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The effect of experience and rearing environment on the behaviour of crab spiderlings during their first weeks of life

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Abstract

To examine (1) the effect of experience and rearing environment on learning and behaviour over time, and (2) when (or if) newly-emerged young begin to incorporate experience into their choices, we compared the activity levels and hunting-site preferences of newly-emerged laboratory and field-reared crab spiders (Misumena vatia (Clerck, 1757)). We split spiderlings from eight broods into cohorts (1) released on goldenrod (Solidago canadensis) in the field and (2) retained individually in the laboratory, but provisioned with Drosophila melanogaster. We then tested both field-retrieved and laboratory-reared individuals at days 3, 7, 14 and 21 for their (1) rate of activity in cages over 15 min and (2) choice of either goldenrod or wild carrot (Daucus carota), two frequent hunting sites in the field. The rearing environment clearly influenced the spiderlings' activity levels: field-reared spiderlings became more active than laboratory-reared spiders over time; however, their choice of flowers did not change, even though their experience differed. Thus, innate mechanisms dominated the spiders' early hunting-site choices, and experience only informed their decisions at later stages in ontogeny. The spiders may, therefore, have multiple mechanisms for learning that begin to operate at different times, since spiderlings improve their locomotor performance through experience, while failing to use early experience in choosing hunting sites at this early point in ontogeny.

Keywords

activity, age, flower choice, innate behaviour, laboratory rearing, locomotor performance, *Misumena vatia*.

1. Introduction

Rearing environment can have a profound effect on the development of behavioural traits in arthropods (Papaj & Lewis, 1993; Herberstein, 2011). For

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example, rearing temperatures affect several components of cricket song (Olvido & Mousseau, 1995; Olvido et al., 2010), and light conditions in the rearing environment can influence courtship behaviour in *Drosophila* (Barth et al., 1997a). Rearing environment affects insect brain development (Barth et al., 1997b; Snell-Rood et al., 2009). Several spiders and insects can modify their behaviour in response to previous experience (e.g., Dukas & Bernays, 2000; Nakamura & Yamashita, 2000), a trait with potentially important fitness consequences. For instance, associative learning in grasshoppers enhanced their ability to identify a superior food source, resulting in an increased growth rate (Dukas & Bernays, 2000). Individuals that initially depend completely on innate responses to certain stimuli may subsequently incorporate information gained from experience into their repertoire (Bateson, 1983; Papaj, 1993).

Laboratory-reared animals are often used in studies on the role played by experience in the development of a behavioural repertoire, even though the behaviour of laboratory-reared subjects may not match that of their wild counterparts (Carducci & Jakob, 2000). Different conditions experienced by subjects in the laboratory and field might lead not only to different behaviours, but also to different levels of success. Evaluating the possible effects of captivity on arthropod learning and development, a seldom-explored topic (Carducci & Jakob, 2000; Dukas & Mooers, 2003), provides insight into the more general issue of the role of environment in learning and behaviour.

The crab spider, *Misumena vatia* (Clerck, 1757) (Thomisidae), a small sit-and-wait predator on flowers (Morse, 2007), provides an excellent opportunity to evaluate the effects of rearing environment and experience on arthropod learning and behaviour. Females lay a single large clutch of eggs in July or August, and the resulting young can be easily reared in the laboratory. Females usually mate only once under normal field conditions (Morse, 2010a). Thus, brood mates are almost certainly full sibs. The spiderlings can be dyed and released into the field, facilitating observation and subsequent collection without any apparent effects on predation rate or behaviour (Morse, 1993).

Previous studies have shown that adult foraging success has significant fitness consequences for this species, with choice of a high-quality hunting site playing the largest role (Morse & Stephens, 1996; Morse, 2007). Both previous experience with a flower species and prey capture experience at hunting

sites affect adult choice (Chien & Morse, 1998; Morse, 2000a), and experience as a late-instar juvenile can influence adult hunting-site choices (Morse, 1999). Laboratory-reared spiderlings, which have no experience in choosing hunting sites or capturing prey at those hunting sites, might therefore exhibit different behaviour and hunting-site preferences than their field-experienced sibs, a difference that may provide an opportunity to examine how these behaviours develop.

Over the first few days after emerging, spiderlings display strong innate preferences for goldenrod (*Solidago canadensis*) over wild carrot (*Daucus carota*) (Morse, 2005) and for goldenrod flowers over goldenrod buds (Morse, 2000a). Preliminary data also suggest that older juveniles (fourth and fifth instar) raised in the laboratory may make different flower choices from similar- aged juveniles captured in the field (Morse, 2007). Thus, although previous experience with flowers or prey does not affect second-instar spiderlings, these factors play a critical role later in life. Therefore, when does experience first impact foraging decisions? Comparing naïve laboratory-reared spiders to their free-ranging sibs in the field over time provides a way to explore this question, simultaneously allowing us to address the effect of captivity on behaviour.

We tested the effect of different rearing environments on learning and behaviour by comparing spiderlings reared in the field to spiderlings from the same broods reared in the laboratory. We repeatedly compared the spiderlings over a period of up to three weeks, investigating two aspects of their behaviour: level of overall activity and flower choice. We predicted that if rearing environment affects the development of sensory and motor capabilities of the central nervous system, or if learning and practice are necessary for the development of perceptual or locomotor skills, spiders reared in the laboratory would be less active than their field-reared counterparts. We also predicted that if previous experience with flowers or prey capture on flowers affects spiderling flower preference, the field-reared spiders would exhibit different, or stronger, preferences than the laboratory-reared spiders.

2. Materials and methods

2.1. Collection of spiders

During early summer we collected large, gravid adult female crab spiders from fields and roadsides of Bristol and South Bristol, Lincoln Co., Maine

(centred at 43°57′N, 69°33′W). We maintained the females in round 7-dram vials (5 cm long, 3 cm diameter) and fed them moths and other insects on alternate nights. When eight of these spiders were ready to lay (they repeatedly refused food), we placed them in the field on common milkweed (*Asclepias syriaca*) plants, their favoured nest site (Morse, 1990), and covered the plant with a loosely fitting nylon tricot bag to prevent them from escaping and to prevent subsequent parasitism or predation of the resulting eggs. Field-rearing insures a maximum probability of success and natural condition of the offspring for these experiments (Morse, 2007).

When the spiderlings began to emerge about 26 days later, we brought the nests into the laboratory, separating each spiderling of the eight broods into individual vials. At least 12 spiderlings from each brood were weighed individually and their carapace widths measured. Spiderlings were also weighed when tested at one and two weeks (see below).

2.2. Care and handling of laboratory and field-reared spiders

A subset of spiderlings from each brood was given initial activity level and flower choice trials (described below) to measure baseline activity and flower preferences and then released outside the study area to prevent resampling. Subsequently, we randomly divided the remaining spiderlings into laboratory and field groups and marked them by lightly dusting them with red micronite dye (Morse, 1993). The number of spiderlings placed in the laboratory and field groups varied between broods as a result of the differences in brood size. We released as many spiderlings as possible in order to enhance the chances of capturing adequate numbers for experiments in the later weeks. One brood (Brood 4) only contained enough individuals to permit use in initial (Day 0) trials. In all we released 415 spiderlings (59.3 \pm 6.14 SE per brood, excluding Brood 4, as noted above).

We maintained laboratory-reared spiders at normal day length in 7-dram vials, fed them a *Drosophila melanogaster* (circa 1 mg) every other day, and provided them with dampened toweling as a water source. This feeding regime approximates the intake of small prey frequently observed in the field (Morse, 1993). Although *Drosophila* have been frequently recognized as substandard food for spiders (e.g., Mayntz & Toft, 2001; Wilder & Rypstra, 2008), early-instar *M. vatia* fed *Drosophila* grow at rates comparable to those of wild individuals (Morse, 2000b, 2010b). Second and third-instar *M. vatia* provisioned on *Drosophila* grew and moulted slightly (though not

significantly) slower than spiderlings captured on goldenrod and feeding primarily on dance flies: Empididae) (Morse, 2010b).

We released the spiderlings of the field group on the day following the initial activity level and flower choice trials (treated as Day 0), placing them on clones of goldenrod *Solidago canadensis* containing enough inflorescences to provide adequate hunting space and separated by at least 2 m from any cluster holding another brood, thereby minimizing the chance that broods would mix. We first removed any other spiders from the site and then distributed the spiderlings evenly over the inflorescences, with a maximum of seven individuals per inflorescence, well within the maximum numbers naturally found in this habitat. We then numbered each inflorescence onto which we had placed spiderlings.

We retrieved individuals from the Field group on days 3, 7 and 14 (and a remaining few on day 21) of the study, occasionally delayed by a day due to inclement weather that interfered with trials. Spiderlings were gently shaken out of each inflorescence onto a white sheet, examined by eye and under a microscope for traces of dye and, if marked, used in that day's trials. Fragments of dye often adhered to the mouthparts of moulting individuals, facilitating their identification in the following instar (D.H. Morse, personal observation). Unmarked individuals were released away from the study site. We subsequently redyed the tested spiderlings and returned them to their previous site.

As the goldenrod inflorescences began to senesce it became necessary to move the spiderlings to later-flowering clones. To minimize disturbance, we made all transfers at the end of a trial day.

We placed a subset of Brood 7 on wild carrot, using the same procedure as described for goldenrod. We retrieved these spiderlings on Day 3 only, since all but one had dispersed by Day 7.

2.3. Trials

2.3.1. Activity level trials

All activity level trials took place in the field under sunny conditions on days 0, 3, 7 and 14 of the study. We usually ran four laboratory-reared spiderlings and four field-reared spiderlings each day of testing. We placed each spiderling in a $30 \times 30 \times 30$ cm mesh-covered cage, gave it 5 min to acclimate to the cage and then recorded its movements for 15 min (900 s), tallying the number of seconds, out of a possible 900, that it spent moving

about within the cage. We used the cages to ensure that we did not lose any of the spiderlings.

2.3.2. Flower choice

We conducted flower choice trials under natural light and calm to an occasional light wind, using fresh stems of goldenrod and wild carrot. We secured one inflorescence of goldenrod and wild carrot in a plastic container, with a stem of grass equidistant between them, each approximately 4.5 cm from the central stem, alternating the positions of the two flowers. If necessary, we trimmed the goldenrod to equalize the flowering surface area of the two.

On days 0, 3, 7 and 14 of the study, we tested between 5 and 20 naïve laboratory-reared spiderlings and between 5 and 20 field-reared spiderlings from the same brood. The results also include a small number of individuals at 21 days. We ran as close to 20 spiderlings as possible from each group. Numbers varied because of the differing numbers of spiderlings from each brood and numbers that we could recapture from the field. Numbers thus decreased as the study progressed.

We placed each spiderling on the central grass stem at the start of a trial and recorded its location after 5, 10, 15, 30 and 120 min. After a spiderling moved onto a flower, we recorded its choice and returned it to its vial. If time allowed, we continued to observe spiderlings that remained on the central stem for longer than 120 min. We sometimes reused unvisited flowers between trials, but always replaced the middle grass stem.

We released all laboratory-reared spiderlings outside the experimental area after each set of flower choice trials, since we no longer considered them to be naïve. After the trials we returned field-reared spiderlings to their previous sites. We never used spiderlings in both activity level and flower choice trials on the same day.

We realize that release of the field-reared spiderlings to their previous sites may have resulted in some spiders participating in trials on multiple test days. However, earlier work (Morse, 2000c) led to serious concern whether we could otherwise obtain adequate numbers of known, field-experienced individuals for the experiments. We reasoned that since these experiments resembled the usual experiences of spiderlings reared in the field, previous testing would not affect their performance; however, the true N values may, therefore, fall somewhat below the ones stated. Consequently, we have adopted an alpha of 0.01 for tests involving the field-reared individuals.

2.4. Analysis

We used parametric analyses wherever the data satisfied the appropriate assumptions. Elsewhere, we used nonparametric equivalent tests.

Initially we compared the activity levels of the field and laboratory-reared individuals at 3, 7 and 14 days with a *t*-test for the difference between two means. Those at 0 days were not included in this analysis, since the rearing environment of the two groups did not differ prior to day 0. We then compared the effect of the three basic variables (rearing site, brood, day) on activity levels with a three-way ANOVA.

For the flower choice trials, we initially compared the contributions of rearing site, brood and day to flower choice with a logistic regression. We then compared the summed choices of the spiderlings with binomial tests and the differences in flower choice between field and laboratory-reared individuals with a Fisher exact test.

We also conducted a post-hoc analysis of time to choose. We examined the effect of rearing condition, eventual flower choice, and brood on time to choose with a three-way ANOVA. We then used *t*-tests to compare time to choose between spiderlings choosing goldenrod and those choosing wild carrot, both within and across rearing conditions. We also compared differences by brood between choice time and activity level with a Spearman rank correlation, and proportions of choosers and non-choosers by brood with a χ^2 likelihood ratio. As with the activity level trials, the comparison of overall choice between field and laboratory-reared spiders excluded day 0.

Differences in mass of field and laboratory individuals at one and two weeks were calculated with *t*-tests for paired samples. All variance estimates are reported as standard errors of the mean (SE).

3. Results

3.1. Activity level trials

We ran activity level trials on 169 spiderlings over the course of the experiments (We discarded three other individuals because of timer malfunction). Forty-nine spiderlings were tested on Day 0, prior to being split into laboratory and field-reared groups. Fifty-nine field-reared and 61 laboratory-reared spiderlings were tested across subsequent dates. Combining across days, field-reared spiderlings tested on days 3, 7 and 14 spent nearly half again



Figure 1. Time spent moving on natural substrate in the field by spiderlings of different broods during 15-min (900 s) trials, \pm SE.

as much time moving as laboratory-reared spiderlings (145.05 ± 13.39 s, N = 59, vs. 99.25 ± 11.19 s, N = 61; $t_{118} = 2.63$, p = 0.0097).

A three-way ANOVA comparing activity levels of these spiderlings (time spent moving) on days 3, 7 and 14 showed significant effects of both rearing site (field or laboratory-reared) and brood on activity level ($F_{9,108} = 2.71$, p = 0.0069; rearing site: $F_{6,119} = 8.66$, p = 0.0041; brood: $F_{6,119} = 3.02$, p = 0.0097: Figure 1); but day of trial had no significant effect ($F_{2,119} = 0.014$, p = 0.90), because the field and laboratory trends changed in opposing directions, thereby cancelling each other. Although time spent moving appeared to increase in subsequent trials by the field-reared spiderlings and to decrease in the laboratory-reared spiderlings (Figure 2), the small number of remaining individuals did not suffice to yield a clear result. None of the interaction terms were significant.

3.2. Flower choice trials

3.2.1. Flower choice results across all broods and days of trial

We ran 632 flower choice trials. Of these, 269 individuals chose goldenrod, 192 chose wild carrot, and 125 did not move onto either of the flowers within the 2-h period (an additional 46 individuals were lost or moved off the inflorescence).

A nominal logistic regression of choice by brood, day of trial and rearing condition (field or laboratory) revealed no significant effect of any of these factors on the spiderlings' choice of flowers ($\chi_{13}^2 = 11.80$, p > 0.3; brood: df = 7, p > 0.2; day: df = 3, p > 0.7; rearing condition: df = 1, p > 0.2;



Figure 2. Time spent moving on natural substrate in the field by experienced (dashed line) and unexperienced (solid line) spiderlings in relation to time since emergence from nests, \pm SE.

Effect Wald Test/Wald χ^2). Thus, we could safely pool the data from all broods and days of the trials.

Overall, spiderlings that made a choice preferred goldenrod (N = 269) over wild carrot (N = 192, p < 0.001, binomial test). More of the spiderlings tested on days 3, 7, 14 and 21, combined, in both the laboratory-reared and field-reared groups chose goldenrod than wild carrot, though this preference was only significant for field-reared spiders (laboratory-reared: N = 160, p = 0.24; field-reared: N = 182, p = 0.001; two-tailed binomial tests). Although a higher proportion of field-reared spiderlings chose goldenrod than laboratory-reared spiderlings, they did not differ significantly (p = 0.19; two-tailed Fisher exact test).

3.2.2. Time to choose

Since activity level results suggested that differences in time to act might occur among spiderlings, we looked at the effect of rearing condition, resulting flower choice, and brood on time to choose using a three-way ANOVA. The overall model was significant: $F_{27,314} = 2.47$, p = 0.0001. In common with the activity results, these times differed widely among the broods ($F_{6,314} = 6.69$, p < 0.0001; brood means 28–77 min, overall mean = 40.48 ± 15.56 min, excluding non-responders).

Also, an interaction effect occurred between rearing condition and flower choice on time to choose: $F_{1,314} = 6.61$, p = 0.011. Exploring this interaction, we found that field-reared spiderlings chose goldenrod more quickly than wild carrot ($t_{169} = 2.39$, p = 0.018), but laboratory-reared spiderlings did not differ in time to choose goldenrod and wild carrot ($t_{153} = 0.84$, p = 0.40). Further, field-reared spiderlings chose goldenrod more rapidly than laboratory-reared spiderlings chose goldenrod ($t_{190} = 2.27$, p = 0.024), but the two groups did not differ in the time required to choose wild carrot ($t_{132} = 1.05$, p = 0.30). These results suggest that field-reared spiderlings did obtain information that allowed them to act on their preferred goldenrod flowers more rapidly than those choosing wild carrot.

We also compared the time required to make flower choices by brood with the level of activity of the different broods. Time for the different broods to choose a flower did not vary concurrently with the activity levels of these broods ($r_s = 0.60$, df = 7, p = 0.51 in a Spearman rank correlation).

3.2.3. Choosers and non-choosers

Numbers of spiderlings failing to move onto either flower species within 2 h (choosers vs. non-choosers) differed among broods ($\chi_7^2 = 55.33$, p < 0.0001; χ^2 likelihood ratio) (Figure 3). Brood 1 occupied one end of the spectrum, in which only 40 of 69 spiderlings (58.0%) made a choice within 2 h (11 additional spiderlings made choices in times greater than 2 h). At the other end, Brood 8, in which 83 of 88 spiderlings (94.3%) made a choice within 2 h (two additional spiderlings made a choice in times greater than 2 h).



Figure 3. Percentage of spiderlings that failed to recruit to flower within 120 min when presented with choice of goldenrod or wild carrot.



Figure 4. Size of spiderlings at 0, 7 and 14 days, \pm SE.

3.2.4. Spiderlings retrieved from wild carrot

Although we retrieved too few spiderlings from wild carrot to analyze statistically (N = 11), their preferences did not appear to differ from the other spiderlings. Seven of the spiderlings chose goldenrod (64%) and four chose wild carrot (36%).

3.3. Increase in mass over test period

We obtained complete data on the mass of both field- and laboratory-reared individuals from six of the broods at 7 and 14 days. Field-reared individuals experienced greater gains in mass than did their laboratory-reared sibs (t = 7.44, p = 0.0007 at 7 days, t = 3.78, p = 0.013 at 14 days) (Figure 4).

4. Discussion

4.1. Activity level trials

We predicted that if experience or rearing condition affected spiderling development and behaviour, then laboratory-reared spiderlings would be less active than their field-reared counterparts. Our findings supported this prediction: rearing condition significantly affected the amount of time a spider spent moving during a cage trial, with field-reared spiderlings spending increasingly more (32–100% across days) time moving than laboratory-reared spiderlings. The tendency of field-reared spiderlings to recruit more rapidly to goldenrod in the flower choice trials also suggests that they learned to act more quickly when presented with their favoured substrate.

4.1.1. Learning locomotor skills

Spiderlings may require a certain amount or range of experience to develop their locomotor abilities to the fullest extent. The environment of the laboratory-reared spiderlings differed from that of the field-reared spiderlings in several ways that might have deprived the laboratory-reared individuals of experience required for learning and developing locomotive skills. Laboratory-reared spiderlings had much less space than field-reared spiderlings. and the vials of the laboratory-reared spiderlings provided a much simpler environment than the field, where the spiderlings experienced a variety of surfaces (leaves, buds, stems and flowers), as well as possible interactions with predators and interspecific competitors. The spiderlings might require experience on a variety of surfaces within a normally encountered space to increase their activity or negotiate more complex, open environments, such as the sites used for activity level trials. Carducci & Jakob (2000) found that adult jumping spiders reared in larger, more enriched environments were more active and performed more flexibly than spiders from smaller, unenriched environments, a pattern widely reported in vertebrates (e.g., Rosenzweig, 1966; Pietropaolo et al., 2004). The increasing activity level of the field-reared group over time suggests that cumulative experience affected the spiderlings' activity level. The rapid rate of growth of the field-reared spiderlings argues against their heightened activity resulting from hunger. We have routinely observed the decrease in activity of other stages of *M. vatia* that we have retained in the laboratory for extended periods of time (Lutzy & Morse, 2008).

The consistent increase in activity of the field group resembles that of other studies of activity in the literature (Edwards & Jackson, 1994; Reid et al., 2010), a characteristic usually attributed to the increased skill associated with practice (Dukas, 2008). Although such a change could simply result from ongoing maturation, our study does not support that explanation because of the simultaneous decrease in activity of the laboratory group. Several studies (summarized in Dukas, 2009: 22) suggest a dominant contribution of learning and a minor contribution of physiological improvement to such performances.

4.1.2. Brood differences in activity level

Brood significantly affected the activity level of the spiderlings, a difference that remained even in the laboratory-reared spiderlings. Since we reared all of the laboratory-reared spiderlings under identical conditions, this result

implies an innate difference in activity among broods. Although seldom noted in studies of spiderlings, we have previously recorded similar amongbrood differences of *M. vatia* spiderlings (e.g., Morse, 2000c, 2005). Fast and slow foragers might be favoured under different conditions, as exhibited by the alternate 'rover' and 'sitter' strategies of *Drosophila melanogaster* larvae (Sokolowski, 1980, 1998).

4.2. Flower choice trials

We predicted that the naïve laboratory-reared spiderlings would not exhibit a clear flower preference, whereas the field-reared spiderlings would develop a strong preference for goldenrod, which attracts significantly more suitable prey than wild carrot (Morse, 2007). However, our results only weakly matched these predictions. Both field-reared spiderlings and laboratory-reared spiderlings preferred goldenrod, though the preference was not significant for the laboratory-reared group. The laboratory-reared spiderlings frequently exhibited a weaker preference for goldenrod than did the field-reared spiderlings, but this trend was not significant. However, over time the field-reared individuals apparently learned to recruit more quickly to their favoured goldenrod: perhaps learning characteristics of these flowers permitted a quick adaptive response. In contrast, laboratory-reared ones did not exhibit this change. The small subset of spiderlings reared on wild carrot preferred goldenrod at the same rate as the other spiderlings.

Thus, over the first few weeks of the spiderlings' lives, innate preferences largely dictated hunting site choices. However, although flower choice did not appear to be learned, the discovery that field-reared spiderlings choosing goldenrod did so more rapidly than either field-reared spiderlings choosing wild carrot or any of the laboratory-reared spiderlings suggested that the spiderlings did learn something from their experience. As a consequence, they might maximize their rate of food intake under suboptimal hunting conditions.

The failure to exhibit changes in flower choice, although consistent with earlier results from these spiderlings (Morse, 2000b), somewhat conflicts with predictions for insects in the literature (Dukas, 2008). However, *Drosophila melanogaster* larvae can also learn certain tasks, but not others (Dukas, 1999, 2009). The absence of changes is consistent with goldenrod being such a predictable resource as to facilitate innate behaviour. During late summer, goldenrod is the most abundant and widespread flower in the

fields and roadsides frequented by *M. vatia* and, coincidentally, also the most profitable foraging site of the adult spiders at that time (Morse, 1981). Clearly, goldenrod comes the closest to a predictable resource that the spiderlings will experience. Given the seasonal succession of several similar goldenrod species over a period exceeding that of any other flower type in the region (Morse, 2007), this complex of goldenrod species seems the most likely to facilitate an innate preference on the part of the spiders. Local behavioural adaptations occur in a variety of spiders (e.g., Riechert, 1981; Cerveira & Jackson, 2011), although most of these reports involve studies of adults. Nevertheless, not all of our spiderlings chose goldenrod in tests offering more than one type of flower, typically goldenrod vs. wild carrot (*Daucus carota*) or *Aster* species (Morse, 2000c, 2005). Possibly our tests did not afford some individuals long enough to make 'correct' choices, a particularly relevant concern, given the differences in activity of the eight broods tested.

4.3. Ontogeny of learning

Combined with information from later in ontogeny (Morse & Stephens, 1996; Morse, 1999) the results from this study suggest that *M. vatia* possesses a complex developmental pattern, in which the use of experience presents itself at different stages. The spiderlings appear immediately capable of improving locomotor skills through practice (Morse, 2000b, this paper), while simultaneously failing for the most part to use previous experience in their hunting site (patch choice) decisions until the fourth or fifth instar (Morse, 2007), a pattern that closely fits the changing predictability of the environmental setting they experience over their life cycle.

Earlier work (Chien & Morse, 1998; Morse, 2000a) has demonstrated that previous experience affects adult spiders' flower preferences, whereas newly emerged spiderlings make innate choices not influenced by previous experience (Morse, 2000c). Preliminary data suggest that older (fourth and fifth instar) juveniles also make choices influenced by experience (Morse, 2007). At some point in their life cycle they, thus, alter their method for making hunting site choices, switching from primarily innate choices to choices significantly informed by their environment and previous experiences.

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References

- Barth, M., Helmut, V., Hirsch, B. & Heisenberg, M. (1997a). Rearing in different light regimes affects courtship behaviour in *Drosophila melanogaster*. — Anim. Behav. 53: 25-38.
- Barth, M., Helmut, V., Hirsch, B., Meinertzhagen, I.A. & Heisenberg, M. (1997b). Experience-dependent developmental plasticity in the optic lobe of *Drosophila melanogaster*. — J. Neurosci. 17: 1493-1504.
- Bateson, P. (1983). Genes, environment and the development of behaviour. In: Animal behaviour, Vol. 3: genes, development and learning (Bateson, P., ed.). Blackwell, London, p. 52-81.
- Carducci, J.P. & Jakob, E.M. (2000). Rearing environment affects behaviour of jumping spiders. — Anim. Behav. 59: 39-46.
- Cerveira, A.M. & Jackson, R.R. (2011). Interpopulation variation in kairomone use by *Cyrba algerina*, an araneophagic jumping spider from Portugal. J. Ethol. 29: 121-129.
- Chien, S.A. & Morse, D.H. (1998). The roles of prey and flower quality in the choice of hunting sites by the adult male crab spider *Misumena vatia* (Araneae, Thomisidae). — J. Arachnol. 26: 238-243.
- Dukas, R. (1999). Ecological relevance of associative learning in fruit fly larvae. Behav. Ecol. Sociobiol. 45: 195-200.
- Dukas, R. (2008). Evolutionary biology of insect learning. Annu. Rev. Entomol. 53: 145-160.
- Dukas, R. (2009). Learning: mechanisms, ecology, and evolution. In: Cognitive ecology II (Dukas, R. & Ratcliffe, J.M., eds). University of Chicago Press, Chicago, IL, p. 7-26.
- Dukas, R. & Bernays, E.A. (2000). Learning improves growth rate in grasshoppers. Proc. Natl. Acad. Sci. USA 97: 2637-2640.
- Dukas, R. & Mooers, A.Ø. (2003). Environmental enrichment improves mating success in fruit flies. — Anim. Behav. 66: 741-749.
- Edwards, G.B. & Jackson, R.R. (1994). The role of experience in the development of predatory behaviour in *Phidippus regius*, a jumping spider (Araneae, Salticidae) from Florida. — N.Z. J. Zool. 21: 269-277.
- Herberstein, M.E. (2011). Spider behaviour. Flexibility and versatility. Cambridge University Press, Cambridge, UK.
- Lutzy, R.M. & Morse, D.H. (2008). Effects of leg loss on male crab spiders *Misumena vatia*. — Anim. Behav. 76: 1519-1527.
- Mayntz, D. & Toft, S. (2001). Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. — Oecologia 127: 207-213.
- Morse, D.H. (1981). Prey capture by the crab spider *Misumena vatia* Clerck (Thomisidae) on three common native flowers. Amer. Midl. Natur. 105: 358-367.

- Morse, D.H. (1990). Leaf choices of nest-building crab spiders (*Misumena vatia*). Behav. Ecol. Sociobiol. 27: 265-267.
- Morse, D.H. (1993). Some determinants of dispersal by crab spiderlings. Ecology 74: 427-432.
- Morse, D.H. (1999). Choice of hunting site as a consequence of experience in late-instar spiders. Oecologia 120: 252-257.
- Morse, D.H. (2000a). The role of experience in determining patch-use by adult crab spiders. — Behaviour 137: 265-278.
- Morse, D.H. (2000b). The effect of experience on the hunting success of newly emerged spiderlings. Anim. Behav. 60: 827-835.
- Morse, D.H. (2000c). Flower choice by naïve young crab spiders and the effect of experience. — Anim. Behav. 59: 943-951.
- Morse, D.H. (2005). Initial responses to substrates by naïve spiderlings: single and simultaneous choices. — Anim. Behav. 70: 319-328.
- Morse, D.H. (2007). Predator upon a flower: life history and fitness in a crab spider. Harvard University Press, Cambridge, MA.
- Morse, D.H. (2010a). Male mate choice and female response in relation to mating status and time since mating. Behav. Ecol. 21: 250-256.
- Morse, D.H. (2010b). Diet and growth of newly-emerged crab spiderlings *Misumena vatia*. — J. Arachnol. 38: 309-312.
- Morse, D.H. & Stephens, E.G. (1996). The consequences of adult foraging success on the components of lifetime fitness in a semelparous, sit and wait predator. Evol. Ecol. 10: 361-373.
- Nakamura, T. & Yamashita, S. (2000). Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). — J. Comp. Physiol. A 186: 897-901.
- Olvido, A.E. & Mousseau, T.A. (1995). Effect of rearing environment on calling-song plasticity in the striped ground cricket. — Evolution 49: 1271-1277.
- Olvido, A.E., Fernandes, P.R. & Mousseau, T.A. (2010). Relative effects of juvenile and adult environmental factors on mate attraction and recognition in the cricket, *Allonemobius* socius. — J. Ins. Sci. 10(90): 1-17.
- Papaj, D.R. (1993). Automatic behavior and the evolution of instinct: lessons from learning in parasitoids. In: Insect learning. Ecological and evolutionary perspectives (Papaj, D.R. & Lewis, A.C., eds). Chapman & Hall, New York, NY, p. 243-272.
- Papaj, D.R. & Lewis, A.C. (1993). Insect learning. Ecological and evolutionary perspectives. — Chapman & Hall, New York, NY.
- Pietropaolo, S., Branchi, I., Chiarotti, F. & Alleva, E. (2004). Utilisation of a physicallyenriched environment by laboratory mice: age and gender differences. — Appl. Anim. Behav. Sci. 88: 149-162.
- Reid, A.L., Seebacher, F. & Ward, A.J.W. (2010). Learning to hunt: the role of experience in predator success. — Behaviour 147: 223-233.
- Riechert, S.E. (1981). The consequences of being territorial spiders, a case-study. Am. Nat. 117: 871-892.

- Rosenzweig, M.R. (1966). Environmental complexity, cerebral change, and behavior. Am. Psychol. 21: 321-332.
- Snell-Rood, E.C., Papaj, D.R. & Gronenberg, W. (2009). Brain size: a global or induced cost of learning? — Brain Behav. Evol. 73: 111-128.
- Sokolowski, M.B. (1980). Foraging strategies of *Drosophila melanogaster*: a chromosomal analysis. Behav. Genet. 10: 291-302.
- Sokolowski, M.B. (1998). Genes for normal behavioral variation: recent clues from flies and worms. Neuron 21: 463-466.
- Wilder, S.M. & Rypstra, A.L. (2008). Diet quality affects mating behaviour and egg production in a wolf spider. — Anim. Behav. 76: 439-445.