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WHY ARE THERE NO SOLITARY BUMBLE BEES?

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Bumble bees (Apidae: *Bombus*) comprise about 240 species (Williams 2009), predominantly in cold-temperate and arctic regions of Euro-Asia and North America. Where they are present in the New World and Asian tropics, they mostly occur at high altitudes.

Aside from 30 socially parasitic species, all bumble bees have a typical primitively social colony cycle (Fig. 1a). The critical point, which distinguishes these bees from their solitary ancestors and relatives comes at the beginning of the growth phase. Instead of leaving the colony to nest on their own, the first (female) offspring remain as non-reproductive workers.

Many species are found at high latitudes, where the growing season is relatively short. There are even bumble bees within 900 km of the North Pole, where the colony cycle must be completed within just two months (Heinrich 1979). If the season were to be so short that the bees could not possibly rear more than a single brood cohort, there would be no workers, and the population would necessarily be solitary (Fig. 1b).

Are there any solitary populations of bumble bees? To my knowledge, there are none. The workers -- in particular the first to emerge in the colony cycle -- are usually significantly smaller than queens. Aside from the social-parasitic species, then, any solitary population would almost certainly reveal itself in the almost uniform size of its females, yet no such population is known.

Why are there no solitary bumble bees? Is sociality among bees in some way necessarily superior to solitary life? This is certainly not the case, as much more than 90% of the approximately 20,000 species of bees are solitary (Michener 2000). Could it be that solitary life is somehow impossible for bumble bees? This, too, is not plausible, as the queen lives and behaves just like a solitary female during the founding phase. Entirely on her own, she forms a nest, forages for brood food, and rears the first group of offspring. There is no reason to think that she could not possibly rear males and new queens, instead of workers, on her own, yet such a cycle is not found in any known population.

Two hypotheses arise out of these observations. First, while a solitary cycle is possible in bumble bees, under all conditions it would be less productive (in the number of reproductive offspring) than the observed social cycle. This would appear to have something to do with particular features of bumble bees. Second, these features are so decisive that bumble bees are excluded from regions where the "winter" is too long to permit a social colony cycle.

In my view, the evidence that some species -- in particular *B. jonellus* (Meidell 1968) -- commonly undergo two generations per year in some localities speaks in favour of

these hypotheses. Although *B. jonellus* appears sometimes to be bivoltine, it remains social, i.e. queens always rear workers, which in turn rear the reproductive individuals. Even under these circumstances the growth phase of the cycle is not eliminated. I should note that the signs of bivoltinism in *B. jonellus* are not particularly conspicuous, so that the possibility remains that it occurs regularly in some other species without having called attention to itself.

What features of bumble bees could inhibit a general evolutionary return to solitary life? My working hypothesis is that the key lies in the size difference between the female castes. The queen must be relatively large, with large fat reserves, in order to survive the winter -- lasting more than six months in some regions -- and incubate the first brood (Goulson 2003, Heinrich 1979). In contrast, it is more cost-effective if the workers are smaller. This not to say that a smaller worker is more valuable to the colony than a larger one but that it is more economic to invest a given mass of food in a greater number of small workers than fewer large one.

If this working hypothesis is substantially true, then the absence of solitary bumble bees is explained not by historical but by present ergonomic factors.

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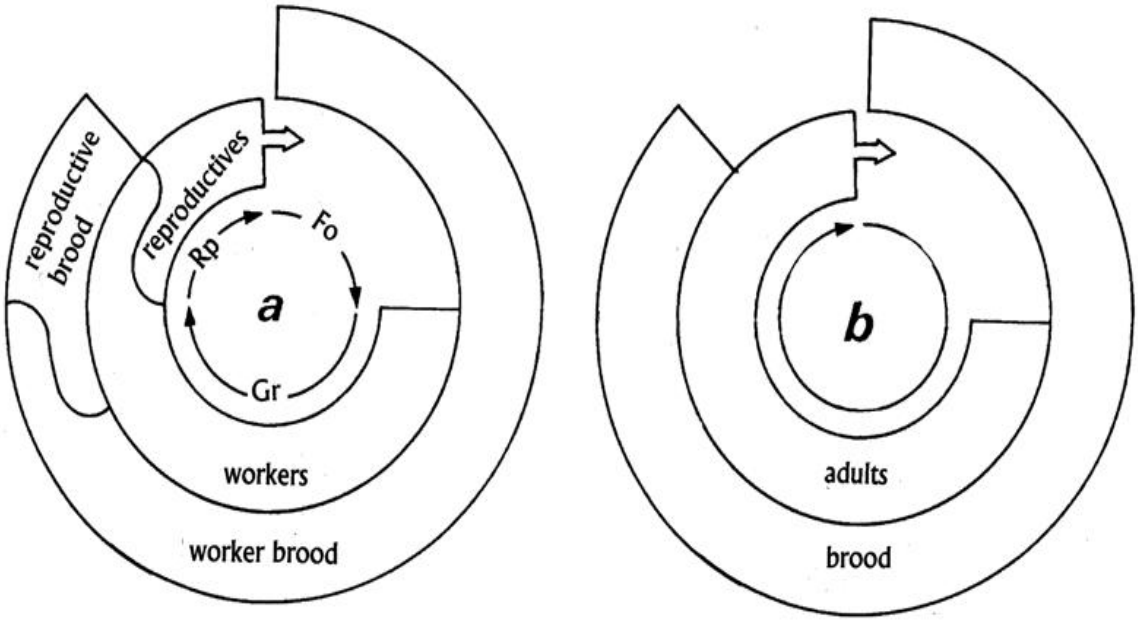

Fig. 1. Colony cycle in primitively social (a) and solitary (b) aculeate Hymenoptera. The difference lies in the absence of the growth phase in solitary species. Outer circle = brood. Inner circle = adult offspring. Fo = founding phase. Gr = growth phase. Rp = reproductive phase.