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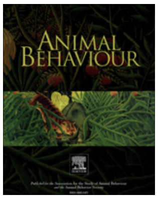

Male mate search for female emergence sites by a parasitic wasp

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To evaluate the use of spatial and temporal information in dictating quantitative search patterns, we investigated the male mate-searching behaviour of a braconid wasp, *Alabagrus texanus*. Specifically, we asked whether these individuals use recently acquired information when establishing their use of space during searching routines. Males find virgin females by patrolling the habitat for pheromone cues, with scramble competition following. To simulate emergences, we placed just-eclosed females in fine-meshed bags that permitted pheromones to disperse. Upon presentation, male swarms formed, reaching maximum numbers within the first few minutes. Males subsequently left the swarming site, and few revisited. Females were removed after 5 min and replaced by a second female. Male numbers remained low, but when the second female was then presented 15 m away, she attracted many males. Repeating the initial experiment with a hiatus of 30 min between first and second females, the second female attracted few males, but with a hiatus of 60 min between females, the second female attracted many males. There was no increase in the number of males that responded to a second female presented closer than 5 m from that of the first female. Wasp emergence patterns revealed that more than one female seldom eclosed within a diameter of 5 m on the same day. Thus, males show short-term memory of space and time that decreases their attention to sites that are unlikely to yield a mating.

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Males have evolved many mating strategies that maximize reproductive success under different conditions (Bateman 1948; Wade & Arnold 1980). Sites of contact with females vary from leks (traditional mating areas), to which females are recruited, to widely spaced territorial or emergence sites (Thornhill & Alcock 1983; Andersson 1994; Shuster & Wade 2003). Males may fight for control of these sites; however, defence of some sites becomes infeasible because of the large numbers of competitors, excessive energy required for defence, or risk of injury, any of which may outweigh the benefits (Thornhill & Alcock 1983; Eggleton 1990).

When and where females become reproductively available presents an important problem for males: should they inspect or defend widely spaced sites? Information about whether virgin females' spatial and temporal distributions of appearances are clumped, random or evenly spaced should greatly enhance a male's searches for females, as should the scale of these patterns and the intensity of competition from other males. Briefly, a clumped distribution increases the probability that another female will emerge from a site, a random distribution does not affect the probability that another female will emerge from a site, and an evenly spaced distribution decreases the probability that another female will emerge from a site. With knowledge that a female has recently emerged from a site, the related probability of a second individual emerging from that site will differ with the type of distribution shown by females in the population. On the basis of the distribution, a clumped distribution would be more likely to generate a rapid return than would either an evenly spaced distribution or a random distribution.

We asked whether males use knowledge of recent appearances of virgin females to establish their spatial and temporal search regime, and tested whether the results permit a quantitative estimate. We used male braconid wasps, *Alabagrus texanus* (Cresson), which engage eclosing females in swarms, a phenomenon referred to as scramble competition polygyny (Emlen & Oring 1977; Thornhill & Alcock 1983). Scramble competition polygyny is understudied (Andersson 1994; Morse 2007), in spite of its likely ubiquity in many insect groups (Thornhill & Alcock 1983; Seidelmann 1999). Explicit spatiotemporal memory is seldom reported among insects (Robacker et al. 1976; Villagra et al. 2008).

To establish this relationship, we measured the frequency and distribution of female eclosions and the number of males in the study area, which permitted predictions about the search behaviour of males. We then tested these predictions with field experiments that evaluated the male wasps' spatial and temporal responses to newly eclosed females, as well as several other potential stimuli. To date, much of the quantitative work on these issues has been conducted in laboratory and flight cages. However,

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we conducted our observations and experiments in the field, so the spatial constraints and artificially high pheromone levels likely to be experienced under confined conditions were absent in our study.

These experiments allowed us to measure the recruitment and subsequent dispersal behaviour of male wasps at female emergence sites. When female emergence is distributed evenly or randomly in space, the temporal distribution of eclosed virgin females is predicted to be longer than when female emergence is clumped in space (Thornhill & Alcock 1983). Thus, if searching males learn the distribution of recent eclosions, we predicted that they would avoid sites with evenly or randomly spaced patterns of female emergence immediately subsequent to a female emergence, especially at sites with evenly spaced temporal distributions. Males may also predict the size of the avoided area based on past eclosions.

Few studies have tested whether male insects can learn critical spatial and temporal information that enhances mate search (but see Robacker et al. 1976; Villagra et al. 2008). However, of those tested, male parasitoids show learning abilities comparable to those of the much better studied females searching for hosts (Takasu et al. 2007), a roughly analogous foraging problem (see Stephens & Krebs 1986). Furthermore, several other braconid wasps show similar swarming behaviour (e.g. Southwood 1956; Antolin & Strand 1992). Traditionally, species without a central foraging problem, such as social bees or sphecid wasps recruiting to a nest (Tinbergen 1951; von Frisch 1967), have been assumed to search using simple resource-based cues (Nicholson 1933; Stephens & Krebs 1986), rather than spatial and temporal memory.

Males that eschew the site of a recent eclosion might simply be responding to a cue related to that eclosion, perhaps an odour left at the time of that event. However, if their avoidance resulted solely from experience (spatial and temporal memory) rather than a chemical cue, males from the original swarm attending the eclosion should eschew such a site, but those without that experience should not hesitate to visit. Although swarms sometimes consist of 30 or more males, not all individuals attend each eclosion event (personal observation). Thus, we predicted that the reduction or decline in the number of males visiting an eclosion site over time results from experience rather than a total absence of chemical cues.

In this study we thus asked whether mate-searching *Alabagrus texanus* wasps use knowledge of recent emergences of virgin females to set their short-term search patterns. We predicted that if they do use such cues, they should modify their search patterns in response to these emergences, lowering their visits to sites of recent emergences on the basis of known emergence patterns of females.

METHODS

Study Area

The study site consisted of a low-lying area of approximately 3000 m^2 surrounding two adjacent, intermittent streams in an old field of 3.5 ha at the Darling Marine Center, South Bristol, Lincoln Co., Maine, U.S.A. (43°57′N, 69°33′W). It contained a dense stand of sensitive *Onoclea sensibilis* L. (Dryopteridaceae) and marsh *Thelypteris palustris* Schott (Thelypteridaceae) ferns averaging 45–60 cm tall. The site was bordered on two sides by higher-lying grassland containing several species of forbs and by mixed coniferous–deciduous forest on the other sides. At the time of this study, the field was regularly mowed in October, but was otherwise unmanaged (Morse 2009).

Subjects

Alabagrus texanus (Cresson) (Braconidae) is a showy black and red parasitoid wasp, approximately 1.5 cm long. Female *A. texanus* oviposit in young moth larvae, and the larval endoparasitoids overwinter inside the developing host (koinobionts: Askew 1971; Godfray 1994). The fern moth *Herpetogramma theseusalis* (Walker) (Crambidae) is the most important (and perhaps only) host in our study area (Morse 2009). The moths, which fly from mid-July to late August at this site, lay their eggs inside shelters (see below) or on the underside of the lower pinnae of ferns. Upon emerging from the litter in the spring, fern moth larvae climb to the tops of new fern fronds, which they notch and bend into shelters (Ruehlmann et al. 1988). Although these shelters are not conspicuously clumped, they are often dense (D. H. Morse, unpublished data). Many (>30–70%) of these shelters are occupied by moth larvae parasitized earlier by *Alabagrus* (Morse 2009). Given the female-skewed sex ratio of *Alabagrus* (Morse 2009), 20–40% of these shelters contain female *Alabagrus*. Fern moth larvae hatch in August and feed in the shelters on still-living fern tissue or on the exposed pinnae, during which time they become susceptible to ovipositing *Alabagrus* wasps. In the following year, the wasp larvae emerge from the last larval stage of their hosts, then pupate and eclose from mid-July to late August (Morse 2009).

We conducted observations of wasps during both the morning and afternoon, recording the times that males spent flying and perching for a maximum of 5 min or until they flew out of sight. We also recorded all occurrences of female emergence as well as males' subsequent behavioural responses. During female eclosion, males typically fly continually over the ferns, intermittently landing on the fronds. When a female begins to eclose, males congregate at the female's incipient emergence site, presumably attracted by the female's pheromones. After the female mates with one of the males (i.e. the winner of an intense scramble competition), these aggregations quickly disperse, and the males return to searching until the next female ecloses.

Background Data

We censused the numbers of wasps flying across or along a 1 × 80 m census strip in the study area on every second or third day of the experimental period, which coincided with the main period of female eclosion. At this time, females are primarily confined to the fern canopy (D. H. Morse, unpublished data). Thus, these counts consisted almost entirely of males, allowing us to relate the size of the male population to the eclosion pattern of the females.

To evaluate patterns of female eclosion in time and space, we covered shelters at four sites with 10 × 20 cm nylon tricot bags (25 shelters at each of three sites, 100 at the fourth), which we checked daily for emergences. All sets were separated from each other by more than 15 m, with individual diameters of less than 5 m.

The wasps used in experiments were collected as pupae from shelters in the study area, placed in 7 dram vials (5 cm tall, 3 cm diameter), and reared to eclosion under ambient light and temperature. We recorded the emergence dates and weights of these wasps and used them in field experiments within a day of eclosion, subsequently releasing them at their collection site.

Experiments

Based on our observation that male swarms disperse relatively rapidly once a newly eclosed female is mated, we attempted to ascertain how aggregations form and dissipate. To assess the attraction of males to newly emerged virgin female wasps, we

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