *MDH-2*, were obtained from 323 individuals from 52 colonies; 282 females and 48 males. For each colony, a minimum of 2 and a maximum of 10 individuals were used ($x = 6.3$). Electrophoretic data were analyzed using the Relate program, version 3.2 (see Queller and Goodnight, 1989). Estimates were calculated for all 52 colonies, and for a subset of the females only from 25 reproductively active colonies.

Results

A summary of contents for the 38 completely excavated nests is provided in Table 2. Colonies were not completely synchronized. Twenty-five colonies of the 35 contained eggs and young brood, while 10 contained only older brood and adults. For the 25 productively active nests, the number of adult females is positively associated with the number of immatures in nests. The slope of this Model II regression is 1.516, and the 95% confidence interval is between 0.893 and 2.139, it accounts for 50% of the variance in the number of young immatures ($r = 0.724$, $p = 0.0001$). In addition, the slope of a Model II regression of the natural logarithms of brood size and adult number of 0.957, is also indistinguishable from 1.0 ($r = 0.593$, $p = 0.003$) (Fig. 1).

Nest parasitism was rare and was not significantly associated with either the number of adult females or macrocephalic males. Of 173 pupae, only 10 were those of a cleptoparasitic, ichneumonid wasp, *Labium sp.*

Nineteen of 31 enzymes initially screened in *L. hemichalceum* were resolvable. A survey of these systems, however, revealed only two of 23 presumptive gene loci to be polymorphic (*G3PDH-2* and *MDH-2*). The majority of enzymes listed in Table 1 produced only one zone of activity. The *GPI* enzyme system, however, did produce a double banded pattern, but because no variation was observed in this system, it was treated as a single locus. Additional, poorly resolved loci were observed for *PEP-LA* and *GK*, but staining of these enzymes on other buffer systems failed to sufficiently resolve the loci. Banding patterns identical to those observed in the *PEP-LA* locus were also visualized using glycine-leucine, as a substrate, but

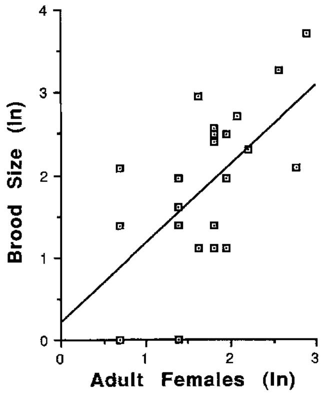

Figure 1. The natural logarithms of the number of immatures (Brood Size) and the number of adult females found in 25 active colonies of *Lasioglossum (Chilalictus) hemichalceum* from a single nest aggregation in Cabboboonee State Forest, southwestern Victoria, Australia. Excavations were carried out in mid February, 1991

Table 2. A summary of contents from 35 nests (25 actively provisioning and 10 not) of *Lasioglossum (Chilalictus) hemichalceum*, completely excavated in February, 1991 at Cabboboonee State Forest, near Portland, Victoria, Australia

Variable (Active Nests/Inactive Nests) (N = 25) (N = 10)	Mean	Std. Error	Range	Sum
Adult Females	6.1/4.1	0.89/1.0	0-18/1-9	153/41
Adult Small Males	0.44/0.3	0.18/0.21	0-3/0-2	11/3
Adult Macrocephalic Males	1.8/1.0	0.41/0.26	0-7/0-3	46/10
Female Pupae	4.0/3.3	0.41/1.47	0-24/0-14	100/33
Small Male Pupae	0.6/0.2	0.24/0.20	1-5/0-2	15/2
Macrocephalic Male Pupae	0.8/0.3	0.25/0.30	1-5/0-3	20/3
Prepupae + Larvae	2.4/0	0.50/0	0-10/0	59/0
Pollen Balls	1.2/0	0.29/0	0-6/0	30/0
Parasites	0.3/0.3	0.17/0.21	0-4/0-2	7/3
Empty Cells	0.3/0.2	0.56/0.20	0-3/0-2	8/2
Moldy Cells	0.2/0.1	0.10/0.13	0-2/0-1	5/1
Total Brood	9.0/3.8	1.81/1.90	1-41/0-19	224/38

Table 3. Relatedness values (r), inbreeding coefficients (f), standard errors (S.E.) and 95% confidence limits (C.L.) calculated from two loci for *Lasioglossum (Chilalictus) hemichalceum* from a single nest aggregation. Standard errors were obtained by Jackknifing over colonies (n = 52) and confidence limits were computed using the tabled value for $t_{[0.05]}$ for $df = 51$

Weight	r	S.E.	95% C.L.	f	S.E.	95% C.L.
Individual	0.119*	0.037	0.045 to 0.193	0.018	0.042	−0.066 to 0.102
Group	0.148*	0.049	0.049 to 0.246	0.031	0.049	−0.068 to 0.125

* Significantly greater than zero and less than 0.25 at the 0.05 level of probability.

Table 4. Relatedness values (r), standard errors (S.E.), and confidence limits (C.L.) by lanus for *Lasioglossum (Chilalictus) hemichalceum* from a single nest aggregation.Standard errors were obtained by Jackknifing over colonies (n = 52) and conficence limits were computed using the tabled value for $t_{[0.05]}$ for $df = 51$

	G3PDH-2			MDH-2		
Weight	r	S.E.	95% C.L.	r	S.E.	95% C.L.
Individual	0.079	0.040	−0.001 to 0.159	0.167	0.059	0.048 to 0.286
Group	0.078	0.058	−0.039 to 0.195	0.220	0.080	0.059 to 0.381

Table 5. Relatedness values (r), standard errors (S.E.), and confidence limits calculated from two loci for *Lasioglossum (Chilalictus) hemichalceum* from a single nest aggregation. Data from 25 nests containing larvae or eggs. Standard errors were obtained by Jackknifing over colonies. 95% confidence limits were computed using the tabled values for $t_{[0.05]}$ for $df = 24$

Weight	r	S.E.	95% C.L.	f	S.E.	95% C.L.
Individual	0.076	0.037	−0.006 to 0.158	−0.016	–	–
Group	0.064	0.048	−0.042 to 0.170	−0.027	–	–

the leucyl-alanine substrate gave much stronger bands. The proportion of polymorphic loci (P) observed was 0.087. The average expected mean heterozygosity (H_e) and average observed mean heterozygosity (H_o) were 0.0316 and 0.0312 respectively.

The overall intracolony relatedness estimate for *L. hemichalceum* at the 5-Way site is significantly greater than 0.00 and less than 0.25 (Table 3) while the inbreeding coefficient is not significantly different from zero. Estimates based on equal weighting for individuals, or equal weighting for groups, are similar. There is variation between the two loci with values for *G3PDH-2* not significantly different from 0.00, while values for *MDH-2* are greater than 0.00 and less than about 0.35 (Table 4).

Relatedness estimates calculated for the 25 reproductively active colonies were about 0.07, on average, and the confidence limits overlap zero (Table 5). This is apparently lower than the above zero estimate calculated for all 52 colonies, but the confidence intervals for the two estimates overlap.

Discussion

There is a positive Model II regression between the number of adult females per nest and the number of immatures, with a slope indistinguishable from one. This association explains about one-half of the variance in the number of young immatures in *L. hemichalceum.* Similarly, the slope of the Model II regression of the natural logarithms of these two variables is indistinguishable from one indicating that as the number of females per colony increases, the average reproductive success per female (reproductivity) remains the same. A similar result was noted for the communal euglossine bee *Eulaema nigrita* (Santos and Garófalo, 1994). This result is in contrast to the decrease in reproductivity with increased colony size for a variety of eusocial hymenopteran species (Michener, 1964).

This comparison is valid, because it compares similar data sets. However, there remains a problem in interpretation because no data from inactive colonies are included in any of the data sets. It seems likely that colonies consisting of small numbers of females suffer higher mortality rates and they would be under-represented in a sample of successful colonies. Moreover, if adult survival is associated with colony size, the interpretation suggested above would mask positive fitness benefits gained by living in groups. To more fully understand the fitness consequences of colony size, a study following colonies from the initiation of activity in the spring combined with excavation of colonies later in the summer would provide data on colony persistence and reproductive output that could be related to the number of females originally comprising the colony. In spite of this difficulty, it does appear that reproductivity in communal species does not decrease with colony size in the same way as it does in eusocial species.

In social insects, the presence of eusociality and the consequent reduction of effective population size may promote low heterozygosity through drift (Berkelhammer, 1983; Graur, 1985; but see Owen, 1985; Reeve et al., 1985). The low proportion of polymorphic loci, and the low allelic diversity at the polymorphic loci in *L. hemichalceum* is consistent with results found for other haplodiploid insects (Crespi, 1991; Packer and Owen, 1992). The expected heterozygosity of 0.0316 is within the range of that reported for all haplodiploid insects and also within the range for both eusocial and non-eusocial species. This supports Crespi's (1991) conclusion that it is not necessary to invoke eusociality to explain low levels of genetic heterozygosity in social Hymenoptera; haplodiploidy is a sufficient condition.

The overall relatedness value for all 52 colonies *L. hemichalceum* is about 0.13. If these individuals represented a single generation, this result would imply the presence of multiple reproductive females in each nest in the previous generation. Alternatively a similar relatedness value could be achieved by a single female mated to more than 20 unrelated males, a very unlikely possibility. However, the colonies obtained for this study were not synchronous.

Twenty-five colonies contained signs of reproductive activity; that is they contained fresh pollen balls, eggs, or young larvae. The inactive colonies may have contained more than one generation, i.e. an old female(s) with recently enclosed daughters. The 25 active colonies, on the other hand, probably consisted of a single generation of females in a brood rearing phase of the colony cycle. The relatedness estimate for the active colonies was lower than the estimate for all 52 colonies and it is not significantly different from zero. This is compatible with the notions that 1) unrelated females nest and reproduce together and 2) there is a slight overlap of generations so that mother-daughter pairs occur in some nests elevating the overall ($n = 52$) relatedness.

As for the relationship beween intracolony relatedness and communal sociality, the meager data suggest that communal sociality in the Hymenoptera is often but not always associated with low intracolony relatedness. The intracolony relatedness of reproductively active colonies of *L. hemichalceum* is zero. DNA fingerprint evidence indicates that intracolony relatedness in the communal bee *Perdita texana* is also zero (Danforth et al., submitted ms). In addition for two communal species of andrenid bee, *Andrena ferox* and *A. jocobi*, neither of which show any electrophoretic variation, no distinction between colonies was found in Dufour's gland secretions (Ayasse et al., 1990). The composition of the Dufour's gland secretions is correlated with kinship in other bee species (Hefetz et al., 1986; Smith and Wenzel, 1988). On the other hand, intracolony relatedness of the sphecid wasp, *C. antipodes*, is fairly high (McCorquodale, 1988).

Within the halictine bees, data on intracolony relatedness indicates that colonies of two eusocial species, *L. zephyrum* and *L. laevissimum* consist of close relatives and are within the range of values known for behaviorally eusocial wasps (Crozier et al., 1987; Gadagkar, 1991; Kukuk, 1989; Packer and Owen, 1994; Strassmann et al., 1989). They are significantly higher than the value reported here for *L. hemichalceum.*

An additional important consideration is that in some apparently communal species, where all females have well developed ovaries, a high variance in reproductive success among group members may still occur. This was demonstrated for the orchid bee *Euglossa cordata.* In reused nests, colonies usually consisted of sisters all exhibiting well developed ovaries. Behavioral observations indicated that one female remained in the nest and cannibalized the eggs of the other group members (Garófolo, 1985).

No clear pattern exists concerning the relationship between intracolony relatedness and social organization in foundress associations in the Hymenoptera as a whole. The trend noted by Strassman (1989) does not hold for two allodapine bee species in the genus *Exoneura* in which closely related females appear to be communal. However, there may be high variance in reproductive success among these cofoundresses (Schwarz, 1987; Schwarz and Blows, 1991; Schwarz et al., in prep.). This again draws attention to the possibility that some apparently communal species may have, on closer inspection, a reproductive division of labor, i.e. a high variance in reproductive success or "reproductive skew" (*sensu* Reeve, 1991).

The low relatedness values for four communal bee species plus this occurrence of high variance in reproductive success among sisters in *Euglossa cordata* and among relatives in foundress associations of two *Exoneura* species suggests that intracolony relatedness may be positively associated with reproductive skew. Additional genetic and behavioral data from *C. antipodes* examining reproductive skew in this species would be illuminating. Clearly, genetic and behavioral data as well as assessment of reproductive state for colony members are required to examine this critical issue and any firm conclusion would be premature.

Changing focus to the mechanistic level, it is clear that relatedness values in a communal species can be influenced by one or more proximate factors. Colony initiation patterns and movement among colonies will influence the relatedness in groups of reproductively active females. Relatedness among their offspring will be influenced by the mating system, and the variance in reproductive success among group members. Colony longevity, the number of generations that a colony persists, may interact with any of these factors.

What evidence is available for communal species concerning each of these possible influences? Nest initiation in communal species is not well understood. A laboratory study of nest initiation in *L. hemichalceum* indicates that this species nests in suitable indentations in the soil without regard to whether or not they are already occupied by another female, and without regard to whether or not the female occupying the incipient nest is familiar or nonfamiliar (Kukuk, in prep). This suggests that foundresses in the wild are unlikely to consist of related individuals. This may contribute to the lack of relatedness in groups of reproductively active females. In the communal wasp, *C. antipodes*, colonies are founded each spring by single females (McCorquodale, 1989a). Because colonies are founded by single females and are annual, relatedness is rather high in this species because nests will be largely occupied by the daughters and granddaughters of a single female.

Second, once colonies are established, if females migrate from nest to nest this will depress relatedness. Such movement, "nest switching", was reported for the communal bees *Agapostemon virescens* (Abrams and Eickwort, 1980), *Andrena jacobi* (Ayasse et al., 1990), and for the communal wasp *C. antipodes* (McCorquodale, 1989) suggesting that this is an important, general characteristic of communal species. The absence of preferential treatment of familiar individuals indicates that nest switching is possible in *L. hemichalceum*; and anecdotal observations suggest nest switching occurs in the field. The ease of nest switching in communal species may provide a relatively cost free way for females to avoid potential dominants and so escape subordination.

For long-lived colonies, if each female mates with a different unrelated male, and variance in reproductive success among females is low, intracolony relatedness will decrease over generations. Colonies of *L. hemichalceum* are long-lived when compared to those of *C. antipodes*. Nearly, 50% of nests that were active in the spring of 1992 remained so when last checked in the fall of 1994 (Kukuk, unpublished data). However, there is a combination of extra- and intranidal mating in *L. hemichalceum* due to the differences in behavior of small versus macrocephalic males. Small males do not remain in nests and probably mate with females on flowers, presumably outbreeding. Large, macrocephalic males remain in nests where they may mate with several resident females (Kukuk and Schwarz, 1988). The proportion of matings obtained by small versus large males would be important in this regard. If a single macrocephalic male mates with several females in a single nest, the resulting female offspring would be members of the same patriline and intracolony relatedness would be elevated. The lack of relatedness in colonies of actively reproducing *L. hemichalceum* females is therefore remarkable and must be strongly influenced by patterns of nest initiation and/or nest switching. In addition, several communal species are known to have macrocephalic males (cf. Kukuk and Schwarz, 1988) but relatedness values are unavailable for them.

Intracolony relatedness would be increased in colonies by high variance in reproductive success among reproductive individuals. The levels of relatedness detected for *L. hemichalceum* also provide evidence of a low variance in individual reproductive success. Even more remarkable is that these low relatedness values are found in a species with very high levels of cooperative behavior. In particular, this is the only species of halictine bee in which trophallaxis is known to occur (Kukuk and Crozier, 1990).

In conclusion, high intracolony relatedness is not a necessary condition for evolution of complex, cooperative behavior in Hymenoptera. However, it can be high in some communal species, as in *C. antipodes*, if colonies are short lived. While it is tempting to conclude from the available data that low intracolony relatedness is associated with low variance in reproductive success among colony members, such a conclusion would be premature. It is crucial to obtain more genetic and behavioral data for communal species to examine this association. In addition, it is important to obtain such data from species in a taxon that includes both communal and eusocial species, such as the halictine bees.

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