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A parasitoid wasp's odd pupal vigil

Thousands of insect species build shelters in a bewildering array of forms, which not only affect their fitness, but also affect the success of others. Caterpillars of the fern moth *Herpetogramma thesausalis* (Walker) (Crambidae) roll up the ends of several fern species into shelters the size of ping pong balls. Inside the shelter, the developing caterpillar feeds on the apex of the fern for several weeks until it pupates in the middle of a carefully curated ball of feces, which it has been collecting for some weeks.

Like nearly all caterpillars, fern moths host several parasitoids. At our field site (an old field in coastal Maine), during the summer of 2012, the usually uncommon pupal parasitoid *Phaeogenes hebrus* occurred in unusual abundance. While collecting moth pupae to measure parasitism levels (a yearly census), we twice found male wasps inside the shelters clinging to the pupae (Fig. 1). These males remained on the pupae as we removed the shelters from the plant, transported them to the laboratory, and held them for several hours during processing. Even when their shelter was opened, the males remained crouched on the pupa. Removing the pupa from the shelter, gently prodding the wasp with a pencil and photographing with a flash all failed to distract them from their pupal vigil.

FIG. 1. A male *Phaeogenes hebrus* clutching the pupa of the crambid moth *Herpetogramma thesausalis* (the brown object that the wasp's front two pairs of legs are on), from which a female *P. hebrus* is waiting to emerge. The wasp and pupa are inside a cutaway shelter made of sensitive fern pinnae, created by the caterpillar in which it lives and feeds. The whitish mass behind the pupa is the frass ball of the caterpillar, which is sequestered inside the shelter and often the caterpillar pupates inside it (though not in this case).

Having previously chased escaped *P. hebrus* about the laboratory, this behavior struck us as extremely curious—most parasitoids would fly away well before one had time to contact them. Why didn't these males flee—were they injured, stunned, in torpor, or was this an adaptive response? We suspected that the males were waiting for females to emerge, a behavior well known in parasitoids (e.g., Matthews et al. 1979). In both cases, a female *P. hebrus* emerged from the pupa upon which the male was sitting within a day. Still, this day-long vigil seemed excessive; in the laboratory, with access to nectar and no predators, males lived an average of 14 ± 6.3 d (mean ± SD, $n = 14$). They would not mate for 2 d after emergence or for several days before dying. Therefore, attending a female's pupa for a day might use up more than 10% of that male's reproductive lifespan! The benefits of precopulatory mate guarding are expected to outweight the costs in species, like *P. hebrus*, where females are receptive (or accessible, as in this case) for only a short time, and is further beneficial when encounter rate of females is low, which we believe is also true in this case (Jormalainen 1998).

Previously, we had experienced erratic success at mating *P. hebrus* in the laboratory. The mating behavior of many parasitoids involves an intense and sometimes injurious precopulatory struggle (Teder 2005). In these mating attempts, the *P. hebrus* female repeatedly bit, kicked, and escaped from the male until it gave up, and the female remained unmated. If males similarly lost matings in the field, a day-long pupal vigil would become even more costly to his reproductive potential. We deduced a possible explanation: by waiting inside the shelter, these males limited the space available for the female to struggle and maximized their chances of a successful mating. To test whether a small space increased mating success, we staged mating trials in containers of varying size. Supporting this hypothesis, mating success significantly increased as container size decreased (Fig. 2). By being present when a female emerged from her pupal case, the male minimized the area of the female to struggle and escape, and maximized his opportunity for reproduction.

Intact leaf shelters protect fern moth caterpillars from *P. hebrus* (LoPresti and Morse 2013), yet the shelter is also integral to reproductive assurance for the wasp. This intriguing relationship has important implications because guarding of females by male *P. hebrus* may be common. All members of the genus *Phaeogenes* parasitize caterpillars that build shelters or bore into plants. In fact, in an examination of *P. nigridens* as a biocontrol agent, Smith (1932) found that males were attracted to parasitized pupae at least a day prior to female wasp emergence and suggested mating them in small vials stuffed with cotton for maximum success. This procedure likely mimicked the stem holes in which its host pupates

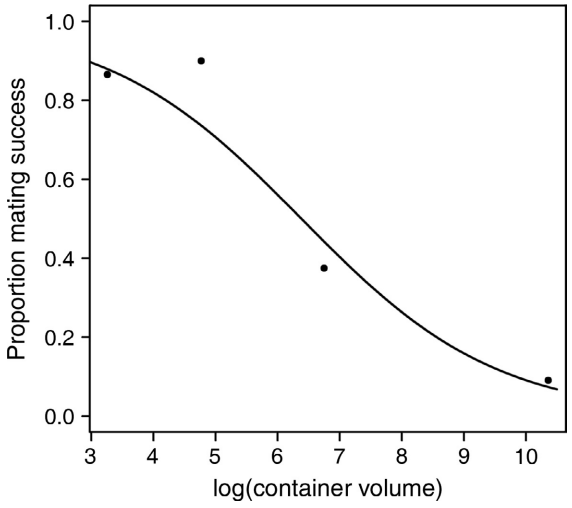

FIG. 2. Mating success as a function of increasing volume of container (log-transformed, measured in cubic centimeters). These data come from 89 trials in which males exhibited mating behaviors (antennating and "dancing" with their wings); in 16 others (excluded), males exhibited no mating behaviors and ignored the females. For ease of visualization, points plotted represent averages for each container volume and not the individual points upon which the binomial regression is based. The regression line is that of the best-fitting model, which incorporated only container volume as an independent predictor (coefficient of log[container volume] = 0.97 + 0.30, $z = -3.3$, $P < 0.001$). Note that the model predicts predicts a few unsuccessful matings in small containers and a few in large containers; we believe that both rare occurances likely occur under field conditions as well.

and suggests the same space-related relationship as that of *P. hebrus*. More generally, internally feeding caterpillars, including leaf miners and stem borers, are often parasitized at higher levels than those that feed externally (Hawkins and Lawton 1987), and many of these mate immediately upon emergence.

More broadly, the effect of this insect-produced structure on the mating repertoire of an exploiting species reflects a larger pattern. Small-scale habitat modifications can have big effects. The key to the mating success of male *P. hebrus* lies in their ability to access females in cramped quarters. Since females are often choosy in their reproductive choices, this tactic should enhance the ability of the male to control mate choice, and the invasion of shelters may be an act of exploitation competition: the first to make a claim wins the race.

The next time you notice a leaf shelter, gall, bark beetle gallery, wasp nest, spider web, or other small, arthropod-engineered structure, don't forget to think and look beyond the primary occupant, to other occupants as well. These may be tricky to find if they are phenologically or spatially separated from the primary occupant. Our observations suggest that behavioral interactions between pupae and their parasitoids can be influenced by these structures. Community-level changes can occur from insect shelters as well. Wetzel et al. (2016) demonstrated an effect of predatory jumping spiders overwintering in oak apple galls: when galls were removed from trees, herbivore abundance increased by up to 59% over gall-intact control trees. This suggests that the spiders used the galls as shelters while waiting for the emergence of herbivorous prey. Shelters created by one insect during a particular stage of its life history may integrate a great many life history and behavioral modifications across several interacting organisms in the community. That small, often overlooked, but diverse and intricate arthropod creations may have large consequences for other organisms is not a new realization (Robert Marquis and lab have done many excellent studies on caterpillar leaf ties), but should be reiterated and considered in natural history and life history studies. After all, the presence of these leaf rolls turned normally flighty wasps into motionless participants in an excruciating vigil that apparently enhances their reproductive success.

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