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Queen polymorphism in the North American harvester ant, *Ephebomyrmex imberbiculus*

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Summary

In the North American harvester ant *Ephebomyrmex imberbiculus*, in addition to dealate queens, wingless female reproductives occur that have greatly reduced ocelli and thoracic sutures (intermorphic queens). Both queen types are equivalent in function, and do not differ in ovarian morphology. Colonies may contain several inseminated and egg-laying intermorphic queens. We discuss queen polymorphism in respect to the biology of this desert-dwelling species.

Introduction

The myrmicine genus *Ephebomyrmex* (Wheeler, 1902) (treated as a subgenus of *Pogonomyrmex* by some authors) comprises some twenty species of medium-sized, seed-harvesting ants from dry desert habitats throughout North and South America. In two detailed investigations, life history and behavior of a nearctic representative, *E. imberbiculus*, were studied (Wheeler, 1902; Creighton, 1956) and in both it was unusually difficult to secure winged male and female sexuals of this species. Creighton (1956) therefore suggested that sexuals are produced only in especially favorable years. We here provide an alternative explanation for the rareness of winged female sexuals: *E. imberbiculus* produces wingless, female sexuals in addition to winged queens.

Brachypterous (short-winged) queens occur in *Ephebomyrmex huachucanus* (Cole, 1968) and "workerlike", wingless queens have been reported from neotropical species of *Pogonomyrmex* and *Forelomyrmex* (Santschi, 1931; Kusnezov, 1951; Kugler, 1978). Complete wing reduction and queen polymorphism have as yet not been reported in *Ephebomyrmex*, and neither has the ecological significance of wingless queens been examined.

Material and methods

Complete colonies of *Ephebomyrmex imberbiculus* were collected in August 1990 by of the authors (SPC) in the Chiricahua Mts. and the adjacent San Simon Valley, southeastern Arizona and southwestern New Mexico. The ants were cultured in three-chambered plastic boxes with a plaster floor. Colonies were fed diluted honey, pieces of insect tissue, and crushed sunflower, sesame and linseeds three times a week.

Queens and workers were dissected by removing the subgenital sclerites and the attached sting apparatus and genital tracts with a pair of forceps.

Results

Nest structure and queen polymorphism

According to Krombein et al. (1979), *Ephebomyrmex imberbiculus* lives in various regions of the southwestern United States and Mexico. In southern Arizona, it occurs in most desert habitats, but appears to be replaced in the Sonoran Desert by the closely related *E. pima*. In the Chiricahua Mts. and adjacent San Simon Valley (our study area), *E. imberbiculus* is common in most desert habitats up to elevations of 1500 m. Colonies have also been collected on bare, rocky, south-facing slopes in Cave Creek Canyon at elevations of 1600 to 1700 m. Nests are built in sandy or rocky soil and are rather shallow. To date, 75 colonies have been excavated, and all but two were less than 60 cm deep, with most ants concentrated in the upper 30 to 40 cm of soil. No ants have been found deeper than 80 cm.

As shown by Wheeler (1902) and Creighton (1956), societies of *E. imberbiculus* are quite small. Colonies censused by us consisted of 10 to 42 individuals ($n = 10$, $\bar{x} = 20.7$), and the largest colony (not censused) contained approximately 80 to 90 workers and a dealate queen. We found only three other dealate queens in the field: one was dispersing on the soil surface, and the other two were foundresses, each in a small burrow under a rock. Dealate queens were absent from all other nests; however, a closer examination of 15 of these apparently "queenless" colonies revealed that all contained wingless queens with a simplified thoracic structure.

The morphological queen castes, i.e. winged queens as well as wingless ergatoid queens *sensu* Peeters (1991), are clearly defined. However, terms for wingless female reproductives with thorax structures intermediate between those of winged females and workers are controversial. In Buschinger and Winter's terminology (1976), the latter group are referred to as "intermorphic" queens, winged queens are "gynomorphic". On the other hand, Peeters (1991) used "intercaste" for both regularly and erratically produced intermediate phenotypes, supposedly resulting from deviations from the normal pattern of caste differentiation. We here use the term "winged queen" for female reproductives which eclose with wings (or "dealate queen" for those which have shed their wings), and "intermorphic queen" for wingless reproductives. In the case of *E. imberbiculus* we prefer the latter term instead of "intercaste", in order to distinguish clearly between regularly reared functional

Table 1. Measurements from workers, intermorphic and dealate queens of *E. imberbiculus* (in mm)

	Worker	Queen	
		Intermorph	Dealate
Individuals	10	9	1
Head length	1.04–1.10	1.04–1.25	1.21
Head width	0.96–1.09	1.10–1.21	1.15
Scape length	0.64–0.79	0.69–0.81	0.85
Eye diameter	0.19–0.21	0.19–0.24	0.27
Thorax length	1.12–1.34	1.31–1.54	1.69
Thorax width	0.69–0.77	0.77–0.89	0.94
Petiole width	0.23–0.32	0.32–0.40	0.40
Postpetiole width	0.42–0.50	0.54–0.61	0.60
No. of ovarioles	2	7–8	8

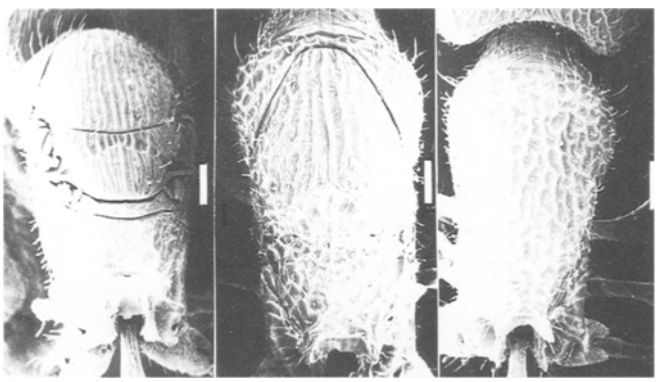

Figure 1. Thorax of a dealate queen, an intermorphic queen, and a worker of *Ephebomyrmex imberbiculus* as seen from above. Whereas all examined intermorphs have a strong promesonotal suture, the thoracic sclerites are completely fused in workers. (Scale = 0.2 mm)

reproductives, which are an important part of the species' life history, and accidentally produced intergrades.

Workers, intermorphic queens and dealate queens of *Ephebomyrmex imberbiculus* differ in the following characteristics:

1. Female reproductives are significantly larger than workers (as indicated by Weber's thorax length, T_L. Dealate queens: $n = 2$, $T_L = 1.71 \pm 0.02$ mm; intermorphic queens: $n = 9$, $T_L = 1.41 \pm 0.08$ mm; workers: $n = 27$, $T_L = 1.25 \pm 0.06$ mm, $p < 0.001$, t test; see Tab. 1).
2. Whereas the thoracic sclerites of workers are completely fused, in intermorphs at least pronotum and mesonotum are separated by a clearly visible suture (Fig. 1). The degree to which thoracic structures are retained in intermorphs varies from individual to individual (Fig. 2). Some intermorphs have small, heavily pigmented spots at the site of the wings of winged queens.

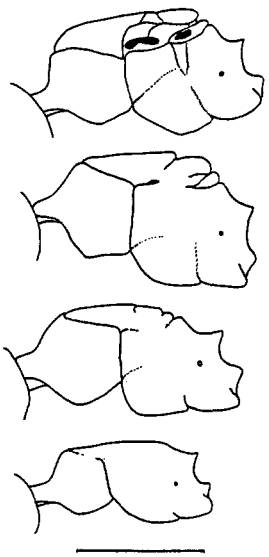

Figure 2. Lateral view of the thoraces of a dealate queen, two intermorphs and a worker of *E. imberbiculus*, showing the stepwise reduction of thorax sclerites. (Scale = 1 mm)

3. In workers, the thorax sculpturing is coarsely rugo-reticulose, while the dorsal part of the intermorph's thorax has strong, irregular rugae, similar to the dorsal scutum of the winged queens.
4. Workers do not have ocelli; in intermorphs their place is marked by small grooves and gaps in the frontal sculpturing. Ocelli are clearly visible in winged queens.
5. The ovaries of 14 dissected workers invariably consisted of two ovarioles and lacked a spermatheca. In contrast, the ovaries of 12 intermorphs had seven or eight ovarioles and a spermatheca, which was filled with sperm in all but one individual. The ovaries of the only dissected dealate queen consisted of eight ovarioles and a spermatheca. The number of ovarioles is extremely small compared to species of the closely related genus *Pogonomyrmex* (*P. barbatus* 50–60, Holliday, 1903; *P. badius* appr. 200, Tschinkel, 1987), but is well in accordance with the assumption that the ovariole number is correlated with the fecundity of a queen and average colony size (Tschinkel, 1987).

Hence, intermorphic queens of *E. imberbiculus* are morphologically intermediate between workers and dealate queens, but identical to the latter in the anatomy of their ovaries and also in their function: both dealate and intermorphic queens laid eggs which developed into callow workers within six to eight weeks.

Polygyny

As far as is known, colonies of *Pogonomyrmex* harvester ants, to which *Ephebomyrmex* is closely related, are strictly monogynous, although short-lived foundress

associations may occasionally occur (Hölldobler, 1976; Pollock and Rissing, 1985; Hölldobler and Wilson, 1990). One of our *E. imberbiculus* colonies contained five intermorphic queens and a few larvae, and no workers, suggesting that new nests may be founded by pleometrosis. In ten mature nests, two, three or more intermorphs were present, and dissections in three colonies showed that several inseminated and egg-laying intermorphs may coexist within a single colony. True polygyny is therefore likely to occur in field colonies of this species.

Dissections revealed the presence of yellow bodies in the ovaries of workers, but in our laboratory nests no males were reared.

Discussion

The finding of intermorphic queens in the North American seed-harvester ant, *Ephebomyrmex imberbiculus*, provides further evidence of the widespread occurrence of wing loss in ant queens. Until recently, primarily wingless female reproductives have been thought to be restricted mainly to the Myrmeciinae, Ponerinae and army ants, and among the Formicinae and Myrmicinae to some highly-specialized social parasites and island endemics (Wilson, 1971). However, during recent years, detailed investigations have revealed an increasing number of myrmicine and formicine species in which short-winged or completely wingless queens have either replaced or occur together with "normal" queens (Bolton, 1986; DuBois, 1986; Brandão, 1987, 1990; Heinze and Buschinger, 1987, 1989; Cagniant, 1988; Tinaut and Heinze, 1992).

The evolutionary significance of wing reduction has as yet only occasionally been examined. The loss of wings is considered to be the ultimate step in a shift of dispersal strategies, during which nuptial flight and solitary colony founding are replaced by stationary sexual behavior, return to the maternal nest, and budding. Environmental conditions favoring queen adoption and budding (Hölldobler and Wilson, 1977, 1990; Rosengren and Pamilo, 1983) may therefore be important also in the evolution of winglessness in ant queens; however, additional factors are required to explain morphological modifications which go beyond behavioral and sociometric changes.

Resource limitation is thought to promote the replacement of winged queens either by wingless female reproductives or "gamergates" in ant species from arid habitats (Taylor, 1978; Briese, 1983; Ward, 1983; Forder and Marsh, 1989; Tinaut and Heinze, 1992). As has been suggested explicitly for species of the *Monomorium salomonis* group, there might be a twofold benefit for queens to rear and adopt wingless daughters: firstly, the success of budding might be higher than that of independent founding; secondly, the production of wingless, "workerlike" sexuals requires less energy than to rear winged queens with enormous flight musculature and large fat bodies (Bolton, 1986).

Resource limitation might also underlie wing reduction in queens of *Ephebomyrmex imberbiculus* and related taxa, such as *E. huachucanus*, *Forelomyrmex mayri*, *Pogonomyrmex laticeps*, and *P. longibarbis andinus*. All these species live in dry desert habitats, and furthermore, their colonies are comparatively small (Kusnezov, 1951; Creighton, 1956; MacKay, 1981). Solitary founding queens in arid habitats

have to dig through thirty of more centimeters of rock-hard soil to reach nesting sites which are relatively safe from desiccation, and many of them fail. Especially for species with small colonies it might be difficult to produce the large numbers of energetically expensive, winged queens necessary to compensate the low survival of individual foundresses. A shift to queen adoption and budding and additional energy-saving modifications of queen morphology might therefore be advantageous. Indeed, *E. imberbiculus* colonies with multiple intermorphic queens appear to be common in the field, and observations suggest that short-winged queens of *E. huachucanus* either mate in the nest or return to it after mating (Creighton, 1952; Cole, 1968). However, budding of multiply-queened colonies has as yet not been observed.

A fair number of winged *Ephebomyrmex imberbiculus* queens in museum collections suggest that winged female sexuals consistently occur in the field. Wheeler (1917) witnessed ground swarming of winged queens, and there is evidence that they disperse and found nests solitarily (Hölldobler unpubl., this study). *E. imberbiculus* is hence one of the few ant species in which both winged and wingless queens occur. Although it may be advantageous in constant environments, and even more so in spatially and temporally heterogeneous habitats, to retain long-range dispersal capabilities (Hamilton and May, 1977; Roff,1986; Roff and Fairbairn, 1991), in most species in which wingless or short-winged queens occur, they appear to have completely replaced winged female sexuals (Peeters, 1991). However, as the winged queen morph is often extremely rare in polymorphic species, it appears likely that further investigations will reveal additional cases of wing polymorphism especially among the Myrmicinae and Formicinae.

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