

OVARIAN DYNAMICS AND HOST USE

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■ **Abstract** Oviposition behavior in herbivorous and frugivorous insects and parasitoids is dynamic at the level of the individual, responding to variation in host quality and availability. Patterns of variation in egg load in response to host presence and quality suggest that ovarian development also responds to variation in the host environment. Ovarian dynamics are mediated by feedback from oviposition, by host feeding, and by sensory input from the host. The last of these mechanisms, host sensory cuing, is known to occur in three major orders and provides strong evidence that ovarian dynamics are adaptive by design. Conditions favoring host effects on ovarian development include trade-offs between egg production and either survival or dispersal, uncertainty in the host environment, and a correlation in host conditions between the time that oogenesis is initiated and the time that eggs are laid. Some host defenses block ovarian development, suggesting that ovarian dynamics in host-specific insects should be viewed from a coevolutionary perspective.

INTRODUCTION

A substantial body of theoretical and empirical literature on phytophagous, frugivorous, and parasitic insects has been devoted to understanding how variation in the quality and abundance of host resources influences oviposition behavior (9, 37, 71, 106). An equally substantial body of literature has sought to describe how aspects of an insect's internal state, such as level of experience and motivation, influence oviposition behavior (9, 37, 54, 69, 71, 87, 88, 94, 102). Taken together, this work indicates that oviposition behavior in host-specific insects is highly dynamic at the level of the individual, responding to variation in host quality and abundance in adaptive ways that depend on an individual's physiological state, including its stage of ovarian development.

One attribute of ovarian development of particular interest to students of insect-host interactions has been egg load. Egg load (defined here as the total number of mature oocytes in the ovaries) exerts a variety of effects on oviposition behavior. Females with high egg load typically expend more effort in foraging for hosts, are less selective regarding the quality of hosts used, lay larger clutches, allocate

sex differently, and invest more in contests with other females over host resources than do females with low egg load (12, 33, 48, 73, 88, 103, 119).

Issues relating to egg load and, hence, ovarian development have taken center stage in a recent debate on the relative importance of egg and time limitation in host use (40, 42, 68, 93, 99). Egg limitation occurs when females deplete their egg supply before opportunities to oviposit are exhausted. Time limitation occurs when females die or otherwise lose reproductive competence before all mature eggs have been laid. A high risk of egg limitation should cause females to become choosier with respect to the quality of hosts used in oviposition, even if such choosiness reduces the rate at which eggs are laid (53, 67). A high risk of time limitation should, in contrast, cause females to adopt strategies that increase the rate at which hosts are found, even if such strategies reduce the quality of hosts on which eggs are laid (105).

Egg and time limitation are a consequence of trade-offs, most plausibly trade-offs between survival and reproduction in an unpredictable environment (93, 99). An animal has a finite amount of resources to allocate to survival and reproduction; investment in one trades off against investment in the other. To the extent that opportunities for reproduction cannot be predicted with certainty in advance of egg maturation, natural selection cannot generate a perfect match between reproductive opportunity and allocation to reproduction (93). However, selection is expected to provide the best possible match. Adjustment of selectivity, clutch size, and other behavior in response to egg load can be regarded as adaptations for reducing an insect's risk of egg limitation (68). Egg maturation processes that contribute to egg load have been cited as central to our understanding of how behavior balances the opposing risks of time and egg limitation (41, 42).

Notwithstanding its significance for the dynamics of oviposition behavior, ovarian development is itself under selection (18, 24, 25, 27, 57, 86, 89) and is conceivably dynamic in ways that permit insects to cope with variation in the host resource. How ovarian development responds to variation in host quality and availability is the subject of this review. Attention is devoted to patterns of egg maturation in relation to host quality and availability, mechanisms underlying those patterns, and trade-offs thought to favor those mechanisms.

BASIC DESIGN AND CONTROL OF OVARIAN DEVELOPMENT

Insect ovaries appear to be well suited for adjusting egg production to environmental conditions. First, once initiated, egg production is rapid. Commenting on the diversity of mechanisms associated with oogenesis in animals, Eckelbarger (25) noted:

A major reason for [the arthropods'] success has been the evolution of specialized ovaries and vitellogenic mechanisms that enable them to manufac-

ture, sometimes in a single day, an egg mass exceeding half their body weight.

Key to rapid production of ovaries of large mass are heterosynthetic mechanisms of yolk synthesis, wherein yolk material is produced not only within the oocyte but in other tissues as well. Vitellogenesis in insects, for example, is marked by manufacture in the fat bodies of a class of yolk proteins known as vitellogenins that are transported through the hemolymph to the developing ovarioles. In the meroistic-type ovaries characteristic of more derived orders, abortive germ cells known as nurse cells, or trophocytes, furnish oocytes with metabolites and organelles via cytoplasmic bridges. As a consequence of such nourishment, vitellogenesis in meroistic ovaries is often completed in just one to two days.

Second, the quantity of eggs available to lay can be adjusted at the level of the individual. Females of many species (sometimes labeled "synovigenic;" 29) mature eggs throughout adult life, sometimes eclosing with few or no mature eggs. Egg production in such species is regulated through two jointly acting processes: oogenesis, in which follicles form in ovarioles, yolk is deposited in oocytes within those follicles and a chorion laid down (25); and oosorption, in which vitellogenesis ceases and yolked oocytes degenerate (7). Less commonly, females eclose with their entire complement of eggs ready to lay. In such species (sometimes labeled "pro-ovigenic;" 29), the quantity of eggs matured is probably regulated little or not at all in the adult stage, but may nonetheless be modified in the juvenile stage.

Third, timing of egg maturation can be adjusted at the level of the individual. An elaborate system of neural and hormonal control regulates the timing of ovarian development (58, 97, 114, 126, 127). Via this system, a variety of extrinsic factors influence the timing and degree of ovarian development, including temperature (6, 32, 117), humidity (64), photoperiod (1, 6, 70, 108, 117), mating (8, 34, 126), social context (11, 97, 114) and diet (126).

PATTERNS OF EGG MATURATION IN RELATION TO THE HOST RESOURCE

In principle, the ability to mature eggs rapidly, in variable quantity and at the appropriate time, should permit insects to adjust rates of egg maturation to variation in host quality and availability. Yet discussions of egg load as a factor in oviposition behavior have routinely treated ovarian development as blind to such variation. In one scenario, eggs accumulate in an insect's abdomen as time since last oviposition elapses (17, 54, 80, 81). The increase in egg load affects oviposition behavior, for example, by reducing selectivity. When eggs are next laid, egg load declines and selectivity is recovered. Eggs begin again to accumulate, completing the cycle. In some models, eggs mature at a linear rate until either

egg load reaches some capacity set by the physical limits of a female's abdominal cavity or nutrient reserves are depleted (17, 67, 71). The host has no effect on ovarian development except through egg deposition or, in species that feed on hosts, nutrient input.

Direct evidence in support of this paradigm is lacking. No one has directly tracked changes in an individual's egg load and correlated these with changes in behavior, owing to the difficulty of counting mature oocytes without killing the individual whose behavior is being followed. Support has instead been marshaled from two independent lines of evidence, one showing that variation in egg load among individuals affects selectivity (12, 48, 73, 88, 103), and one showing that an individual's selectivity increases with time since last oviposition (102).

Resorting to indirect evidence might merit little concern if such evidence uniformly supported the existing paradigm. As this review will illustrate, it does not. While variation in egg load is a powerful predictor of variation in behavior in many host-specific insects, it has little or no significance in others. At the same time, patterns of ovarian maturation in relation to host use appear to be more complex than sometimes assumed.

Responses to Variation in Host Availability

Effects of host availability on egg load and behavior are typically assessed by depriving females of hosts. In some insects, host deprivation has no detectable effect on egg load. In the pollen beetle, *Meligethes aeneus*, egg load of individuals deprived of oviposition sites did not differ significantly from that of individuals exposed continuously to such sites (45). Neither a beetle's propensity to oviposit nor its clutch size showed detectable changes over time since last oviposition. Mediterranean fruit fly (*Ceratitis capitata*) females deprived of hosts for three weeks similarly retained no more eggs in their ovaries than females deprived for two weeks (79). Nevertheless, the difference in deprivation period was accompanied by a difference in behavior. More deprived flies foraged more persistently for fruit and were more aggressive in defense of fruit than less deprived flies.

In other insects, eggs accumulate under host deprivation. In *Bemisia tabaci* whiteflies, total vitellin and vitellogenin content increased steadily over a 24-hour period during which females were denied access to host melon leaves (121). Similarly, in pear psylla (*Cacopsylla pyricola*), eggs accumulated over a 16-hour period of host deprivation. Increased egg load in pear psylla was associated with increased oviposition activity when host leaves were subsequently made available (47).

In yet another group of insects, host deprivation is associated with smaller egg loads, not larger ones as expected. Females of an aphidiid parasitoid, *Monoctonus paulensis*, provided with host aphids during day one post-eclosion had higher egg loads on day three than females deprived of hosts continuously from emergence (72). Egg loads for females of an encyrtid parasitoid, *Leptomastix dactylopii*, declined slightly as host deprivation progressed over ten days (90).

Variability in results may partly reflect the timescale over which responses to host deprivation were evaluated. In synovigenic parasitoids, egg load increases initially under deprivation, but declines subsequently as eggs are resorbed (23, 29). Waxing and waning of egg load is paralleled by changes in host selectivity. The early literature on parasitoids described a “faculty of restraint” in oviposition that broke down as eggs accumulated (29, 65). As deprivation continued, females were progressively less likely to attack hosts. Generally, the appearance of hosts restores egg maturation (23). If the period of deprivation continues for too long, however, ovarian development may not revive and females may not lay eggs again, a phenomenon termed “ecological castration” (30).

Timescale probably does not account entirely for variation in ovarian responses to host deprivation. Some variation may reflect species differences in synchrony of ovariole maturation. In order for egg load to change gradually in response to host deprivation, development within different ovarioles within the ovaries must necessarily be asynchronous. Some insects, such as sheep blow flies (*Lucilia cuprina*), which lay just a few large clutches in their lifetime, appear to be constrained to mature oocytes synchronously across ovarioles (13). Oviposition site deprivation in *L. cuprina* affects neither egg load nor oviposition behavior.

Variability in results may also reflect variation in strategies for coping with host deprivation. An intriguing alternative response to host deprivation has been reported in females of a tachinid fly species, *Chetogena edwardsii* (111). Host-deprived females retain no more eggs in their ovaries than females given unlimited access to their nymphalid caterpillar hosts. However, host-deprived females differ from undeprived counterparts in one key respect: They retain a fertilized egg in a uterus where it undergoes embryogenesis. Maggots hatching from embryonated eggs reach pupation sooner than maggots hatching from eggs fertilized shortly before oviposition. By incubating eggs, females conceivably broaden host range to include late-instar caterpillars that offer a relatively narrow window of time for parasitoid development. In short, *C. edwardsii* females may effectively increase host availability by generating embryonated eggs that fare better in low-quality hosts, and expanding host range to include those hosts. Ovoviviparity in females denied access to preferred breeding sites has also been reported in some Hawaiian *Drosophila* and *Scaptomyza* flies (57).

While insects surely experience periods of complete host deprivation in nature, host abundance often varies in a more graded fashion. Data, though sparse, indicate that ovarian maturation responds to patterns of graded variation. The egg parasitoid *Trichogramma minutum* is highly opportunistic, adjusting its fecundity schedule to current host density (5). Females offered host flour-moth eggs at low density and just once every three days spread out egg production evenly over a period of several weeks. In contrast, females offered eggs daily in essentially unlimited supply realized 50% of their lifetime fecundity in the first few days after emergence, after which egg production plummeted below levels achieved by females offered hosts at low density.

In a study exceptional for its strong focus on ovarian dynamics (90), female *Leptomastix dactylopii* parasitoids provided with mealybug hosts at high density had egg loads resembling those of host-deprived females and females provided with hosts at low density. Because wasps foraging at high density were depositing eggs at relatively high rates and retaining no fewer eggs on average, it follows that wasps in that treatment were producing eggs at higher rates than wasps in other treatments.

In encyrtid parasitoids, oosorption leaves visible chitinized remnants. By counting remnants, the boost in egg production at high host density was determined to be due to an increase in oogenesis and not a decrease in oosorption. Finally, effects of host regime on egg production vanished immediately upon deprivation of hosts; in terms of ovarian development, there was no “memory” of the host environment experienced prior to deprivation.

Responses to Variation in Host Quality

Ovarian maturation is also sensitive to variation in host quality. In *M. aeneus* pollen beetles, egg load in individuals offered highly acceptable cruciferous host plant species was greater than egg load in individuals offered species of low acceptability—not less, as might be expected if individuals provided with less acceptable plants were accumulating eggs that those provided with acceptable plants were depositing (45). Egg maturation was linked to oviposition. Given free access to highly acceptable hosts, more eggs were laid, but proportionately more were matured. In beetles given free access to less acceptable hosts, in contrast, egg maturation was virtually shut down. Finally, individuals proved capable of adjusting egg production in response to changes in host quality. Being switched from low-quality to a high-quality host boosted egg production; switches in the opposite direction depressed egg production (46).

In seedcorn flies (*Delia platura*), rates of egg maturation were likewise matched to rates of oviposition (125). Seedcorn flies develop as larvae on both living and dead plant material, and females oviposit in moist sand even in the absence of germinating host lima beans. However, females provided with lima bean produced two to three times more eggs and produced them sooner than host-deprived females. Bean-exposed females retained no fewer eggs in their ovaries at death than bean-deprived females, suggesting that rate of egg maturation was matched to rate of egg deposition. When flies were switched from lima bean and sand to sand only, egg production and deposition initially slowed but soon matched the rate at which flies maintained continuously on lima bean and sand produced and laid eggs.

In the bethylid parasitoid, *Goniozus nigrifemur*, rates of egg maturation depended on the size of host pink bollworm larvae recently encountered (66). Females permitted to oviposit in a large host (20–28 mg) and dissected five days later retained nearly twice as many eggs in their ovaries as females permitted to oviposit in a small host (2–6 mg) (means of 12.6 versus 6.8 respectively), despite

the fact that large-host females laid larger clutches than small-host females. Same-aged, host-deprived females retained just two eggs on average. Large-host females also oviposited over a day sooner in the next host than did small-host females.

Adaptiveness of Patterns

Many studies cited here were not intended to evaluate ovarian dynamics in relation to the host resource. Nevertheless, data suggest that ovarian development responds to variability in host quality and availability in adaptive ways. For example, boosting egg production when hosts are common, as observed in *Trichogramma* wasps (5), reduces risk of egg limitation, at least in the short term. Slowing egg production when the quality of the host is low, as observed in *Meligethes* pollen beetles, may allow females to wait out periods of poor host quality, at least if egg production trades off against survival (as discussed below: a common trade-off). In an insect such as a pollen beetle, which has a relatively long reproductive season, the benefits of delaying a commitment to reproduce may be particularly high (45). If host quality remains low, restoring rates of egg maturation to high levels, as observed in *Delia* flies (125) makes adaptive sense too. Eggs that are made and laid on poor-quality hosts have some chance of survival; eggs that are never made and never laid do not. Hence, if poor conditions persist, an insect should “make the best of a bad job” and resume laying eggs. Finally, oosorption under host deprivation has long been regarded as adaptive; by reallocating nutrients from eggs to somatic tissues in times when oviposition resources are scarce, an insect may survive periods of host shortage (7, 29).

MECHANISMS UNDERLYING OVARIAN DYNAMICS

Ovarian development responds to variation in the host environment by three mechanisms: (a) Egg maturation is triggered by oviposition, and oviposition varies in frequency with host quality and abundance; (b) hosts serve as a source of nourishment for oogenesis to a degree related to their quality and abundance; (c) host stimuli directly promote egg maturation, again to a degree related to host quality and abundance.

Oviposition-Mediated Effects of the Host

Many patterns in egg maturation cited here can be explained by a simple mechanism: Oviposition begets oogenesis; failure to oviposit begets oosorption. Because oviposition behavior is sensitive to host quality and abundance, a cause-and-effect relationship between oviposition and ovarian development would generate a de facto match between ovarian development and variation in the host resource.

That failure to oviposit begets oosorption is well known (7, 29, 30, 32). Likewise, oviposition is known to facilitate oogenesis. In cockroaches, oogenesis is

stimulated by oothecal deposition (97); oothecal release delivers input (possibly via stretch receptors) along the ventral nerve cord to the brain. Stimulation of the corpora allata by the brain results in production of juvenile hormone (JH); high JH titres transmitted through the hemolymph stimulate oogenesis. In cyclorrhaphous flies, a different mechanism serves the same end. An oostatic hormone produced by the primary follicles in the ovaries inhibits development of more distal follicles. Once eggs are laid, inhibition is released and a subsequent gonotrophic cycle begins (2, 15, 128); involvement of neural input has not been demonstrated in this case.

Does the effect of an oviposition on egg maturation depend on the quality of the last host on which eggs were laid? Does rate of host encounter influence the degree to which oviposition promotes egg maturation? To date, no study has manipulated oviposition history systematically enough to answer these questions [although a step in that direction, with negative results, has been made; (90)].

Nutritional Effects of the Host

Adult nourishment is profoundly important for oogenesis in many insects (126). Of interest here are instances in which insects feed as adults on the same kind of host used for juvenile development. If hosts nourish oogenesis to a degree related to their quality and abundance, ovarian development might, as a consequence, respond adaptively to variation in the host resource.

Adult host feeding in relation to oviposition has been considered in depth for hymenopterous parasitoids (40, 56, 118). The relationship between host feeding and oviposition constitutes a classic example of a trade-off between current and future reproduction, particularly when host feeding renders individual hosts unsuitable for oviposition. Dynamic programming models predicated on this trade-off routinely predict that parasitoids should host feed when egg loads are low (and risk of egg limitation correspondingly high), a prediction generally supported by laboratory data (40, but see 95). Models also predict that parasitoids will restrict feeding to hosts of lower quality and use higher-quality hosts for oviposition, a prediction also supported by data (40).

Developmental realism has been added to models in the form of egg maturation delays and costs of oosorption (16). Nevertheless, in most discussions, ovarian maturation simply tracks oviposition, albeit through an indirect path: Oviposition reduces egg load to levels low enough to stimulate feeding, which in turn facilitates egg production. Does the effect of host-nutrient input on egg maturation depend on the quality of the host used in feeding? Does host abundance influence the degree to which nutrition promotes egg maturation? Can parasitoids regulate allocation of nutrients to reproductive versus somatic processes according to the quality and quantity of host nutrients imbibed? At this point, too little is known about the physiological details of nutrient allocation to reproduction to answer these questions.

DIRECT SENSORY EFFECTS OF HOSTS ON OVARIAN DEVELOPMENT

The discussion thus far provides little evidence of adaptive design in ovarian dynamics. Based on current understanding, both oviposition- and nutrient-mediated mechanisms simply link ovarian development to oviposition, which responds in turn to variation in the host environment. Conceivably, it is oviposition behavior that responds by design to variation in host quality and availability; ovarian dynamics follow only as an incidental consequence. Evidence that host stimuli act as sensory promoters of ovarian development, independent of oviposition or host nourishment, would constitute stronger evidence of design in ovarian dynamics.

Many studies on egg production in host-specific insects were not intended to evaluate direct sensory effects of the host on ovarian development and their experimental design precludes that evaluation. Investigators counted eggs laid rather than dissecting ovaries or, if ovaries were dissected, performed dissections only after eggs were laid. Such methodology cannot distinguish between a direct effect of host stimuli on ovarian development and an effect on egg deposition, which then stimulates production of more eggs (60). In cabbage root flies, for example, exposure to cabbage stimulates oogenesis, but only after some eggs are laid (59). Only by using periods of host exposure prior to dissection that are too brief to permit oviposition, or using surrogate hosts that somehow prevent oviposition, can oviposition-mediated effects be ruled out.

Likewise, in cases where females feed on hosts, it can be difficult to distinguish between nutritional and sensory influences (58). These issues notwithstanding, solid evidence for sensory effects of hosts on ovarian development spans three major orders (Lepidoptera, Coleoptera, and Diptera) in work dating back to the 1960s.

Order Lepidoptera

Host plant stimuli commonly have direct effects on ovarian development in Lepidoptera (4, 8, 21, 44, 82, 91, 112, 113). Hillyer and Thorsteinson's classic work on the diamondback moth, *Plutella xylostella*, showed direct effects of host plants on ovarian development and demonstrated that a single volatile component of the insects' cruciferous host plants, allyl isothiocyanate, induced effects of a magnitude similar to that of whole plants (44). This work is noteworthy for the completeness with which it surveyed the effect of host stimuli and the effects of other factors, such as non-host plants and mating on ovarian development. Exposure to host cabbage for three days following emergence of an adult female hastened onset and degree of ovarian maturation. Two non-host species, pea and wheat, had no effect. An experiment in which screening prevented contact with a cabbage leaf failed to find evidence of an effect of host odor. Nevertheless, females exposed for three days to paper treated with allyl isothiocyanate, a volatile com-

pound known to be an oviposition stimulant for *P. xylostella* (38), retained almost as many eggs per ovariole as females provided access to cabbage, and many more than control females.

Implicit in some of Hillyer and Thorsteinson's experiments is the assumption that male behavior is not influenced by host stimuli. In fact, exposure to host plants accelerates reproductive maturity in males (82). Because mating promotes egg maturation in *P. xylostella* (44), an effect of the host on egg maturation was likely due in part to an effect of the host on mating.

Order Coleoptera

Bruchid beetles have been the subject of a large literature on the role of host stimuli on ovarian development. Egg production in *Acanthoscelides obtectus* has long been known to be greater in the presence of its leguminous host seeds than in their absence (123). This result does not depend on oviposition: After just two days of exposure to host beans and before any eggs were laid, egg load exceeded that of control females not exposed to host beans (62).

Because females do not feed on the beans (83), input from the host must be non-nutritional in nature. Facilitation of egg production required females to make physical contact with beans: Bean odor alone had no effect (83). Assays with ether extracts of beans further suggested that host stimuli were gustatory in nature (75, 83). Amputation experiments indicated that the maxillary palps were required for detection of active components (83).

While *A. obtectus* has been studied most, effects of host beans or bean pods on ovarian development have been demonstrated in at least four other bruchid species (*Brucidius atrolineatus*, *Callosobruchus maculatus*, *Zabrotes subfasciatus*, and *Caryedon serratus*) (20, 84). Ovarian development in all four species is facilitated only when the host plants are at, or nearly at, the phenological stage suitable for feeding by first-instar larvae. Lower-quality hosts do not promote oogenesis. In *B. atrolineatus*, a number of factors, including short photophase, high humidity and host presence, trigger an end to reproductive diapause in both adult males and females. These factors stimulate the previtellogenic phase of ovarian development, during which nurse cells transfer metabolites to oocytes; however, the presence of host inflorescences and bean pods alone or in combination appears to be required for vitellogenesis (36, 51, 64). Inflorescences furnish nutrients in the form of pollen; however, volatile, non-nutritive compounds play a role as well (51). While a nutritional contribution of the pods has not been ruled out, the effect of pods is specific to host cowpeas; presence of non-host legume pods has little or no effect on maturation (64).

The only other beetle family subject to detailed analysis of host resource effects on ovarian development is the carrion-feeding Silphidae. Both the behavioral context and underlying physiological mechanism by which the oviposition resource enhances ovarian development have been described for the burying beetle, *Nicrophorus tomentosus*. During a 15- to 20-day period of post-

emergence feeding on carrion, ovaries increase in mass to a “resting stage” characterized by low titres of juvenile hormone (JH) (114). In this stage, females forage for an oviposition host (a small vertebrate carcass). Upon discovery of a carcass, beetles make dorso-ventral circuits around the carcass. During transits, beetles remove hair or feathers from the carcass, deposit anal secretions that delay decomposition, and shape the carcass into a ball. The prepared carcass is eventually buried in a chamber around which eggs are laid.

Within 24 hours of carcass discovery, ovarian mass increases two- or three-fold (98, 114, 115). To determine whether feeding on the carcass was sufficient to stimulate oogenesis, some females were provided with a mouse carcass and some with pieces of a mouse large enough to feed upon but not large enough to prepare and bury. Proportionately fewer females in the mouse-parts treatment developed ovaries, relative to the whole-mouse treatment, suggesting that feeding alone does not facilitate oogenesis. Evidently, carcass preparation behavior is a prerequisite for ovarian maturation.

The precise stage of host use contributing to stimulation of oogenesis was resolved by assays of JH titres (115). Within 10 minutes of discovery, JH titre approximately doubled and rose to a peak over the subsequent 50 minutes. During that first hour, females palpated, lifted, and circumambulated the carcass, and occasionally plowed through the soil around the carcass. No feeding on the carcass was observed during that period, excluding nutritional input from the host as a factor in stimulation of oogenesis (114, 115).

The primary significance of the burying beetle work lies in its demonstration that the process of host examination is associated with a rapid rise in JH titre that initiates vitellogenesis and consequently egg production (114). No other study of host-specific insects has clearly demonstrated a role for this so-called “master regulator” (sensu 97) in mediating a sensory effect of the host resource on ovarian development. In other respects, this work demonstrates the difficulty of studying host sensory effects on egg production. Precisely what stimuli facilitate oogenesis is not known and could be difficult to determine. Is it host stimuli detected during carcass assessment, proprioceptive input associated with assessment, or something else, perhaps even input from anal secretions deposited on the carcass? If host stimuli are directly involved, during execution of which behavior patterns (palpation, lifting, circumambulation, or plowing) are those stimuli detected? Palpation seems an obvious candidate and ablation studies might furnish answers.

Order Diptera

Both preoviposition period length and number of ovariole cycles in the frit fly, *Oscinella frit*, were influenced by exposure to hosts (43). The number of cycles, computed as egg load divided by the number of ovarioles, for females exposed to hosts was higher than the number of cycles in females held with non-hosts or no plants at all. Among host species, oats stimulated oogenesis more than other graminaceous plants.

Most work relating to host sensory effects on ovarian development involves fruit flies of the family Tephritidae. The difficulty of distinguishing sensory effects of the host resource on ovarian development from nutritional effects is illustrated in work on the olive fly, *Bactrocera oleae*. In field cage assays (31, 32), olives enhanced development of the first clutch, but the effect was attributed to adult feeding on olive juice. It was proposed that flies imbibe bacteria on the olive surface that liberate nutrients in the gut and thereby promote ovarian development (32, 61).

Evidence of direct sensory effects of host olives on oogenesis was put forward in two studies relating presence of wax domes (a kind of surrogate fruit) to high rates of egg maturation (35, 60). However, one study (35) used oviposition counts exclusively, possibly confounding direct sensory effects on ovarian development with indirect effects mediated through oviposition (60). Experimental design helped eliminate this problem in the second study, but results were mixed (60). In three assays, wax domes had a significant effect (though substantially weaker than that of real fruit) but in four assays there was no effect at all. In all assays, olives strongly promoted ovarian development.

Work on a tephritid fly, the walnut-infesting *Rhagoletis juglandis*, demonstrated that host fruit influenced egg maturation and ruled out both oviposition and host feeding as factors (3). In initial experiments, host fruit enhanced egg load; host foliage, by contrast, had no effect. A small number of eggs were laid in fruit during these manipulations, leaving open the possibility that egg maturation was facilitated by oviposition. This possibility was ruled out with the use of yellow plastic spheres that resembled fruit in shape and size. Females vigorously attempted to oviposit into these surrogate fruit, but because the plastic could not be penetrated with their ovipositors, eggs were never laid. Mean egg load of flies held with surrogate fruit was significantly higher than that of control flies and similar to that of flies held with real fruit. Because surrogate fruit provide nothing in the way of nutrition, oogenesis enhancement evidently does not require nutrients from host fruit. The possibility remains that host stimuli promote non-host-based nutrient uptake. In the absence of a protein source, no eggs are produced, regardless of the presence of surrogates (D Papaj, H Alonso-Pimentel, and C Nufio, unpublished data).

In *R. juglandis*, both shape and color play a role in the enhancement of oogenesis by host fruit (3). In one experiment, mean egg load of flies held with a yellow sphere was significantly greater than that of control flies or flies held with a yellow cube of like surface area. Either tactile or visual stimuli could account for the shape effect. In another experiment, mean egg load of flies held with green and yellow spheres (colors most similar to yellow-green walnut husks) was significantly higher than that of flies held without spheres. By contrast, mean egg load of flies held with blue, black, or red spheres was not significantly higher than that of flies held without spheres. Whether ovarian development is responding to hue, saturation, intensity, or some combination of these factors is unclear, but visual stimuli are almost certainly involved.

Finally, exposure to host stimuli both hastens onset of vitellogenesis and increases the proportion of oocytes undergoing vitellogenesis. A detailed morphological analysis (A Lachmann and D Papaj, unpublished data) revealed that host experience during the first gonotrophic cycle influenced maturation of each of the first two follicles in a given ovariole. Maturation of the second follicle in a given ovariole does not ordinarily begin until the first follicles in all ovarioles contain mature, chorionated eggs. Females provided with surrogate fruit commonly matured eggs in all first and many second follicles; in contrast, females deprived of access to a surrogate fruit almost never matured the full complement of first-follicle eggs and, evidently for this reason, rarely initiated vitellogenesis in second follicles.

Host Sensory Cuing in Relation to Host Quality and Availability

Whether efficacy of sensory cuing of ovarian development depends on host availability (beyond mere presence versus absence) is an open question. Manipulations of host availability have simply not been carried out in this context. However, data cited here indicate that efficacy of sensory cuing of ovarian development depends on host quality. First, effects of plant stimuli vary according to host status. Non-host stimuli have little or no effect. Second, different host species vary in their effect on ovarian development. Whether such effects correlate with either oviposition preference or juvenile performance is often unclear. Only in bruchid beetles is there clear evidence that sensory cuing is sensitive to variation in the suitability of the host for juvenile growth and survival.

The overall impact of host sensory input on egg maturation is difficult to gauge. Evidence for direct host sensory effects on ovarian maturation to date is restricted to the first gonotrophic cycle; effects in subsequent gonotrophic cycles (which may comprise the greater part of a female's lifetime fecundity) have not yet been distinguished from facilitative effects of oviposition.

CONDITIONS FAVORING OVARIAN RESPONSES TO HOST VARIATION

Sensory cuing of ovarian development by host resources constitutes reasonably strong evidence that ovarian development is matched, by design, to variation in the host environment. But is it good design? Why should ovarian development be forestalled until host stimuli are detected? At least three conditions favor adjustments in ovarian development in response to variation in the host resource. First, the host environment must be unpredictable over time and/or space (although, as later discussed, not too unpredictable). Second, there must be a trade-off, such that costs and benefits of ovarian development trade off against those of some other process contributing to fitness. Finally, host stimuli must be

more useful indicators of the status of the host environment than other stimuli. Each condition is addressed in turn below.

Uncertainty of the Host Environment

For sensory cuing of ovarian development to be adaptive, the host environment must be unpredictable in time and/or space. To take an obvious example, if hosts were continuously available, timing of development could be regulated internally (or according to another extrinsic factor). Illustrative of the role of uncertainty in host cuing of ovarian development is a pattern of inter-population variation in the bruchid beetle *A. obtectus* (49, 50). Females of a strain originating from higher elevations (2000 m) develop more slowly and depend more on the presence of host pods and seeds for onset of vitellogenesis than females originating from lower elevations (1000 m). The greater reliance of high-elevation females on host stimuli is evidently a consequence of a higher level of uncertainty in host conditions. At low elevations, hosts are continuously and reliably available; at high elevations, there is considerable year-to-year variability in host availability. An analogous pattern of population variation was reported in the parasitoid *A. tabida* (27).

Trade-Offs Associated with Ovarian Development

In order for host sensory cuing or other host effects on ovarian development to be adaptive, egg maturation must trade off against another process or set of processes important to fitness. Otherwise, all insects would have all eggs ready to lay at the time that reproductive competence is first achieved. The body of life history theory equipped to deal with these trade-offs is only now being brought to bear upon the details and diversity of ovarian development. At present, two kinds of trade-offs, survival-reproduction trade-offs and dispersal-reproduction trade-offs, appear to have special significance for ovarian dynamics in relation to the host resource.

Survival-Reproduction Trade-Offs

Pouzat et al (84) suggested that forestalling oogenesis until suitable host beans were available improved bruchid beetle survival during periods unfavorable for oviposition and so accounted for an observed effect of host stimuli on oogenesis. This proposition implies that investment in reproduction trades off against survival. Survival-reproduction trade-offs are common in insects (26, 27, 92). In *Asobara tabida* parasitoids, for example, females allowed to deposit eggs die sooner on average, indicative of a survival-reproduction trade-off. Egg production appears to involve a "borrowing" against lipid reserves that could otherwise be used to prolong longevity (26).

In a lady beetle, *Epilachna niponica*, a specialist herbivore on thistle, females turn egg production on and off according to the availability of larval food plant (77, 78). Oosorption increased seasonally as host availability declined, a change coincident with increased female survival. Oosorption also increased in response

to habitat perturbation such as flooding, which reduced host availability. Increased female survival associated with oosorption demonstrably improved chances of future oviposition in a subsequent season, thereby increasing a female's lifetime reproductive success.

Precisely how reproduction affects survival is rarely known and may be complex. In the bruchid beetle *Callosobruchus maculatus*, two distinct survival trade-offs are associated with egg production (110). An early trade-off was conditional upon current diet and possibly related to depletion of energy reserves. A late trade-off was independent of diet and may reflect senescence. Both trade-offs depended on an interaction between early reproduction and nutritional state at the time of reproduction. High food availability at a time of intensive egg production abolished the early trade-off and mitigated the late trade-off.

Sensitivity of survival-reproduction trade-offs to diet can profoundly affect patterns of senescence in host-specific insects. Mediterranean fruit flies postpone senescence when deprived of protein, a nutrient required for egg production (14). The remaining life expectancy for a protein-deprived individual that had already lived 60 days, for example, was not detectably shorter than the remaining life expectancy for a deprived fly that had lived just 30 days. In effect, protein-deprived females entered a "waiting mode" during which they evidently minimized reproductive costs that would reduce survival. Once protein was furnished in the diet, females began producing eggs and remaining life expectancy rapidly declined. Curiously, the decline depended little on the length of time over which protein was deprived. This dual mode of aging presumably results in higher reproductive success than a single determinate mode that is independent of protein intake. It would be interesting to know if, in addition to protein, host stimuli facilitate transfer to a reproductive mode.

Finally, while survival-reproduction trade-offs must often reflect competition between egg maturation and survival-related processes for a limited pool of nutrients, there may be other causes. Reproduction may, for example, inflict some somatic insult that directly reduces survival (110). Only by manipulating both egg production and nutrient availability in assessments of trade-offs can these alternatives be distinguished. This is rarely done and so little can be said regarding the extent to which nutrient allocation underlies reproduction-survival trade-offs.

Dispersal-Reproduction Trade-Offs

In an environment that is patchy with respect to host quality or availability, females may need to disperse to find hosts. Host sensory cuing of ovarian development or, more generally, any matching between ovarian development and host conditions, might be of particular benefit if producing eggs trades off against effective dispersal (3, 44). Dispersal-reproduction trade-offs are common in host-specific insects (52, 100, 101) and are central to the so-called oogenesis-flight

syndrome, wherein oogenesis and dispersal tend to be separated in time over an insect's life (22).

In some cases, dispersal-reproduction trade-offs are a special case of survival-reproduction trade-offs. Long-winged forms of the cricket, *Modicogryllus confirmatus*, for example, have lower fecundity during early adult life than short-winged forms have (107). Forms did not differ in fat content at emergence, implying that the difference in fecundity is related to nutrient allocation in the adult (109). Moreover, longevity was strongly negatively correlated with egg production, suggesting that the apparent dispersal-egg production trade-off is actually a survival-egg production trade-off, in which long-winged females mainly allocated energy from food to flight muscle development and somatic maintenance, whereas short-winged females allocated it to egg production and longevity.

In other cases, dispersal-reproduction trade-offs are better framed as egg production-reproduction trade-offs. If egg maturation reduces an insect's ability to find a resource required for oviposition, for example, realized fecundity may paradoxically be diminished by egg maturation, even if survival is unaffected. Under such conditions, an insect may profit by forestalling egg maturation until hosts are found. How maturation of eggs hinders dispersal to host habitats is not well understood. Possibly, nutritional investment in eggs trades off against investment in flight muscle, as in crickets (74; see also 126). There may be a basic metabolic cost of maintaining an egg load (3, 7, 16, 90). Alternatively, dispersal effectiveness may be affected by the eggs themselves. In one of few measurements made of this type, a batch of mature eggs in a sarcophagid fly's ovaries reduced lift production during flight by 40% (10).

Host Stimuli As Useful Indicators Of Host Conditions

Phenotypic plasticity theory predicts that the adaptive value of tracking environmental change will depend on the occurrence of cues that are reliably correlated with changes in the environment (76). It is not a given that host stimuli, whether through ovipositional, nutritional, or sensory routes, are predictive of host conditions. Because making eggs takes time (16, 120), host stimuli will be predictive only if conditions at the time that oogenesis is stimulated are correlated with conditions at the time of egg laying readiness. Thus, while uncertainty in the host environment is a prerequisite for sensory cuing of ovarian development, the host environment must not be too uncertain. To paraphrase a remark made by Stephens in regard to learning, today's host environment must tell the insect something about tomorrow's host environment, or host-mediated cuing of ovarian development will have little value (104).

Even if host stimuli are the most reliable signals of changes in host conditions, they are not necessarily the most useful. For example, where host availability is highly seasonal, photoperiod or temperature changes may be nearly as reliable as host stimuli in predicting the appearance of hosts. Moreover, such cues may provide an earlier indication of host availability than stimuli from the host itself.

Where intraspecific competition places a premium on having eggs ready as soon as hosts are available, the early warning provided by photoperiod or temperature cues may make these cues more valuable than host cues themselves. In fact, photoperiod (1, 6, 55, 70, 108, 117) and temperature (6, 32, 117) commonly influence both reproductive diapause and termination of diapause in host-specific insects. Similarly, where mating occurs in close association with the host, mating rather than host input may regulate ovarian development. In the seedcorn fly, *D. platura*, host priming of egg production may reflect in part a facilitatory effect of the host on mating, which in turn stimulates egg production (124, 125).

Host stimuli must commonly interact with a variety of factors, including temperature, humidity, photoperiod, mating status, and social context (11, 19, 64, 82, 125). In *Anastrepha* flies, extensive systematic manipulations of host stimuli, adult diet, male pheromone, and social context revealed the existence of complex, higher-order interactions among factors in effects on egg production (63). Presumably, such interactions permit insects to cope better with uncertainty in an assortment of ecological factors than in the absence of such interactions.

Finally, certain host stimuli might be more useful than other host stimuli as predictors of host conditions. Long-range cues, such as host odor, may be less useful than short-range cues, especially if egg production trades off against the ability to travel to far-away hosts. Some host stimuli such as nutrients may act more directly on oogenesis than other stimuli and may be less costly in terms of sensory reception and neural processing. In this regard, JH itself, or a JH mimic that directly regulates onset of vitellogenesis, might be an ideal signal. In *Varroa* mites, the host honey bee's JH, ingested during host feeding, promoted oogenesis (39). Conceivably, specialist herbivores might exploit JH analogs found in host plants for the same purpose.

COEVOLUTIONARY ASPECTS

Plant Defenses Aimed at Ovarian Development

In examining the adaptive value of ovarian dynamics in relation to the host resource, the evolutionary interests of the host have so far been neglected. Yet hosts and their insect enemies are involved in a coevolutionary arms race, and hosts might conceivably evolve defenses that suppress oogenesis or facilitate oosorption in insects that attempt to consume the hosts (cf. 85). The evolutionary potential for such defenses is illustrated in a recently discovered pattern of resistance in Sitka spruce against white pine weevils (*Pissodes strobi*) (96 and references within). Feeding on resistant spruce genotypes causes ovarian regression in female weevils, an effect attributable neither to decreased feeding nor to reduced oviposition. Resistant and susceptible trees do not differ in content of phagostimulants and deterrents; moreover, JH treatment of weevils feeding on resistant leaders restores ovarian function. The possibility that feeding on resistant

leaders blocks JH function suggests that *P. strobi* may be affected in diverse ways. Because JH regulates oogenesis and dispersal in a complementary manner (22), blocking of JH function may not only inhibit oogenesis but also increase insect dispersal from the resistant tree. Given the central role of JH in insect development (97), circumventing such a defense may pose an evolutionary challenge to the weevil.

Ovarian Dynamics and Host Specialization

Ovarian development has received surprisingly scant attention in discussions of the evolution of host specialization. Yet surely host specificity (sensu 102) could be as much a function of specificity in sensory cuing of oogenesis as it is a function of specificity in host acceptance behavior, for example. Estimates of host preference that do not take into account the effects of the host on ovarian development may be misleading (121).

Level of specialization is associated with the pattern of ovarian maturation in some tephritid fly species. In the specialist olive fly, *Bactrocera oleae*, the proportion of gravid females in a population declined as an early-season olive crop disappeared (32). This decline was due in part to suppression of oogenesis in newly emerging females and in part to ovarian regression (including both cessation of oogenesis and onset of oosorption) in older females. Ovarian maturation resumed as a late-summer crop of olives became available. Similarly, egg maturation in three Australian dacine specialist species, *Bactrocera cacuminatus*, *B. cucumis* and *B. jarvisi*, was retarded when females were deprived of hosts (28). The first two Australian species exhibited no decline in host selectivity in response to deprivation, whereas the third did.

Egg maturation in the highly polyphagous *B. tryoni*, in contrast, continued unabated and egg load increased steadily over a period of host deprivation, a pattern accompanied by a decline in selectivity (28). These species differences in ovarian development make sense intuitively. A specialist faced with a shortage of hosts can either disperse to find hosts or wait out the period of scarcity. In the face of a dispersal-reproduction and/or survival-reproduction trade-off, reducing egg production might improve dispersal and/or ensure survival. A generalist faced with a shortage of a host species, by contrast, can resort to use of alternative species. At emergence, the generalist would use the most preferred host. However, if that species was not available, eggs would accumulate, selectivity would decline, and less preferred species would be used.

Trophic Patterns in Sensory Cuing

Evidence of host sensory effects on ovarian development in entomophagous parasitoids is conspicuously lacking. Possibly, the absence of evidence on sensory cuing of ovarian development in parasitoids reflects a lack of attention to the appropriate cues. Signals that influence ovarian development might derive not from the host directly but, as is the case for signals involved in host finding (116,

122), from the host's resource (for example, a plant exploited by a parasitoid's host). The rationale for involvement of a third trophic level is derived from co-evolutionary theory. The host insect is expected to evolve ways to conceal itself from a parasitoid and thus its cues, though reliable, may not be highly detectable. The host's food plant is under no such selection and may, in fact, be selected to signal the herbivore's presence to natural enemies. Such signals, while highly detectable, are indirect indicators of host presence and may be less reliable than host cues; in terms of host finding, this reliability problem is mitigated by parasitoids through learning (116, 122). It is conceivable that a third trophic level plays a role in sensory cuing of ovarian development in parasitoids, and even that something analogous to learning is involved.

Alternatively, conditions favoring sensory cuing may be uncommon in parasitoids. Synovigenic parasitoids frequently host feed (29, 40, 56), perhaps precluding and at least obscuring sensory cuing. Moreover, use of yolk-deficient, hydroptic eggs by some hymenopterous parasitoids (29) may significantly lower costs of egg maturation and thereby relax selection for its timing. Not surprisingly, parasitoids with hydroptic eggs are often pro-ovigenic, oogenesis being completed by eclosion and, thus, well before females encounter hosts (29, 30).

CLOSING REMARKS

Biologists tend to put physiology in one box and behavior in another. Evidence of sensory cuing of oogenesis suggests that, in terms of mechanisms, insects blur the boundary between ovarian physiology and oviposition behavior. In this regard, one future direction for research is an in-depth comparison of host stimuli cuing ovarian development and host stimuli used in oviposition. Evidence to date suggests that stimuli affecting oogenesis overlap broadly with those eliciting oviposition. However, if each set of stimuli is tuned to the particular ecological context (for example, the phenological context) in which ovarian development or oviposition behavior is initiated, differences in stimuli might be subtle and require close examination to detect.

Another issue worthy of attention is the extent to which our understanding of dynamics in oviposition behavior (an area of intensive research in host-specific insects) depends on an understanding of ovarian dynamics. We need to intensify our study of mechanisms underlying ovarian dynamics. Such knowledge is worthwhile for its own sake but will also improve the sophistication with which models of oviposition behavior depict ovarian development.

We also need to give thought to the separate contributions that ovipositional and ovarian dynamics make to effective host use. One obvious difference between the two sets of dynamics is the scale of variation over time and space to which each is best suited to respond. Ovarian responses to environmental change, though dynamic and adaptive in form, are comparatively slow (16). As such, oviposition behavior can respond to a finer scale of variation in the host resource than can

ovarian maturation. Other differences may be found in the details of trade-offs affecting oviposition on one hand and ovarian development on the other. The diversity in patterns of host use is likely to reflect in part a diversity of interactions between ovarian development and oviposition behavior.

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