POINT-OF-VIEW

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On the assessment of prey suitability in aphidophagous Coccinellidae

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Abstract. Empirical protocols for assessing the suitability of prey for aphidophagous coccinellids are examined and a modified scheme of categorization is presented. It is argued that prey suitability should be assessed independently for larval development and adult reproduction because of potentially divergent nutritional requirements between these life stages. A scheme is proposed for assessing prey suitability for larval development using conspecific eggs as a reference diet against which diets of various prey types can be compared both within and among coccinellid species. Among suitable prey (those that support ca. 100% survival of larvae to the adult stage), those that promote faster development and yield larger adults relative to a conspecific egg diet are considered "optimal" for larvae. Prey that yield viable adults with similar or reduced adult weight after a similar or extended period of development relative to a diet of conspecific eggs are classified as "adequate". Prey are "marginal" if they support the survival of some larvae, but significantly less than 100%. Supplementary water should be provided with any non-aphid diet (e.g. pollen and alternative sources of animal protein) given the potential for food-specific diet-drought stress interactions. For adults, suitable prey are classified as "adequate" if they support the production of viable eggs when fed as a monotypic diet, or "marginal" if they merely prolong adult life relative to a water source. Prey that comprise an optimal or adequate diet for both larval development *and* adult reproduction are termed "complete" and these can be indexed for relative suitability according to derived estimates of r_m. Potential sources of error in diet evaluation studies are identified and discussed.

INTRODUCTION

Effective and standardized approaches to evaluating the various life-history consequences of prey consumption are essential to laboratory assessments of the biological control potential of predatory insects. Relative prey suitability for development and reproduction is a primary determinant of the numerical response of predator populations, just as host suitability is for parasitoid populations. Determination of prey suitability for insects that are aphid predators only in their larval stages (e.g. Chrysopidae, Hemerobiidae, and Syrphidae) is relatively straightforward: prey that support completed development are suitable – the faster the development and/or the larger the adult, the more suitable the prey. However, evaluation of prey suitability becomes more complex for insects that are predatory in both immature and adult stages since both developmental and reproductive criteria must be examined. Such is the case for aphidophagous coccinellids.

CLARIFYING THE CONCEPT OF ESSENTIAL PREY

For the Coccinellidae as a group, it has been proposed to classify prey types as "essential" if they support both completed larval development and successful adult reproduction, or "alternative" if they serve only as an energy source to extend adult longevity (Hodek & Honek, 1996). These concepts have proven useful to the study of coccinellid nutritional ecology, but I will suggest that modifications and refinements of these designations are required because they fail to adequately account for a wide range of intermediate situations. Although patterns of prey suitability for larval development often closely parallel those for adult reproduction (e.g. Omkar & James, 2004), this is not always the case. It is now known that larvae and adults may differ in nutritional requirements, such that a particular prey may represent a suitable diet for larval development, but not for adult reproduction, or vice versa. For example, Michaud (2000) demonstrated that larvae of a population of *Harmonia axyridis* Pallas from Florida could develop successfully on a diet of *Aphis spiraecola* Patch (albeit with extended developmental time and reduced adult weight relative to more suitable diets) but that adult females could not produce viable eggs on a monotypic diet of this aphid species. Thus, although *A. spiraecola* does not meet the requirement to be classified as an essential prey, it is clearly an adequate food for larvae and an important food source in both citrus (Michaud, 2003) and apple (Brown, 2004) where *H. axyridis* serves as a primary biological control agent. Similarly, adult females of *Hippodamia convergens* Guerin had good fecundity and fertility on a diet of *Toxoptera citricida* (Kirkaldy), even though larvae could not complete development on a monotypic diet of this prey species (Michaud, 2000). A similar effect was noted by Morales & Burandt (1985) studying a South American population of *Cycloneda sanguinea* L. feeding on *T. citricida*; adults were fertile feeding on this prey, but larvae failed to complete development successfully despite voracious consumption. Since differences may exist between the nutritional requirements of larvae and adults, prey suitability should always be assessed independently for larval development and adult reproduction. To avoid confusion with well-established usage of the term "essential" sensu Hodek & Honěk (1996), I propose the term "complete" be used to refer to those prey species that support both development and reproduction.

UNSUITABLE PREY

Prey that are readily consumed by either larvae or adults are considered to be "acceptable", regardless of the physiological consequences for the beetle, whereas prey that are consistently rejected following encounter are unacceptable (Hodek & Honěk, 1996). For example, *Megoura viciae* Buckton is an acceptable, but unsuitable, prey for *Adalia decempunctata* L., regardless of the beetle"s life stage (Dixon, 1958), and the same is true for *Aphis sambuci* L. when preyed on by *Adalia bipunctata* L. (Blackman, 1965). As noted in Hodek & Honěk (1996) lack of suitability in acceptable prey species may occur because of simple nutritional inadequacy, or toxicity arising from compounds sequestered from the host plant by the prey, e.g. *Macrosiphum albifrons* Essig on *Lupinus mutabilis* (Gruppe & Roemer, 1988) and *Aphis nerii* Boyer de Fonscolombe on *Nerium oleander* (Malcolm, 1990).

Although toxicity can conceivably arise from metabolites produced de novo in prey species, and independent of host plant, no examples of this have been reported in the literature for aphids as yet. However, recent evidence indicates that aphids containing parasitoid larvae in later stages of development may become toxic to coccinellid larvae. Larvae of *H. convergens* fed nymphs and mummies of *Schizaphis graminum* Rhondani parasitized by *Lysiphlebus testaceipes* Cresson fail to form viable pupae (K. Giles, pers. commun.). Similar results were obtained by feeding larvae of *C. sanguinea* nymphs of *T. citricida* parasitized by *L. testaceipes* (J.P. Michaud, unpubl.). Thus parasitized aphids may represent a previously unrecognized, yet potentially important, toxicity risk for larval coccinellids in the field and pose a hazard for laboratory studies of diet suitability whenever there exists a risk of parasitoid infiltration in prey aphid colonies.

When a prey item is decidedly unsuitable for coccinellid larval development, the first instar is rarely completed; although larvae may survive for a number of days, very little growth is achieved. However, nutritional inadequacy may also arise when one particular nutrient becomes limiting in later stages of development. This could result from a paucity of a particular amino acid in the protein profile of an aphid relative to the amino acid requirements of the beetle larva during development. Diet switching experiments can sometimes be used to confirm a hypothesis of nutritional inadequacy. For example, Michaud (2000) found that larvae of *Coleomegilla maculata fuscilabris* (Mulsant) could not complete development on a monotypic diet of *T. citricida*, but had excellent survival when fed a proprietary artificial diet during the first instar. In this case, the monotypic diet resulted in normal development to the pupal stage, with a large proportion of these yielding adults that were either deformed or otherwise non-viable, i.e. surviving only 2–3 days. Thus *T. citricida* cannot be considered an adequate prey for *C. m. fuscilabris* development, but could nevertheless represent an important protein source in habitats where complementary foods are available.

Any significant degree of prey toxicity, such as noted by Dixon (1958) for *A. decempunctata* fed *M. viciae*, typically results in rapid death of the coccinellid larva following consumption, although death by poisoning is more commonly a gradual process. If acceptable prey are suspected of toxicity arising from the sequestration of secondary plant compounds, the issue can sometimes be resolved by rearing the prey aphids on related host plants, or even different parts of the same host plant, that vary in concentrations of the active compounds (Gruppe & Roemer, 1988; Malcolm, 1990) in order to see if mortality scales accordingly when they are fed to larvae.

PREY SUITABILITY FOR LARVAE – CRITERIA AND RECOMMENDED PROCEDURES

By all available accounts, feeding prey to larvae as monotypic diets is probably the best approach for assessing their suitability for coccinellid growth and development. Coccinellid larvae, being less vagile than adults, likely feed on a single species of aphid throughout their course of development in nature more often than not, so monotypic diets are probably the norm. Furthermore, the few studies that have sought to demonstrate nutritional complementation of low quality aphids by feeding them in mixed diets or including higher quality aphids in mixed diets (e.g. Nielsen et al., 2002) have concluded that no such effects occurred.

Prey suitability can be categorized as either "optimal", "adequate" or "marginal" by comparing larval performance on a particular monotypic prey diet to that obtained on an exclusive diet of conspecific eggs (see rationale below). Eggs for larval feeding experiments can be collected from ovipositing females and refrigerated to arrest their development until a sufficient supply is obtained. The relative suitability of prey types for coccinellid larvae can be assessed on the basis of three empirical criteria: survivorship, adult weight, and developmental time, with physical factors such as temperature, humidity and day length held relatively constant within a range of values known to be favorable for the species in question. These criteria are listed in their inferred order of importance to fitness. Obviously, survivorship is paramount, and adult weight is likely to have far greater impact on fitness than developmental time, potentially influencing adult longevity, mating success, fecundity, and resilience to environmental stresses. Developmental time can be measured in days from eclosion of the neonate larva to emergence of the adult. This period can be divided into larval, prepupal and pupal stages for sake of interest, but most variation is usually reflected in the duration of larval development. Typically, larval developmental time and adult weight are negatively correlated, such that diets producing the largest adults also yield the fastest developmental times (Kalushkov, 1998; Dixon, 2000; Michaud, 2000; Omkar & Bind, 2004; Omkar & James, 2004). Emerging adults should be sacrificed on their first day of life following hardening of the cuticle, without permitting them access to food or water by freezing them individually in glass vials and then drying them in an oven at 50°C for 72 h before weighing.

CONSPECIFIC EGGS AS A REFERENCE DIET FOR LARVAE

Egg cannibalism is an adaptive behavior common to aphidophagous coccinellids that lay clustered eggs (Dixon, 2000). Not only does cannibalism of sibling eggs by eclosing larvae improve their survival when prey are scarce (Dixon, 1959), but cannibalizing first instars also benefit from faster development and increased adult size relative to non-cannibalizing larvae (Osawa, 2002). Michaud & Grant (2004) confirmed these results for *H. axyridis* and two other species, *C. sanguinea* and *Olla v-nigrum* Mulsant, demonstrating that this effect may be generally applicable to the group. In addition, Michaud & Grant (2004) showed that the magnitude of the impact of early egg cannibalism on life history traits is largely contingent on the quality of the subsequent larval diet. Since consumption of just one conspecific egg by a neonate larva can favorably influence subsequent larval performance (Osawa, 2002), neonate egg cannibalism likely represents an unrecognized source of variation in life history parameters in many larval feeding experiments and should be carefully controlled (i.e. selectively permitted or denied) in all experiments that seek to assess prey suitability for larval development. This can be accomplished by observing hatching egg clusters and carefully removing larvae as soon as melanization occurs, or selectively placing other larvae to feed on chilled egg masses.

A monotypic diet of conspecific eggs appears to reliably yield successful larval development and healthy, fertile adults in all species tested to date (Michaud, 2003; Michaud & Grant, 2004; Cottrell, 2004). Thus, a conspecific egg diet can be used as a universal reference diet against which the suitability of particular prey species can be assessed in a uniform manner for any aphidophagous coccinellid species. Eggs for such studies should be obtained from coccinellid females reared and fed on prey that are known to support both completed development and successful adult reproduction in the species. Only prey items of the highest suitability support faster development and/or heavier adult weights than an exclusive diet of conspecific eggs (Michaud, 2003; Michaud & Grant, 2004) and these can be considered optimal prey. Prey types that yield larval survival not significantly less than 100%, but with adult weight and/or developmental time comparable, or inferior to, a conspecific egg diet, can be considered adequate, but sub-optimal. Marginal prey are then those that support the completed development of only a small proportion of larvae (i.e. significantly less than 100%). For example, of the six aphid species tested by Omkar & James (2004) as food for *Coccinella transversalis* F., only *Aphis gossypii* Glover and *Aphis craccivora* Koch qualify at least as adequate prey, all others being only marginally suitable, although whether or not the former two species represent optimal prey cannot be ascertained because there was no reference diet of conspecific eggs.

The data presented by Cottrell (2004) include a reference diet of conspecific eggs and provide a good illustration of its utility for assessing prey suitability for larvae. Examining their data for conspecific egg diets begun in the first instar reveals that *Monelliopsis pecanis* Bissell is an optimum prey for *Olla v-nigrum* Mulsant, yielding higher adult weight and faster development than the conspecific egg diet. In contrast, this species is merely an adequate prey for *H. axyridis*, yielding adult weights and developmental times comparable to the conspecific egg diet, but not superior. Note also that *H. axyridis* eggs were completely unsuitable for both of the "native" coccinellids tested, whereas they yielded 100% survival of conspecific larvae and adult weights comparable to, or greater than, those obtained with any prey offered in the test.

PREY SUITABILITY FOR ADULTS

Determination of relative prey suitability for adult coccinellids has more potentially confounding elements, and more empirical problems, than do similar studies with larvae. One consequence is that many studies ignore reproductive performance on prey and focus entirely on larval development (Michels & Behle, 1991; Munyaneza & Obrycki, 1998). However, a species' numerical response in the context of biological control depends on both completed development and successful reproduction and the designation "essential prey" cannot be made on the basis of successful larval development alone. Similarly, recent work on parasitic Hymenoptera has sought to complement existing parasitoid host range data with studies comparing various nectar sources for their relative contributions to the fertility and fecundity of adult wasps (e.g. Jacob & Evans, 2000; Lee et al., 2002; Wratten et al., 2003), thus generating a more complete perspective of the species' ecological requirements.

ADEQUATE PREY VS MARGINAL PREY FOR ADULTS

Among foods that are suitable for adult coccinellids, only those types that support successful reproduction when consumed as a monotypic diet can be classified as adequate. Thus various pollen sources comprise adequate adult food for *C. maculata*, even though a diet including animal protein usually results in higher fecundity (Riddick & Barbosa, 1998). Adequate prey species can be scaled for relative suitability according to the mean numbers of fertile offspring females produce in a specified reproductive period measured from the first day of oviposition.

Prey that do not support reproduction may nevertheless extend adult lifespan in the absence of adequate prey, i.e. they are "alternative" prey sensu Hodek & Honěk (1966). However, these prey are not functionally alternative to adequate prey, but rather serve as dietary supplements that sustain adult survival without directly supporting the key function of reproduction. In this sense, they are analogous to the proposed definition of marginal prey for larvae. Marginal adult prey (or food) can be anything that, when consumed by adults as a monotypic diet, extends longevity significantly beyond that obtained when only water is provided. This category will include vegetable sources of protein and carbohydrate (e.g., pollen and nectar), as well as animal sources (e.g., honeydew and aphids or other prey that do not support reproduction without some complementation). In terms of biological control, marginal prey are especially important for sustaining coccinellid populations that survive largely on aphid species that exhibit "boom and bust" cycles of abundance, as they can function to reduce local extinction events when adequate prey are scarce.

CRITERIA AND RECOMMENDED PROCEDURES

The appropriate criteria for determining relative prey suitability for adult coccinellids are, in order of biological importance, fertility (determined by egg viability), fecundity (egg number), longevity and the pre-reproductive period. Omkar & James (2004) measured these variables for adult *C. transversalis* fed on six species of aphid prey. Linear regression of the mean values presented in Table 3 (Omkar & James, 2004) produces r^2 values ranging from 0.977 to 0.993 for all possible pair wise combinations of these variables, suggesting considerable interdependency. Providing *C. transversalis* is representative, the shortest pre-oviposition period, the longest oviposition period, and the longest lifespan will all tend to be obtained on the same diet that yields the highest per capita production of viable eggs. Since fecundity declines quite steeply with adult age (Dixon & Agarwala, 2002), measurements of the quantity and fertility of eggs produced by a series of females over a fixed period in early adult life is likely sufficient to assess relative prey suitability for adults. Estimates of total lifetime reproductive success are of interest in theoretical models of fitness, but they are not requisite for assessment of diet suitability.

Differences in prey suitability for reproduction can normally be resolved by collecting eggs from mated females held in isolation over a period of either three weeks of reproductive life, or 10–12 days of actual oviposition, and incubating egg clusters until eclosion so that viability can be tallied. However, a measurement of fecundity and fertility over a period equal to, or greater than, the generation time of the species on the same diet is required if an approximation of r_m is desired. Since generation time is required for the r_m calculation (see below), the length of the female pre-oviposition period must also be measured on each diet and this is a life history character that can vary substantially among females independent of diet. For example, the pre-oviposition period of first generation, mated *H. convergens* females in Kansas, U.S.A. ranged from 2 d to 32 d following isolation and provision with *S. graminum*, an essential prey for this species (J.P. Michaud, unpubl.).

Provided an estimate of pre-oviposition period is not required, groups of newly-emerged adult beetles can be housed in ventilated jars with food and water for a period of 10–20 days, reducing maintenance labor considerably. Females of most species are deterred from oviposition under these crowded conditions, but will mate with a variety of males, improving their average fertility.

Mated females are then removed and isolated in small containers for oviposition. Water should again be made available in any non-aphid diet treatment and this can be accomplished using a small cube of sponge wetted every 24–48 h depending on ambient humidity. Switching ovipositing females from one diet to another may also reveal differences in the nutritional value of prey; significant changes in female fertility may be evident as soon as 1–2 days following a change in diet (Michaud, 2000; Michaud & Olsen, 2004). Switching females to an adequate diet can also provide a means of verifying their reproductive viability in cases where a prey type has proved inadequate for reproduction.

Collection of eggs for assessment of fecundity and fertility should be performed at least daily, or twice daily if there is evidence of cannibalism by females. Care should also be taken to immediately remove early hatching larvae from asynchronously hatching egg clutches to prevent egg cannibalism that can confound estimates of egg fertility. Hatching rates are then recorded for each egg clutch following incubation at a standardized temperature.

CHALLENGES IN MEASURING REPRODUCTIVE PERFORMANCE

Reproductive females consume much larger quantities of food than do developing larvae, so assessments of reproductive performance require the rearing of much larger numbers of prey than assessments of larval development. and render conspecific eggs impractical as a reference diet for comparative purposes. The intrinsic reproductive potential of coccinellid females is often quite variable, such that a small fraction of females is sometimes responsible for a large fraction of the cohort's reproduction (J.P. Michaud, unpubl.). Intrinsic variation in female fecundity increases standard errors in estimates of reproductive success and thus the sample size of females that must be tested in order to resolve more subtle effects of diet.

Repeated matings may be necessary to maintain female fertility in some coccinellid species (Majerus, 1994), raising the question of whether or not females should be provided with repeated access to males. Typically, egg cannibalism by males renders continuous confinement of pairs impractical, although even the females will sometimes consume their own eggs as an artifact of confinement. A period of 10–12 days of actual oviposition is probably short enough to avert problems with sperm depletion in most species. However, where precise estimates of lifetime reproductive success are desired, females should be permitted periodic mating opportunities, followed by subsequent isolation for oviposition. It is also notable that no studies of coccinellids have yet addressed the issue of possible diet effects on male fertility, likely due to the difficulties associated with determining sperm viability. It is usually implicitly assumed that nutritional requirements for fertility are similar for male and female, but there have been no efforts to verify this to my knowledge. Nevertheless, variation in male fitness may be of little or no consequence to biological control in the field provided females have opportunities to engage in multiple matings.

Of more potential significance to diet evaluation studies is the fact that larval diets may influence the subsequent fertility of adult females (Michaud, 2000). The implication is that some nutrients obtained during larval feeding may be retained in the insect through the pupal stage and utilized to supplement a nutritional deficit during adult reproduction. If insects are reared on an optimal diet as larvae and then evaluated for reproductive performance as adults fed on a range of diets, the risk arises that residual nutrition obtained during development might serve to mask the inadequacy of a marginal food for the first week or more of reproduction. One way to avert such a possibility is to ensure that adults employed in such tests are reared as larvae on the same monotypic diet they will be tested on as adults. However, this leaves the problem of what to use as larval food when the goal is to evaluate adult performance on a prey type that does not support development. In this case, larvae could be reared on several different prey types that vary somewhat in adequacy for larval development and their adult performance compared on the same inadequate larval prey so as to detect possible nutritional legacies from the larval diets.

INDEXING THE SUITABILITY OF COMPLETE PREY

Truly complete prey should, when fed as a monotypic diet to both larvae and adults, support the development and reproduction of successive generations of a coccinellid species (i.e. two or more) without measurable decline in any index of biological performance. For these prey, one may wish to obtain some estimate of relative suitability that incorporates both larval and adult performance criteria. Since these prey are adequate for both larval development and adult reproduction, one can calculate and compare r_{m} values obtained on diets of various prey types. Abbou-Setta & Childers (1991) proposed a procedure for simple estimation of r_{m} without the need to measure lifetime fecundity and showed that it provided accurate results for various species of Coleoptera. The only parameters required are generation time and an estimate of fecundity and fertilty over the same period. Generation time can be calculated as the sum of the egg incubation period, larval developmental time, pre-pupal and pupation periods, and pre-oviposition period. Effects of larval diet on adult size are ignored in the r_{m} estimation, but will still be reflected via effects of adult size on female fecundity, provided insects for reproductive performance trials are reared as larvae on the same prey that they receive in adult feeding trials. Species representing complete prey can then be indexed according to their relative suitability for a particular coccinellid species using r_{m} values derived from an objective methodology that incorporates distinctive life history consequences of the diet for both larval and adult life stages.

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