

## MINI- REVIEW

**Minireviews** provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

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### Modification of adverse conditions by insects

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Many insects modify their environments directly, rather than merely choosing available sites that are already favourable. The modifications are carried out by making excavations in soil and other substrates, constructing feeding or resting shelters, inducing plant responses such as galls, aggregating, building colonial nests, and through parental actions. Such environmental modifications are briefly reviewed and related to the conditions that they modify. Some of the modifications offset physical factors such as dryness or flooding and cool or freezing temperatures. Others reduce the effects of natural enemies or enhance food resources. These effects have seldom been quantified and much of the evidence is anecdotal, but preliminary generalizations are made from existing information. Although potential roles often overlap, excavations and shelters protect especially against physical factors, while aggregations, colonies and parental actions more often influence the acquisition of resources. How modifications affect the impact of natural enemies differs among different kinds of enemies and is especially difficult to test. In any event, adaptive local modifications of the environment by insects are shown to be widely distributed and important. However, their specific roles have often been assumed rather than tested, or have been overlooked along with the potential interdependence of different effects. Therefore, environmental modifications should be considered explicitly and examined with greater rigour during the study of insect life cycles.

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Many insects escape or shelter from potential adversity by moving elsewhere for lesser or greater distances. Others withstand or tolerate extreme conditions directly through physiological and other adaptations. These two sorts of responses have been reviewed many times (Danks 1991, 1996, 2000a, and references cited there, Drake and Gatehouse 1995). However, many insects also mitigate the impact of adverse conditions by mod-

ifying local environments, for example by actively excavating or constructing shelters, rather than simply choosing existing protected sites. This paper considers these mechanisms of local environmental modification, which have not previously been examined as a whole in this way. Potentially adaptive modifications influence three sorts of conditions: physical factors such as temperature and moisture; natural enemies such as preda-

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tors and parasitoids; and resources, including both the quantity and quality of food.

Excluded here, however, is the simple choice of alternative but already available microhabitats. For example, many species bask in sunshine while active in favourable microsites, feed preferentially in pre-existing shelters (Larsson et al. 1997), or enter protected sites such as litter for dormancy (Danks 1991). Certainly the conditions they experience are thereby different from ambient, but the environment has not been modified by the insect in any way. The same exclusion applies to nests or other pre-formed cavities when they are adopted by species that did not make them (Kojima 1993, McIntyre 1999). Even when the choice of habitat is assisted by chemical signals, as for the oviposition cues of mosquitoes, the habitat is only "modified" if it is then more easily altered by group action (see Aggregation). Also excluded are instances in which the habitat is modified incidentally and not as an adaptive component. For example, ants may change the chemistry of soil near their nests, influencing local plants (Dean and Yeaton 1993). In the same way, periodical defoliation of host trees by certain caterpillars is a by-product of the feeding of dense populations, and is not "adaptive" for those caterpillars in a consistent and focussed way. Excluded here too, of course, are individual morphological adaptations, such as those that allow water vapour to be condensed.

Based on available information in the literature, this paper briefly reviews the types of local modifications by insects and the likely conditions that they modify. It demonstrates that such adaptive features are widely distributed and thus significant for the study of life cycles, but it also demonstrates that little critical or quantitative analysis of their roles has been undertaken. These findings highlight the need for more rigorous examinations of the functioning and value of local environmental modifications, in the same way that Price et al.'s (1987) assessment of the role of plant galls in improving micro-environments, supplying resources, or protecting the occupants from predators helped to foster more critical tests of these hypotheses. Some preliminary generalizations are made from existing information in order to promote such examinations.

## Excavations

Digging into substrates allows species to construct a shelter by simply removing rather than secreting or collecting material. Many species build such burrows or mines for short-term or long-term use. For example, some males of the bee *Andrena nivalis* Smith excavate short sleeping burrows in soil (Miliczky et al. 1990), although females sleep in the nest. Special overwintering burrows are built in soil (e.g. some spiders and

carabid and chrysomelid beetles: Miyashita 1997, Montero and Lietti 1998, Noronha and Cloutier 1998) and wood (Sugiura 1995), and other species overwinter in stems and seed heads and other substrates. Soil burrows or earthen cells may be stabilized by a silk lining, as are the pupation chambers of many moths.

The likely values of such excavations are summarized in Table 1. Burrows certainly protect against physical conditions. Many authors have noted the protection against desiccation afforded by the burrows of desert arthropods such as scorpions, spiders, termites and tenebrionid beetles (Crawford 1981, Hadley 1994, pp. 292–4, Rasa 1994, Henschel 1998), which may adjust burrow depth and location in response to desiccation stress (Rasa 1994, 1999; cf. Williams 1995). The mines of the moth *Nepticula castanopsiella* Kuroko are warmer in sunshine than the air temperatures in winter (Kino 1981). The burrow nest of the anthophorid bee *Epicharis zonata* Smith is lined by resin, allowing the occupants to survive below the water table (Roubik and Michener 1980).

Such shelters also protect some species from predation and parasitism (Table 1). *Cotesia* parasitoids of stem borers suffer 30 to 40% mortality in the boring as the host larvae can defend themselves by biting and spitting inside the boring (Potting et al. 1997). Chironomid larvae that burrow more deeply into the substrate suffer lower predation (van de Bund and Groenenkijk 1994). Nevertheless, except for their role in maintaining humidity, the function of many excavations has not been tested directly. For example, Connor and Taverner (1997) believe that the leaf-mining habitat avoids climatic stress, predators, surface plant defences and diseases, and also combines shelter with feeding, and Shook (1978) supposed that the entrance turret of the burrow of the spider *Lycosa carolinensis* Walck. may protect against predators as well as against sand and flooding. Moreover, the adaptations reflect compromises. For example, mining in the shoot is more protective than mining in the leaves for the cabbage webworm *Hellula undalis* (Fab.), but the quality of the food that the shoot supplies is poorer (Sivapragasam and Chua 1997).

## Feeding and resting-stage shelters

Many species construct shelters during the feeding stage. Leaf eaters may make a leaf shelter by curling or rolling leaves, and many lepidopterous larvae tie leaf edges together with silk. For example, first instar hesperiid larvae cut and curl the leaf (Nakasuji 1987); feeding by aphids reduces leaf turgor and may roll the leaf (Burd et al. 1998); even some spiders use rolled leaves to shelter and mate (Taylor and Jackson 1999). Some insect larvae are communal, constructing silken

Table 1. Insect modification of adverse conditions by means of excavations.

Major element	Modifications demonstrated or reliably inferred against:	Modifications less prevalent or inadequately tested against:	Widespread features	Other correlations
Physical factors	Dryness, flooding, heat, cold, freezing, displacement, mechanical damage	Toxicity	Especially for protection against water loss and heat or cold	Especially in desert and steppe habitats in summer, and in cool temperate habitats in winter
Natural enemies	Predators, parasites	Diseases		Deeper burrows have more potential protection
Resources	Some excavations are made in edible substrates	Excavations seldom respond to the adversity of resources as such		
Combined elements	Interaction between physical protection and food quality	Multiple roles (e.g. physical factors and predation) often assumed but seldom demonstrated		Most combinations reported for herbivores

tents over the leaves (Floater 1996). Many of these shelters appear to combine protection and feeding. For example, some species that tie or web the leaves to form a shelter also skeletonize them (Davis 1991). Spider webs, of course, are primarily food snares, and there are even species that elaborate complex communal webbing (Downes 1994). Although a few species remain in these shelters (which typically are fairly lightly constructed) when feeding is complete, and pupate or even overwinter there (Goeden and Teerink 1997, Day et al. 1998), most species leave them to pupate in still more protected sites or structures.

A second set of species constructs separate protective structures, either mobile or stationary. The feeding tube of some chironomid midge larvae is made chiefly of salivary proteins (Galli and Wieslander 1993), although other larvae (e.g. other chironomids, caddisflies, coleophorid moths) cement together substantial amounts of substrate material. The palisade sawfly *Stauronematus compressicornis* (Fab.) constructs around itself a barrier of dried saliva (Codella and Raffa 1993). Larvae of the chrysomelid beetle genus *Oulema* construct a faecal case over the thorax and abdomen that is considered beneficial for camouflage, repelling predators and reducing water loss, although the faecal particles may attract parasitoids (Wellso and Hoxie 1988). Some caterpillars construct frass chains to rest on, which do not cover the larvae but rather isolate them from predators walking on the leaf surfaces where the larvae have been feeding (Machado and Freitas 2001).

A very large number of species build longer-lasting cocoons or other shelters to modify the conditions to which their potentially vulnerable resting stages are exposed, for example during diapause. Some parasitoids use modified host remains or mummies in the same way (Hippa and Koponen 1984, many aphid parasitoids). It has proved easier to test the effectiveness for various purposes of these relatively durable and immobile structures than to test the generally more flimsy and ephemeral feeding shelters. Resting-stage structures of generations that survive prolonged adversity characteristically are much more robust than those of non-diapause generations (Bartell et al. 1976, Mello and Garafalo 1986, Donovan 1991; many examples described in Danks 1987, Table 6). At the least, shelters are sealed for winter (Olsson 1981, Elliott 1982). Many such shelters are firmly attached to their substrates, presumably reducing potential mechanical injury of immobile individuals by wind and other forces.

The roles of shelters are summarized in Table 2. Feeding shelters have generally been supposed to enhance physical conditions. For example, temperatures are increased in the shelters of tent caterpillars (Joos et al. 1988). The tents of feeding larvae of the moth *Yponomeuta mahalebella* Latr. tend to be orientated to the south, raising the temperature and producing better

Table 2. Insect modification of adverse conditions by means of feeding and resting shelters.

Major element	Modifications demonstrated or reliably inferred against:	Modifications less prevalent or inadequately tested against:	Widespread features	Other correlations
Physical factors	Dryness, flooding, heat, cold, freezing, oxygen limitation, toxins, displacement, mechanical damage		Most resting shelters are relatively robust	Several simultaneous protective roles, especially in difficult habitats such as unstable substrates and where ice formation is likely
Natural enemies	Predators, parasites	Diseases	Shelters commonly more effective against generalist than specialist invertebrate enemies	Structures may serve in camouflage or diversion as well as direct protection
Resources	(See below)	Some shelters may secure food from competitors, or help exploit it by allowing mass feeding		
Combined elements	Combined shelter and use of food resources		Shelters are often made from leaves or other food material	

survival and growth and so heavier adults (Alonso 1997). Cases of some caddisfly larvae retain water and help the occupants to resist drying (Zamora-Munoz and Svensson 1996). The tubes of chironomid larvae can be ventilated by body undulations (Leuchs 1986), so increasing oxygen supply. A bubble held in the nests of terrestrial spiders acts as a physical gill, preventing drowning (Rovner 1987).

Cocoons of many species protect against dry environments. For example, cocoons of a range of species have been shown to act as a humidity buffer and reduce transpiration of their occupants (Nowbahari and Thibout 1990, Rosner and Führer 1996, Tagawa 1996). Aestivating chironomid larvae survive in special aestivation cocoons (and see below) (Hinton 1960, Edward 1968, Hudson 1971, Jones 1975, Grodhaus 1976, 1980, Delettre 1988). Finally, some cocoons can absorb water (Nowbahari and Thibout 1990). Alternatively, cocoons modify conditions that are too wet. For example, the cocoon of the lacewing *Chrysopa perla* (Linn.) protects the prepupa from immersion in water (Sagné and Canard 1984). Cocoons of the moth *Leguminivora glycinivorella* (Matsumura) protect against flooding, and also against ice inoculation (Sakagami et al. 1985).

Most rather small structures would be expected to have little effect on the temperatures of their occupants. However, pupal cocoons of the arctic moth *Gynaephora groenlandica* (Wocke) accelerate development by trapping solar heat (Kevan et al. 1982 (as "*G. rossii*"), Lyon and Cartar 1996).

Cocoons may protect the occupants from the effects of freezing temperatures, especially by preventing contact of the insect with ice which otherwise would lead to freezing by inoculation (example cited above; see also examples below for egg structures made by parents). The winter cocoons of chironomids, tightly applied to the folded larvae, appear to protect against damage from ice which otherwise would cause mechanical injury as it expands during the freezing process in aquatic habitats (review by Danks 1971b; Danks and Jones 1978, Kornijów 1992). The similar chironomid drought cocoon would likewise protect against mechanical injury of the dormant animal (Hinton 1968).

Protective coverings also change predation rates (Table 2). For example, caterpillars within folded leaves are less susceptible to predators (Loeffler 1996). Dragonfly larvae take more naked than covered chironomid larvae (Dillon 1985). Caddis cases protect the soft posterior body from predators. Otto (1983) showed that a caddis with a stout case remained there under simulated bird attacks, whereas a species with a flimsy case left it at the first disturbance. Likewise, the retreats and barrier webs of spiders can act as a physical barrier against natural enemies (Silverman and Appel 1984, Morewood 1991, Cloudsley-Thompson 1995). The spittle of spittle bugs has been supposed to protect the occupants against desiccation, but it does not appear to

Table 3. Insect modification of adverse conditions by means of induced plant responses.

Major element	Modifications demonstrated or reliably inferred against:	Modifications less prevalent or inadequately tested against:	Widespread features	Other correlations
Physical factors	Desiccation, displacement	Other physical factors	Desiccation is a particular challenge for small organisms	All gall formers are relatively specialized, and relatively small in size
Natural enemies	Predators, some parasites	Some parasites, diseases	Gall tissue protects some species against generalist enemies	Convincing evidence for protection against natural enemies is more limited than for other elements
Resources	Reduced or unavailable food or nutrients, plant defences	Competitors	Plant induced to actively supply resources	
Combined elements	Physical factors and resources		Concurrent adaptations to physical factors and plant resources well demonstrated	

reduce water loss (Turner 1994); presumably the spittle protects chiefly against predators. Some of the silken webs or shelters, as well as faeces for example, also deter parasitoids (Gross 1993) although, again, the level of protection they afford is often uncertain (Lei and Camara 1999).

The longer-lasting external structures built by resting stages, such as cocoons, also protect against natural enemies. Some cocoons comprise two or more layers, such as a protective shell and a layer of loose threads or flocculent silk, which can serve to impede different types of predators (cf. Hieber 1992 for spider egg cocoons). Cocoons could also serve for diversion against predators or camouflage, and some spiders include silk structures or detritus in their webs, apparently for this purpose (Cloudsley-Thompson 1995). The cocoons of some species differ in colour at different times of year (Danks 1987, Table 6).

### Induced plant responses

Many kinds of insects induce galls on plants. The relationships are specialized ones on particular plant parts. Galls can supply the gall former with physical protection, protection from natural enemies, and food resources (Table 3) (see Cornell 1983, Price et al. 1987, Price and Pschorn-Walcher 1988, Clancy 1993, Stone and Cook 1998 for sample discussion). Of course, not all gall-insect relationships show all of these potential features. Because galls are high-value resources that combine food and shelter, they may be occupied for more than one generation and often are defended (Crespi 1992, Inbar 1998).

Most galls are relatively small, and so provide little temperature buffering (Baust et al. 1979, Layne 1991, 1993). However, they supply a potentially moist environment compared to the surroundings, or at least a source of water. For example, galls of the cynipid *Antistrophus silphii* Gillette have increased photosynthesis and increased xylem potential, which may buffer the gall maker from stress during drought (Fay et al. 1993).

Galls provide protection from natural enemies, especially more generalized ones, at least when the galls are fully formed. For example: parenchymatous gall tissues protect cecidomyiid gall makers from predation by moth larvae (Abe 1997); cynipids found deepest in the gall are least attacked by parasitoids (Jones 1983); tortricids in galls have less parasitism than free-living ones (though gallers are relatively rare) (Mills 1993). Abrahamson et al. (1991) supposed that the phenolic “defensive” reaction of the plant to the gall maker might protect the gall maker from predators. However, although in the tephritid fly *Eurosta solidaginis* (Fitch) larger galls give much better protection against insect parasitoids they elicit more attacks by birds (Weis and Abrahamson 1985, 1986, Walton 1988).

Table 4. Insect modification of adverse conditions by means of aggregation and social colonies.

Major element	Modifications demonstrated or reliably inferred against:	Modifications less prevalent or inadequately tested against:	Widespread features	Other correlations
Physical factors	Dryness and cold for aggregation; Dryness, flooding, heat, cold, freezing, displacement, etc. for social insects	Other factors for aggregation	Many features can be modified, but there are wide differences among species	Potential group effects such as synchronized development
Natural enemies	Predators, some parasites	Diseases, some parasites	Chiefly effective only for some kinds of predators; less defence against specialist parasitoids	
Resources	Unavailable food, defences	Competitors	Group actions condition the food or overwhelm host defences	Colonies can obtain dispersed resources
Combined elements	All elements combined in advanced social insects			

Galls provide resources as a result of the plant's response to the gall maker. In this way, the gall comes to be lined with specialized nutritive cells (Shorthouse 1993) or a direct phloem supply (Wool et al. 1999), for example. Nevertheless, plant resources and the gall maker are in balance, so that galling fails on small shoots that have too few resources (Roininen and Danell 1997), or on large shoots that cannot be stimulated enough by the gall former (McKinnon et al. 1999).

Modification of plant structures by galling may also prove to be adaptive on a longer time scale. For example, shoot killing by high populations of gallers stimulates more gallable shoots the next season (Craig et al. 1986). Aphids feeding on maple inflorescences change the pattern of alternate-year seed production, reducing key fruits and thus leading to more inflorescences to feed on the next year (Furuta 1990).

### Aggregation and social insects

Under some circumstances, individuals improve their local environment by aggregating (Table 4). For example, aggregated young caterpillars of *Imbrasia belina* (Westwood) maintain their bodies at a relatively high temperature that is equivalent to that of the solitary larger instars (Klok and Chown 1999). Benton and Crump (1979) reported that temperatures were higher and buffered in aggregations of the lady beetle *Coleomegilla maculata* (DeGeer), though elevated temperatures have not been reported in aggregations of some other species. Aggregations form at low humidities in some cockroach nymphs (Dambach and Goehlen 1999), and water loss is reduced in aggregations of *Imbrasia belina* (see above) and other caterpillars (Willmer 1980, Fitzgerald 1993), desert tenebrionid beetles (Rasa 1997), and a tropical endomychid beetle (Tanaka et al. 1988, Yoder et al. 1992, Denlinger 1994).

The role of aggregation in protecting against predation is equivocal, because vertebrates may feast on aggregated dormant insects (Mattson et al. 1991, White et al. 1998). However, aggregation has been supposed to provide some protection to individuals against predators, for example by reinforcing aposematic colouration or by dilution (Sillén-Tullberg 1988, 1990, Stamp and Bowers 1988, Vulinec 1990), though not necessarily against all kinds of predators (Stamp and Bowers 1988). Aggregation may also confuse predators (Foster and Treherne 1981 for marine water striders), or reduce the cost of providing rewards to ant "guards" (Axen and Pierce 1998). On the other hand, aggregation may increase vulnerability to some parasitoids, especially those attacking undefended egg-masses. Of course, aggregation can have other benefits independent of the environment, such as synchronizing development or facilitating mating.

Group action by aggregated larvae of a few species modifies food resources. Feeding by multiple blow fly larvae helps to raise the temperature and liquify the food (Marchenko and Vinogradova 1984). Palestini et al. (1998) raised the possibility that the chemical status of the food would be improved by aggregated dung beetle larvae. Scolytid beetles overwhelm the host defences more easily when aggregated as both larvae and adults (Grégoire 1985). Aggregation facilitates growth in a number of other species (Fitzgerald 1993). Larvae of *Chlosyne* butterflies (Clark and Faeth 1997, Denno and Benrey 1997) achieve this effect by creating a nutrient sink or by overwhelming plant defences, because the effect is seen only on living plants (although the mode of action is unknown).

Insects that aggregate as organized societies in colonial nests achieve substantial environmental modification (Table 4). Apart from the general shelter provided by the nest, within the nest envelope many species can control moisture, avoid the effects of rain, and thermoregulate with varying effectiveness, depending on species (Rosengren et al. 1987 for ants, Martin 1992 for wasps, Engels et al. 1995 for bees). Thermoregulation is done by such means as mass incubation or shivering, entrance closures, wing fanning, covering, withdrawal, and evaporation of water. Even in species that do not thermoregulate actively, the nest buffers the colony against potentially lethal sudden drops in temperature (Cannon and Fell 1992). The structure of the nest also controls its general environment: termite nests can be engineered to prevent overheating without risk of drying (Luscher 1961); ant nests with many passages are colder than those with few (Francke et al. 1986); complex nests can be designed against flooding (Peeters et al. 1994).

The conditions in honey bee colonies are relatively well known. Temperatures well above ambient can be achieved by bee clusters within the nest even in the winter, although clusters of 30,000 to 40,000 bees are required for survival in temperate climates (Vickery 1991). The raised temperature not only prevents cold injury to the bees, but also keeps honey stores liquid so that they can be used to obtain energy. The temperature of the cluster and the behaviour of the bees have been much studied (Southwick 1987, 1991, 1994, Fahrenholtz et al. 1989, Moritz and Southwick 1992, deToledo and Nogueira-Couto 1999), and the process can be modelled (Lempke and Lamprecht 1990, Sumpter and Broomhead 2000).

Nests serve partly to defend against predators. For example, in addition to the structures themselves, defences such as repellent chemicals (Jeanne 1975) and sticky stalked droplets near the nest entrance (Schremmer 1977) protect against ants. Moreover, many social insects defend their nests against predators by means of a soldier caste, or at least with guards posted at the entrance. In addition, the colony can

exploit diverse resources by co-ordinated effort. Therefore, modifications of physical, biotic and resource elements have allowed a 100-fold increase in life span in social compared to solitary insects (Keller and Genoud 1997).

## Modifications by parents

Parents can improve conditions for their progeny. Eggs are protected at the oviposition site in various ways (overview by Richards and Davies 1977, p. 321). These methods range from simple covering with detritus to robust structures (e.g. oothecae of cockroaches, egg pods of grasshoppers, egg sacs of spiders), elevating eggs on slender stalks (e.g. chrysopids: Duelli 1984), or depositing them in burrows in soil (e.g. earwigs), cavities in wood (e.g. some beetles, solitary wasps) or plant stems (e.g. some bugs, sawflies). Several specialized behaviours protect eggs from the potential responses of plants. For example, some species of *Neodiprion* sawflies use their ovipositors to sever the resin canals of selected needles prior to oviposition in slits higher up the needles (McCullough and Wagner 1993 and references cited there). Such "preslits" drain resin and thereby greatly reduce the host plant's response to injury by the egg slits themselves. Several species of cerambycid beetles that attack vigorous host plants girdle the stems or branches of the host before they deposit eggs (partial review by Hanks 1999). Again, wounding of plant tissue by the ovipositor of membracid bugs may block host plant defences (Tallamy 1986), as well as giving access to feeding sites (Wood 1976).

A second set of adaptations provides direct support for the progeny rather than a more favourable setting for the eggs. Some species, especially those that construct nests or burrows, guard the young. The same effect is achieved by carrying eggs or progeny (exposed, or covered within egg cases or more specialized structures), which allows also for the eggs to be kept under favourable physical conditions. For example, eggs of the belostomatid *Abedus herberti* (Hidalgo) are kept moist and aerated by the male that carries them (Smith 1976). Other adults give provisions to the progeny, typically by mass provisioning before hatch, but also by ongoing care (see Choe and Crespi 1997 for examples). This trait reaches its greatest development in social insects. However, even some orthopterans provide trophic eggs to the young. Finally, eggs may develop inside the mother. Eggs of some species develop fully there and are deposited just before or after they hatch (oviviparity, as in some tachinids), but use only nutrient stores in the eggs. However, the thin-walled eggs of strepsipterans and some paedogenic cecidomyiids lie free in the haemocoel and are supplied with maternal nutrients. Louse flies, bat flies and tsetse flies nourish

Table 5. Insect modification of adverse conditions by parents.

Major element	Modifications demonstrated or reliably inferred against:	Modifications less prevalent or inadequately tested against:	Widespread features	Other correlations
Physical factors	Dryness, flooding, cold, ice by some egg-coverings	Other physical factors	Eggs placed in an excavation or puncture, or in a secreted structure	Effects of other coverings not elucidated
Natural enemies	Some predators, some parasites by egg structures, excavation or guarding	Many natural enemies	Eggs carried, or maintained in a cavity	Extended periods of development
Resources	Hostplant defences by oviposition behaviour; Limited or dispersed food supplies by provisioning or egg retention; Competitors by sequestering or guarding resources		Complex behaviours beyond simple oviposition-site choice	Especially when resources are scattered or contested
Combined elements	Resources and physical factors in some species	Most functions not analyzed in combination		

their larvae by secretions from “milk glands” in an enlargement of the oviduct. The larvae are ejected when mature and pupariate at once (Maa and Peterson 1987 and references there). Similar adaptations are known in some aphids and other insects, notably viviparous cockroaches (Ingram et al. 1977).

The effectiveness of modifications by parents is summarized in Table 5. Typical egg-site modifications appear to offset physical factors such as desiccation, flooding, and ice inoculation in the same way as the burrows and cocoons of later stages, although again the effects have seldom been quantified. However, the spumaline of egg masses of the moth *Malacosoma americana* (Fab.) absorbs water (Carmona and Barbosa 1983). The gelatinous egg matrix of limnephilid caddisflies from temporary pools protects against desiccation (Wiggins 1973, Berté and Pritchard 1983), and it also provides freezing resistance (Wiggins 1973). The silken egg cocoons of some dung beetles allow them to exploit dung that otherwise would be too wet (Gittings and Giller 1998). Air-filled foam around the eggs of the beetle *Galeruca tanaseti* Linn. protects them from temporary flooding (Messner 1983). Egg sacs of the spider *Floronia bucculenta* (Clerck) protect against flooding, desiccation and ice inoculation (Schaefer 1976). A few effects of egg coverings on the temperatures of their occupants have been claimed or demonstrated (Kulagin 1897, Grevillius 1905, Carmona and Barbosa 1983). The overlapped scales of the egg masses of the moth *Thaumetopoeia pityocampa* (Den. and Schiff.) serve to speed development by creating a greenhouse effect in sunlight (Milani 1990).

Like some resting-stage cocoons, egg cases and silk webbing protect against natural enemies (e.g. Duncan and Lindquist 1989 for mite eggs; review for spiders by Cloudsley-Thompson 1995). Different structures are effective against different kinds of attackers (Hieber 1992). The egg stalks of chrysopids protect against some predators and parasitoids as well as preventing cannibalism (Duelli and Johnson 1992, Růžička 1997). One species even applies ant-repellent substances to its egg stalks (Eisner et al. 1996).

The effectiveness of egg coverings and maternal guarding depends on the species (compare Tallamy and Wood 1986, review on pp. 372, 378, Filippi-Tsakamoto et al. 1995, and Kudo and Ishibashi 1996). Some species even perform aggressive lunging and wing fanning that cause the departure of enemies (Tallamy and Denno 1981, Edgerly 1987, Guershon and Gerling 2001). In at least some groups, maternal care occurs only in species especially vulnerable to natural enemies because they deposit eggs in exposed rather than protected places (Tallamy and Schaefer 1997) and few eggs survive without maternal care (Edgerly 1987, Tallamy and Schaefer 1997). Guarding can also defend against mould. Earwigs lick and roll the eggs apparently for this purpose (Buxton and Madge 1974). Cockroaches

tending eggs in damp wood galleries clean the galleries and remove fungi (Nalepa 1988).

Provisioning and maternal secretions provide food resources to the larvae. In many species of scolytid, passalid and other beetles, galleries in wood make food accessible to progeny and even condition it, as well as providing a protective cavity (Schuster and Schuster 1985, 1997, Kirkendall et al. 1997, Paine et al. 1997). Carrion beetles make resources available to the offspring by burying and other behaviours, and also give protection from competitors as well as from predators (reviews by Eggert and Müller 1997, Scott 1998). Some spiders that guard eggs and progeny eventually provide their bodies as a food resource to the spiderlings (Toyama 1999).

## Host behaviour

Some parasitoids modify host behaviour (Horton and Moore 1993) and hence the nature of the host as a habitat. For example, parasitized hosts of some species seek sites that favour survival of the parasite (Brodeur and McNeil 1989, 1990 for *Aphidius*, Pivnick 1993 for *Microplitis*, Reitz and Nettles 1994 for *Eucelatoria*). Predation rates of parasitized hosts tend to be reduced (Fritz 1982). However, the opposite effect has also been reported, through habitat choice (Müller and Schmid-Hempel 1993) or through “suicidal” exposure to predators (Shapiro 1976, McAllister and Roitberg 1987).

## Conclusions

Many insects actively modify local environments to their own advantage, rather than simply choosing more advantageous places among existing alternatives. Modifications through excavations protect against several physical factors (Table 1), especially dehydration and temperature. Deeper burrows generally provide better protection, and can be built more easily by larger species, which also tend to have lower rates of water loss. Nevertheless, in northern climates slow warming of deep layers in spring means that ensuring enough time for development and reproduction by relatively early resumption of activity from shallow overwintering sites can be more important than avoiding cold (Danks 2000b). Burrows and borings also protect against some natural enemies. At a general level, species such as borers (and gallers) that are more protected have lower rates of parasitism (Hawkins 1994). However, notwithstanding the protection against generalist predators and parasites provided by burrows, especially deep ones or those with a narrow bore and those that are closed or defended, many specialist enemies exploit burrowing insects and their resources (Danks 1971a). Some dis-

eases are more likely in confined and humid spaces than in the open; the cleaning of eggs by guarding mothers to prevent mould growth was noted above.

Feeding and resting-stage shelters also protect against various physical factors (Table 2). Like burrows, shelters appear to be more effective against generalist than specialist enemies. Strong or complex structures protect against many invertebrate predators, and also may serve to camouflage the organisms against vertebrate predators. On the other hand, some diseases are favoured in sheltered chambers, as they are in burrows. Many feeding shelters help to secure food resources, whereas resting-stage shelters do not.

Induced plant responses such as galls cause the plant to supply resources (Table 3). They also protect especially against desiccation and some predators. Nevertheless, galls are immobile and resource-rich and there is limited rigorous evidence for protection against the many types of natural enemies characteristic of most gall communities.

Some aggregations modify water and temperature regimes (Table 4), but most evidence is equivocal, as for other physical factors. Group actions condition the food or overwhelm host defenses in several plant-feeding species. Physical factors are controlled by social colonies (Table 4), but this homeostasis is not perfect: limits for adult survival may be relatively wide, and closer control would be less efficient, for example because a higher temperature in winter than the minimum necessary to maintain metabolism and food availability requires more energy to be consumed. Cooperation among individuals allows for the coordinated acquisition of resources and for concerted defence against predators; but mutual grooming, trophylaxis, and other close contact among nest-mates favours the transmission of microorganisms and small parasites, and so may make colonies more susceptible to infection.

Modification of adverse conditions by parents (Table 5) stems from a range of interesting and often complex behaviours that have been widely reported, even though most of their effects on fitness have not been quantified. Best documented are the ways in which resources for progeny are provided or defended.

Environmental modifications by insects through excavations, feeding and resting-stage shelters, induced plant responses, aggregations, social behaviour, and parental actions therefore can alter the impact of physical factors, natural enemies and resources. Current evidence, as summarized in Table 6, suggests that excavations and shelters protect especially against physical factors, while aggregations, colonies and parental actions more often influence the acquisition of resources. Modifications diminish the impact of some natural enemies but are especially difficult to evaluate in this context. Moreover, there are great differences among species and a given adaptation can serve multiple purposes.

Table 6. Summary of insect responses to physical factors, natural enemies and food resources by environmental modifications: +, commonly demonstrated; (+), demonstrated for some aspects only;  $\pm$ , relatively infrequent; -, rare or unlikely.

Means of modification	Major element		
	Physical factors	Natural enemies	Resources
Excavations	+	(+)	$\pm$
Feeding shelters	+	(+)	(+)
Resting shelters	+	(+)	-
Induced plant responses	+	(+)	+
Aggregations	(+)	(+)	(+)
Social colonies	+	(+)	+
Parental actions	(+)	(+)	+
Host behaviour	-	(+)	-

This overview suggests several questions that should be addressed more fully in order to evaluate environmental modifications, including the complexity and diversity of individual adaptations, interactions and combinations, trade-offs, potential impacts on other species, and especially how to measure the effectiveness of the adaptations. Many adaptations are more complex than might be expected, promoting care in arriving at generalizations. For example, the effects of different predators and parasites, notably specialists versus generalists, and also of diseases, are different. Protected conditions that limit predation may favour mortality even from generalized fungi. Combined responses can be especially difficult to evaluate; some examples were summarized in Tables 1–5.

Potential trade-offs provide one way to evaluate modifications of the environment. The costs of time and energy involved in building shelters are traded off against future growth or reproduction, and lost time and energy and increased risk to adults that protect their progeny is traded off against future reproductive possibilities, provided the increased survival of individuals or progeny outweighs the costs. Different fecundity and different investment in parental care in related species provides one index of relative cost (e.g. Table 5-3 in Tallamy and Schaefer 1997). There is considerable theory about the effects on fitness of different strategies of cooperative brood rearing (see Wilson 1971, 1975, Choe and Crespi 1997, Trivers 2002, for an introduction to these ideas), but other trade-offs of interest in the present context have not been examined in the same way, although construction does have a measurable cost (Stevens et al. 1999, 2000).

In a wider ecological context, organisms that modify the environment might have impacts on other species and so are potential “ecosystem engineers” in the sense of Jones et al. (1994). Many modifications influence habitat only for the modifier (and so are not environmental engineering in this sense), and even species that do modify the environment in ways that affect other

species work chiefly over short time frames such as one insect generation. With the exception of termite mounds and some ants nests (Hansell 1993), structures are small and ephemeral, like galls and cases. Again, burrowing, especially by ants but also by aquatic insects, has the potential to disturb substrates and redirect resources (Meadows and Meadows 1991, Wang et al. 2001), but with few exceptions typical insect populations are too low and the size of individuals too small to generate major changes. Therefore, the effects of insect modifiers on overall ecosystem structure are relatively limited. Nevertheless, even small and ephemeral structures modify resources for other species, by increasing habitat complexity for subsequent colonists (Cardinale et al. 2001 for caddisfly structures) and especially by changing the conditions for invading specialists. Indeed, nests and galls support complex and interdependent small-scale communities of considerable ecological interest, with usurpers, inquilines, symbionts, commensals, predators, parasitoids and pathogens that depend on the builders, and some of which depend not on the biomass of the builder (which would not qualify as ecosystem engineering) but on the microhabitat created. The cumulative influence of such small-scale modifications makes some insects noteworthy, though chiefly inconspicuous, ecosystem engineers.

Local environmental modifications clearly have significant adaptive value to the modifier, so that they should be considered more generally in assessing species biology and in designing experiments. The fragmentary nature of the existing information means that even a deliberate attempt to focus on hypotheses generates more unproven possibilities than definitive answers. Therefore, it is not yet feasible to develop general recipes on how to quantify the roles of environmental modifications. Instead, I offer three observations.

First, measuring relevant features and designing explicit tests is more useful than making assumptions. It is beneficial to consider the potential ecological factors that apply to a species relatively broadly, so that observations and experiments can be designed to assess multiple effects. Most studies of the levels of parasitism by polyphagous parasitoids, for example, include very limited data about the exposure, protection or overall physical conditions experienced by the different host species, which would be expected to modify the incidence of parasitism. Most of the functions that have been ascribed to cocoons and egg cases have not been tested.

Second, effects may be interdependent. Surprisingly detailed studies are then required to assess accurately the potential effects of modifications. For instance, a species that enhances local temperatures by means of a silken feeding tent may make a more effective tent if individuals are grouped; predation and parasitism may be reduced simply because development is faster in the warm tent, exposing individuals to attack for a shorter

period; and therefore even a finding that tent-living larvae have reduced predation does not immediately distinguish between the effects of temperature on the time of exposure, and the possible effects of protection through either the structure of the tent or the aggregation of the larvae.

Third, several potentially important features have not been investigated in detail, as suggested by the information in Tables 1–5. These features include even many physical factors (especially those other than moisture and temperature), differences in the impacts of different kinds of natural enemies (e.g. predators vs. diseases, generalists vs. specialists), the roles of competitors (as opposed to enemies), and the factors mitigated by aggregation.

Given the prevalence and complexity of ways in which insects actively modify their environments, I hope that in future the modifications will be recognized explicitly and their roles subjected to more rigorous investigations.

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