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Initial responses to substrates by naïve spiderlings: single and simultaneous choices

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Whether foragers encounter resources sequentially (one at a time) or simultaneously has received relatively little explicit attention, given its potential importance for success. Here I evaluate the efficiency of naïve spiderlings *Misumena vatia* (Thomisidae) in exploiting hunting sites presented in these two ways. The spiderlings significantly preferred goldenrod (*Solidago canadensis*) inflorescences over aster (*Aster umbellatus*) inflorescences, both when these blooms were presented to them one at a time and simultaneously, if they were in physical contact with these blooms, a result that matched the numbers of prey these flowers attract. However, they accepted goldenrod significantly more frequently one at a time than in simultaneous presentations. Even when their substrates were then switched in a reciprocal cross, spiderlings favoured goldenrod over aster, although those moved from goldenrod to aster responded significantly more strongly (negatively) than did the reciprocal crosses. However, spiderlings did not distinguish between goldenrod and aster inflorescences simultaneously presented 10 cm away, and only two-thirds of them managed to recruit via lines to either of the flowers. They responded similarly to two-goldenrod inflorescences or two-aster inflorescences as to mixed goldenrod–aster pairs, and they recruited roughly half as often to a single inflorescence of either species as to pairs. At 50 cm, less than one-fifth recruited to the mixed substrate. Thus, the spiderlings first recruit to a site and then accept or reject it, a time-consuming activity. Costs in time for making simultaneous choices exceed those for one-at-a-time choices, due to their lower success rates in recruiting to the more profitable species.

Foragers' initial responses to resources may be affected by how they encounter and perceive them. Since foraging repertoires often determine their eventual success in resource exploitation and, ultimately, their lifetime fitness (Morse & Fritz 1987; Blanckenhorn 1991; Morse & Stephens 1996), it is important to establish the basis for these patterns. Individuals may experience new substrates either one at a time (sequentially) or multiply (simultaneously), a variable that has only intermittently received direct attention in the foraging literature (Stephens & Krebs 1986; Stephens et al. 1986). Organisms with different learning and perceptual abilities are likely to respond differently under diverse environmental conditions (Balda et al. 1998; Dukas 1998a). Furthermore, the range of environmental variables encountered by most foragers is great enough, and the predictability of opportunities problematic enough, to suggest that environmental factors will often affect the differences in choice expressed (Papaj & Lewis 1993). Eventual adult choices could thus be influenced by differences in previous experience and resultant learning. However, standard models of resource exploitation (prey choice, patch choice, etc.) do not incorporate learning (Dukas & Real 1993; Dukas 1998b).

Most efforts dealing with the discovery of resources have assumed a sequential order of encounters (see Stephens & Krebs 1986), and have not compared the animals' responses to both sequential and simultaneous options. However, many preference tests in behaviour and ecology offer two or more items simultaneously (e.g. Alcock 2001), a procedure that may not reflect the usual way in which such items are encountered. Although this test design may provide qualitative information on a subject's preferences, extrapolation to real-world equivalents may be problematic, particularly if quantitative conclusions are to be drawn from them. If perceptual capabilities are particularly strong relative to the patchiness of the environment, responses to simultaneous presentations should be well developed, but if such capabilities are minimal, responses to options that present items one at

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a time may provide their only option. Not all organisms respond similarly if presented with both sequential and simultaneous problems (e.g. Stephens & Krebs 1986; Read et al. 2001), and the costs of the two alternatives are likely to differ with the context.

The issue of sequential and simultaneous choice in resource acquisition has been well developed in the marketing literature (Simonson 1990; Ratner et al. 1998; Read et al. 2001), and conclusions developed there warrant comparison with natural systems. In particular, when presented with simultaneous choices, human subjects show considerably more variability than with sequential choices. Selections made under simultaneous choice were poorer than those made under sequential choice. Some workers have suggested a possible long-term advantage for this response associated with sampling for the future (Simonson 1990; Ratner et al. 1998; Read et al. 2001), a factor bearing close resemblance to Heinrich's (1979) concept of 'majoring' and 'minoring', in which relatively unprofitable items may prove to be valuable later in the season. Read et al. (2001) suggest that a long-term advantage of variable choice in simultaneous presentations might lie in risk aversion, as in playing the stock market safely.

Mate choice also bears many similarities to foraging choice, and the analogy of foraging for mates is appropriate where search constitutes a major aspect of mate choice. As Andersson (1994) notes, in the systems most frequently studied from a mate-choice perspective, lekking systems, females have the opportunity to use simultaneous choice. However, females of many species are more likely to encounter prospective mates sequentially, a situation that has received considerably less attention, with a particular dearth of invertebrate examples (Parri et al. 1997).

Animals vary greatly in their tendencies towards risk adversity or proneness, a likely consequence of both their phylogeny and the circumstances they are experiencing (Caraco et al. 1980; Stephens & Krebs 1986), and this information could affect their responses to sequential and simultaneous-choice situations. Alternatively, relative performance in sequential and simultaneous tests could reflect their limited ability to process large amounts of information simultaneously (Dukas 2002), with the consequence that decisions are more likely to be impaired in simultaneous than in sequential experiences.

The crab spider *Misumena vatia* (Thomisidae), a small sit-and-wait predator on flowers (Morse 1979; Morse & Stephens 1996), provides an excellent opportunity to investigate sequential and simultaneous choice as they relate to substrate patch choice, learning and perception. Females lay single, large clutches of eggs in July or August that can be collected and the resulting naïve young exposed subsequently to various sets of environmental variables relevant to their development as effective foragers. In northeastern North America young *M. vatia* usually emerge in mid- and late summer to hunt on goldenrod (*Solidago* spp.) (Morse 1993a, 2000a), but they also occupy asters (*Aster* spp.). Since goldenrods and asters differ considerably in floral architecture and also in the number of potential prey they attract, they offer a natural opportunity to examine factors associated with patch choice. Finding and selecting high-quality hunting sites are essential skills for the spiderlings at this time, as they are particularly vulnerable to starvation (Vogelei & Greissl 1989; Morse 1993a).

Spiderlings are highly responsive to their substrate, and this factor alone suffices to dictate whether newly emerged individuals will remain or quickly disperse (Morse 1993a, 2000a). After leaving their natal nest sites (leaves), naïve spiderlings depart rapidly from substrates resembling these sites, which provide minimal foraging opportunities (Morse 2000a). They show strong preferences for goldenrod flowers and retain these patterns when subsequently exposed to the same substrate, showing little tendency to habituate to other sites during daily exposures over a 5-day period (Morse 2000a). On a short-term basis, at least, the actual presence of prey does not heavily influence this behaviour, as it does in the adult females (Morse & Fritz 1982; Morse & Stephens 1996). However, spiderlings respond more rapidly to prey after experience with them (Morse 2000b), as they do to a substrate successively presented to them (Morse 2000a). These results suggest a modest ability to respond to contact or close-range stimuli, which enhances their ability to select some sites over others, these being ones that attract superior numbers of potential prey. Furthermore, they improve their response to prey as a result of contact to them. The spiderlings face a variety of other challenges, however, including the choice of substrates, both on contact and from a distance. Previous experiments did not provide the spiderlings with alternative substrates for comparison or compare their ability to select these substrates when presented sequentially and simultaneously. Their ability to perceive and to respond to these variables will play a major role in how the spiderlings will exploit potentially available resources. The experiments reported here tested those variables.

Here I address the following questions: (1) do the spiderlings make innate choices between goldenrod and aster flowers, and (2) do their choices change with shifts in the substrate presented to them? (3) Does their ability to select high-quality substrates (patches) differ in sequential and simultaneous-choice situations, both on contact and from a distance? The distance factor is potentially important, because it will affect the spiderlings' proficiency at finding favoured substrates in the first place. The shifts in substrate further provide insight into the effect of differentially rewarding sites in aversive learning.

METHODS

Study Area

I performed this field work during August 2001–2003 at the Darling Marine Center of the University of Maine, South Bristol, Lincoln Co., Maine, U.S.A., in a 3.5-ha old field surrounded by mixed coniferous–deciduous forest. The field, mown yearly in October, contained several grasses (Gramineae), and the main forbs flowering during late summer when *M. vatia* spiderlings were emerging