The Frequency of Multi-queen Colonies Increases with Altitude in a Nearctic Ant

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Abstract:

1. Most ants in boreal and alpine habitats are facultatively polygynous, i.e. their colonies may contain one or several queens. It was investigated how the proportion of polygynous colonies varies along an elevation gradient from 60 to 2700 m in the Nearctic ant*Temnothorax rugatulus* (Emery).

2. Across all populations, the proportion of polygynous colonies was positively correlated with altitude. The correlation was considerably stronger when only populations in the narrow area of the Chiricahua Mts, Arizona, were compared.

3. The dominance of polygynous colonies at high altitudes may be associated with selection against solitary colony founding by young queens. In areas with short summers and long winters, hibernation mortality of solitarily founding queens may select for alternative reproductive tactics, such as polygyny and colony founding by budding.

4. Colony founding tactics need to be taken into account to more fully understand altitudinal and latitudinal patterns of ant faunas.

Keywords: Altitude | colony founding | polygyny | queen number | Temnothorax rugatulus

Article:

Introduction

Environmental influences on life history traits of insect societies, particularly the number of queens per colony, are a recurrent topic in ecological entomology. While the presence of a single queen (monogyny) is assumed to be ancestral (Hughes *et al.*, 2008a), many ant species may have colonies with several reproductive queens (facultative polygyny). The occurrence of multi-queen societies appears paradoxical because it results in reproductive conflict among queens, lowers

the relatedness between workers and the brood they care for, and introduces the possibility of nepotism (Keller, 1995).

Facultatively polygynous species are particularly common in boreal and alpine habitats. Most species of non-parasitic ants reported from areas near the tree line in the Northern hemisphere are facultatively polygynous (Heinze, 1993; Bharti *et al.*, 2013), and a recent study has corroborated this pattern for the Swiss Alps (Reymond *et al.*, 2013). Although the prevalence of facultative polygyny at high latitudes and altitudes is thus well documented, it remains unclear how queen number within facultatively polygynous species varies with geographical traits. Reymond *et al.* (2013) predicted dominance of monogyny at higher altitudes because young queens from monogynous nests are typically larger and presumably more capable of dispersal than queens from polygynous nests.

High-quality data sets to test this prediction can be gathered best for species with relatively small and simple nests. Here, we use data from an extensive study on queen size polymorphism in the Nearctic ant *Temnothorax rugatulus* (Emery) (Rüppell *et al.*, 2001; O. Rueppell, unpublished) to determine how the percentage of polygynous colonies varies along an elevation gradient from 60 to 2700 m.

Materials and methods

Temnothorax rugatulus is widely distributed throughout the Western United States. Queens show a bimodal distribution of body size, which is associated with alternative reproductive tactics: microgynes follow a dependent colony founding strategy, i.e. they mate in the vicinity of their natal nest and may return into it to lay eggs. Macrogynes appear to mate away from the nest and to found solitarily (Rüppell *et al.*,2003).

A total of 1030 complete colonies were collected in mixed coniferous forests at different altitudes in Arizona, New Mexico, and Colorado (977 colonies, for details see Rüppell *et al.*, 2001) and in 2012 at Sagehen Creek Field Station, California (1950 m, 18 colonies), Wyeth Campground, Oregon (60 m, 14 colonies), Ellensburg, Washington (760 m, 13 colonies), and Cle Elum, Washington (appr. 750 m, 8 colonies). Queen number was determined directly after collection.

Results and Discussion

Across all 19 collecting sites and more than 1000 colonies, the proportion of polygynous colonies increased significantly with altitude (Spearman's rank correlation, $r_S = 0.600$, $P = 0.0066$). Considering only colonies from eight sites in the Chiricahua Mountains, Arizona, and thus removing possible effects of different latitude and longitude, improves this correlation ($r_S = 0.976$, $P < 0.0001$). In the Chiricahuas, the fraction of polygynous colonies increased from 3/15 (20%) at 1850 m to 22/27 (81%) at 2700 m (Fig. 1). In an earlier

study with about half the number of colonies we could not substantiate such an association (Rüppell *et al.*, 1998).

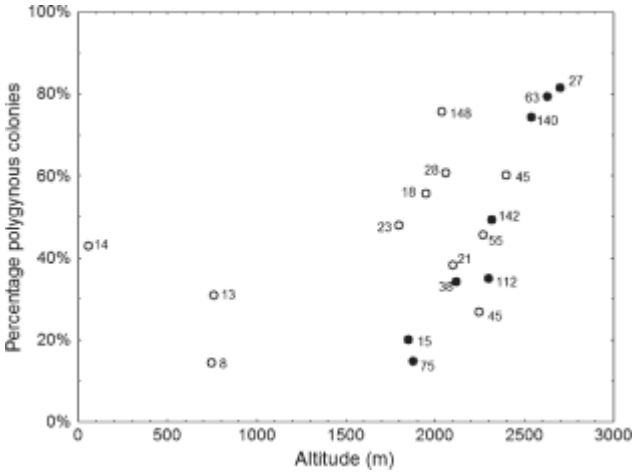

Figure 1. Association between the percentage of multi-queen colonies of the ant *Temnothorax rugatulus* and altitude in the Western United States. Samples from the Chiricahua Mts are indicated by solid circles, all other samples from multiple populations by open circles. Figures next to the circles give the numbers of colonies inspected per population.

Like polyandry (multiple mating of the queen), polygyny can be favoured by selection for larger genetic variability of workers (Rueppell *et al.*, 2008; Hughes *et al.*, 2008b) when different worker lineages specialise in different tasks (Snyder, 1993; Hughes *et al.*, 2003; Helanterä*et al.*, 2013) or are differently resistant against pathogens (Decanini *et al.*, 2007; Ugelvig *et al.*, 2010). However, whether these or other genetic diversity arguments explain the altitudinal clines in polygyny remains to be investigated.

A more direct explanation is that polygyny is favoured at high altitudes because it is associated with the establishment of new colonies by colony budding. Queens thus avoid the risky solitary founding typical for monogynous species. The distribution of the two queen morphs in*T. rugatulus* strongly supports this hypothesis: most queens collected at lower altitudes were macrogynes, which found colonies solitarily, whereas colonies at higher altitudes usually contained microgynes, which found new nests assisted by workers (Rüppell *et al.*, 2001,2003). In areas with short summers and long winters, solitary founding may be selected against because young queens do not have enough time to rear workers before hibernation and solitary hibernation is associated with high mortality (Heinze *et al.*, 1996; Shiroto *et al.*,2011). Accordingly, queens of *Camponotus herculeanus* (Linneaus), the only species with regular independent founding occurring near the tree line in Europe and North America, are not exposed to solitary hibernation by overwintering in their natal nests before mating in early summer (Heinze & Hölldobler, 1994).

Colony founding and dispersal tactics of ant queens are important to understand altitudinal and latitudinal patterns of individual traits, such as body size of queens and workers, and social traits, such as queen number and colony size, of ants (e.g. Geraghty *et al.*, 2007; Reymond*et al.*, 2013).

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