SINGLE SEX ALATE PRODUCTION BY COLONIES OF PHEIDOLE DESERTORUM AND PHEIDOLE XEROPHILA TUCSONICA (HYMENOPTERA: FORMICIDAE)*

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Specialization in production of the sexes is widespread in ants; individual colonies often produce a sex-biased ratio of reproductive offspring (Kannowski 1963, Pamilo and Rosengren 1983, Nonacs 1986a,b). Reasons for specialization are unclear, although there is much speculation (Pamilo and Rosengren 1983, Nonacs 1986b, Frank 1987, Boomsma and Grafen 1990). While some colonies produce unisexual or extremely sex-biased broods, other colonies within the same populations will produce both males and gynes in nearly equal proportions (Pamilo and Rosengren 1983, Nonacs 1986b). A more extreme form of specialization in sexual production occurs within the genus *Pheidole*; all colonies within a population may exhibit specialization to the point of producing only unisexual, or nearly unisexual reproductive broods. We have investigated this phenomenon in two common desert *Pheidole* species.

MATERIALS AND METHODS

Partial excavations and censuses were made of *P. xerophila tuc-sonica* nests at South Mountain Park, Phoenix, Arizona in August 1987. Collections and censuses of *P. desertorum* colonies were made at 2.5 mi. N.W. of Rodeo, New Mexico in June and July of 1988 and 1989. *Pheidole desertorum* evacuate the nest in response to attack by *Neivamyrmex* army ants (Mirenda et al. 1980); this behavior was exploited to trap complete colonies which were censused later. Traps consist of an open (top and bottom) plastic bowl cemented into an uncovered, fluon-lined plastic box. The bottom edge of the bowl extends below the bottom of the box and is pushed into the soil around *P. desertorum* nest entrances. Army ants are introduced ad libitum into the bowl; *P. desertorum* flee from the

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nest, out of the bowl, and fall into the box. The sex produced by *P. desertorum* colonies left intact in the field was assessed by placing a concave stone over the nest entrance and pouring water over and around the stone. Alates moved under the stone into the humid chamber; the stone was lifted and number and sex of alates were recorded.

RESULTS

In *P. xerophila tucsonia*, alate production by colonies appeared strictly unisexual; only males were found in 13 colonies (mean number = 30.62, SD = 33.62) and only gynes were found in 6 colonies (mean number = 16.00, SD = 21.82). In *P. desertorum* colonies assessed and left intact in the field, only males were found in 46 colonies (mean number = 27.30, SD = 40.30) and only gynes were found in 64 colonies (mean number = 15.61, SD = 17.56). Both sexes were found in only 5 colonies (mean number of males = 18.00, SD = 32.08; mean number of gynes = 2.40, SD = 1.34). Complete colony census data (Table 1) suggest mixed-sex reproductive broods are produced by male specialist colonies which produce a small number of gynes.

Table 1. Census of males and gynes present in complete P. desertorum colonies.

	Colony Designation							
	\overline{AI}	A4	A8	X1	A9	X3	A6	A5
# Males	356	535	711	1,076	0	0	0	0
# Gynes	1	0	9	1	3	198	246	434

DISCUSSION

Specialization in production of the sexes is more extreme in *P. desertorum* and *P. xerophila tucsonica* than has been reported to occur in other ants. Droual (1982) observed 40 reproductive *P. desertorum* colonies which evacuated the nest in response to introduction of *Neivamyrmex nigrescens* army ants. Twenty-two colonies produced only gynes; the remaining 18 produced only males or a sex ratio "strongly" male-biased. These observations are consistent with data presented here. *Pheidole desertorum* colonies produce either all gynes, all males, or nearly all males. Only unisexual reproductive broods were observed for *P. xerophila tucsonica*.

Proposed circumstances under which natural selection may result in specialization by ant colonies include avoidance of inbreeding (Marikovsky 1961), queen-worker conflict over investment ratio (Pamilo 1982, Boomsma and Grafen 1990), efficient use of resources (Nonacs 1986b), and intrasexual competition among relatives (Frank 1987). Selection against specialization should be strong in small populations (Taylor and Sauer 1980), and selection to maintain specialization may be weak when population investment ratio is at, or near equilibrium (Frank 1987). Differing magnitude of selection pressures both favoring and opposing specialization might result in differing degrees of specialization, including extreme specialization found within *Pheidole*.

SUMMARY

Pheidole desertorum and P. xerophila tucsonica appear unusual among ants in that colonies produce only unisexual or extremely sex-biased reproductive broods. Specialization in production of the sexes may be more extreme within Pheidole than other ants due to difference between ant taxa in magnitude of selection pressures both favoring and opposing specialization.

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