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Condition-dependent mate choice of a parasitoid wasp in the field

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Recent studies have emphasized that the choosiness of mate-seeking individuals may differ greatly in response to the size and age of both participants. As haplodiploids, parasitoid wasps provide unusual opportunities for studies of mating preferences, since females can produce male offspring without mating, thus changing the consequences of not mating from the standard diploid model. Few studies of wasp mating systems have examined mating patterns in the field, even though the limited dimensions of laboratory cages may prevent normal search patterns or dispersal ranges and thereby potentially alter mating patterns. We thus investigated several size- and age-related variables that may influence the mate choice behaviour of male and female solitary parasitoid wasps *Alabagrus texanus* (Cresson) (Braconidae) under both field and confined laboratory conditions. In the field, similar numbers of tethered virgin females (1) mated with the first male visitor, (2) rejected the first but then mated with a subsequent male and (3) did not mate at all. Heavy females mated more often than light ones, but male mating success did not significantly differ with male or female mass. Early-arriving males of intermediate mass (and age) obtained the most matings, but the youngest (1-day-old) and oldest males were all unsuccessful. Age-related variance of females did not play a significant role, since they mated immediately after emergence. However, under highly constrained spatial conditions in the laboratory, several of the previously field-resistant females mated despite the limited number of males present, demonstrating the importance of space in the *Alabagrus* mating system.

Recent studies have emphasized the importance of variation in mating preferences by both males and females (Brown & Kuns, 2000; Burley & Foster, 2006; Howard & Young, 1998). Increasing recognition that an individual's own phenotype may be important in mating preferences has resulted in studies demonstrating condition-dependent mate choice (Cotton, Small, & Pomiankowski, 2006; Holveck & Riebel, 2010), the focus of this study.

Studies of mate choice have traditionally focused on female choice, because females' individual reproductive bouts generally involve a much greater investment than those of males (e.g. Trivers, 1972). However, recent studies have emphasized that male choice may often occur under a variety of circumstances (Boivin, 2013; Bonduriansky, 2001; Edward & Chapman, 2011), such as when they are the limiting sex or are subject to sperm limitation. Others have recently recognized the possibility of mutual mate choice (Reid & Baruch, 2010; Salehialavi, Fritzsche, & Arnqvist, 2011).

In this study we wished to determine whether either sex demonstrates condition-dependent mate choice (i.e. nonrandom mating) in the field and whether the results resemble those obtained under the constrained conditions of the laboratory. In particular, we wished to establish whether identifiable segments of the population (large, young, etc.) mated more or less often than expected.

The operational sex ratio (OSR, the number of males and females in the local breeding pool at any given moment) is important in mate choice (Andersson, 1994; Emlen & Oring, 1977). Several factors may affect the OSR: the pattern and total number of emerging adult males and females, the timing and frequency of matings and the adult life span.

Male age, a potentially important variable in mate choice, provides females with a variety of advantages and disadvantages. Older males, by virtue of their prolonged existence, have shown their superior survival abilities but may have depleted their supply of sperm (Boivin, 2013; Lewis, 2004) or acquired deleterious mutations during their adult lifetime (Beck & Promislow, 2007; Carazo, Molina-Vila, & Font, 2011; Hansen & Price, 1999). In contrast, young individuals likely possess adequate numbers of sperm and a minimum of new mutations but an untested genotype. Middle-aged males may offer a compromise between the old and the young (Conrad, Paxton, Barth, Francke, & Ayasse, 2010; Jones & Elgar, 2004). Support thus exists for each alternative, providing no clear a priori basis for making a prediction.

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In contrast, females most likely express mate choice in response to the aggregate of male candidates present in the swarms. Females may favour larger males, as seen in many taxa (Capone, 1995; Partridge, Ewing, & Chandler, 1987), since these males may result in larger and more competitive sons (or grandsons in the case of haplodiploid males; Featherston, Jones, & Elgar, 2013) and more fecund daughters, although this outcome remains equivocal (Prokop, Michakzyk, Drobniak, Herdegen, & Radwan, 2012). Alternatively, females may show condition-dependent choice as seen in the gregarious braconid wasp *Cotesia flavipes*, although not in the solitary *Cotesia marginiventris* (Joyce, Bernal, Vinson, & Lomeli-Flores, 2009).

Parasitoid wasps provide unique opportunities for investigating several aspects of mate choice, although relatively few studies have used them for this purpose (Fauvergue, Lo Genco, & Lo Pinto, 2008; Godfray, 1994; Joyce et al., 2009). Size, age and sex ratios can be readily controlled, and the haplodiploid condition enables female wasps to realize a variable degree of fitness in the absence of an acceptable mate by producing male offspring without mating. Although most work on the mating systems of parasitoid wasps has taken place in laboratories or flight cages, mating patterns are influenced by the spatial location and dispersal of receptive females (Godfray, 1994; Godfray & Cook, 1997; Thornhill & Alcock, 1983). Many solitary male parasitoids must forage for widely dispersed mates within a habitat (Godfray, 1994), and, in addition, males may encounter limited numbers of reproductively available females at any given time (Godfray, 1994; Matthews, Matthews, & Crankshaw, 1979; Paxton, 2005), since females of many parasitoid wasp species mate only once (Godfray, 1994, p. 275; O'Neil, 2001; Thornhill & Alcock, 1983, p. 450). Godfray and Hardy (1993) noted how little is known about the foraging behaviour of haplodiploids in the field (reiterated by Fauvergue et al., 2008).

The solitary parasitoid wasp *Alabagrus texanus* (Braconidae) (Cresson), henceforth *Alabagrus* or wasp, is an ideal candidate to test questions of mate choice under natural field conditions (Morse, 2011). *Alabagrus* is relatively large, locally abundant, brightly coloured, slow flying and easy to handle, all traits that facilitate testing patterns of mating behaviour in the field. Female *Alabagrus* mate only once (S. A. Adams & D. H. Morse, personal observations), usually immediately after emergence as adults (Goh & Morse, 2010), therefore remaining only briefly in the OSR. In contrast, males will mate several times if given the opportunity and thus remain in the OSR for most of their adult lives. Therefore, although the *Alabagrus* population produces many more females than males (ca. 65:35%; Morse, 2011), the OSR almost always remains male biased (Morse, 2011). Goh and Morse (2010) found that male *Alabagrus* regularly make nonstop patrolling flights of 20 m or more in their quest for emerging females and that they seldom search an area soon after the emergence of a female there. Thus, male *Alabagrus*'s normal search patterns routinely cover hundreds of square metres and thus invite comparisons with studies conducted in confined laboratory spaces or flight cages.

The chemical cues produced by an emerging female *Alabagrus* wasp (Goh & Morse, 2010) create male swarms whose individuals engage in scramble competition (Alcock et al., 1978; Andersson, 1994), lowering the probability of male mate choice (Kokko & Johnstone, 2002) but not eliminating that possibility. However, if males do show mate choice, they should prefer larger, and likely more fecund, females (Eggleton, 1990; Joyce et al., 2009). Hypothetically, individual males in a swarm might also vary their effort to mate in response to characteristics of the female.

Since female *Alabagrus* typically mate once, usually immediately after emergence (Goh & Morse, 2010), males normally encounter little variation in female age; thus, this factor should not usually affect male mate choice. Among species of parasitoid wasps that do not mate upon emergence, younger females generally attract more males (Godfray, 1990; Steiner & Ruther, 2009).

In this study, tethering experiments in the field revealed a more complex pattern of mating behaviour in *Alabagrus* than previously predicted. Comparisons between field and laboratory mating experiments showed that the space and specific environment in which mating occurs can strongly influence the mating behaviour of female *Alabagrus*, illustrating the importance of studying mating behaviour in the natural environment and suggesting an important role for sexual conflict.

METHODS

Study Area

We conducted this study in an old field of 3.5 ha at the Darling Marine Center, South Bristol, Lincoln County, Maine, U.S.A. (43°57′N, 69°33′W). The study site, approximately 0.3 ha within the field, surrounds two adjacent, intermittent streams and contains a dense stand of sensitive fern, *Onoclea sensibilis* L. (Dryopteridaceae), averaging 45–60 cm in height (Morse, 2009). The study area is bordered on two sides by higher-lying areas of grasses and forbs, and on the other two by mixed coniferous–deciduous forest. The field is mown in October, but is otherwise unmanaged.

Organisms

We briefly describe the life cycles of the solitary parasitoid wasp, *Alabagrus texanus* (Cresson) (Braconidae), henceforth *Alabagrus* or wasp, and its primary (and probably only) host in our study area, the fern moth, *Herpetogramma theseusalis* (Walker) (Crambidae), henceforth *Herpetogramma* or moth (Morse, 2011). Larval *Herpetogramma* emerge from the leaf litter in early June as middle-instar larvae. These larvae climb to the tips of young fern fronds, which they notch, bend and form into round shelters. Feeding on the innermost layers of these shelters, they continue to grow until pupating in early to mid-July. After approximately 12 days, the adult moths eclose, mate and place their eggs in the shelters and on the undersides of the lower fern pinnae. The resulting second-generation moth larvae hatch in late July to mid-August and feed in the shelters and lower pinnae of the ferns.

Alabagrus, a striking red and black species of approximately 1.5 cm in length, searches for and oviposits in young moth larvae during late summer, parasitizing 40–70% of its hosts (Morse, 2011). The resulting young wasps subsequently overwinter as early instars inside their hosts until the hosts reach approximately 50–60 mg in late June–late July (Rose & Morse, n.d.). At this point, the wasp larvae start growing rapidly, emerging when their hosts have reached the prepupal stage. Pupating soon after emergence, the wasps eclose from mid-July to mid-August, with males preceding the females by a few days. Females outnumber males by nearly two to one, but the operational sex ratio is usually strongly male biased, due to the extended reproductive life of the males and the tendency for females to mate only once, usually immediately after eclosion.

Individuals Reared

We collected moth larvae and pupae from sensitive fern shelters from mid-June to late July and reared out the male and female wasps used in our experiments. We placed larvae and pupae individually in 7-dram vials (5 cm tall, 3 cm diameter), providing fresh fern fronds to the larvae every other day under ambient light and temperature. We retained the resulting pupae in these vials until eclosion. All eclosed wasps were sexed, placed in a 7-dram vial (5 cm tall, 3 cm diameter) and weighed to the nearest 0.1 mg