CONVERGENCE PATTERNS IN SUBSOCIAL INSECTS

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INTRODUCTION

Subsocial behavior is the most primitive level of social interaction involving parents and offspring (79). Although preovipositional behaviors such as nest construction (48, 77) or various resource manipulations (10, 162) eventually benefit offspring, subsociality by definition is restricted to postovipositional parental behavior that promotes the survival, growth, and development of offspring (33). Insect parental adaptations comprise a continuum of care ranging from passive egg guarding to an array of complex grooming, feeding, protective, and nesting behaviors (for comprehensive reviews see 33, 54, 171). Although levels of complexity are diverse, parental care can be categorized into three primary behaviors: (*a*) those that physically protect the young from danger, (*b*) those that protect resources vital to offspring, and (*c*) those that facilitate offspring feeding. The effectiveness of these behaviors in neutralizing or alleviating conditions detrimental to young is evidenced by their repeated convergence throughout vastly different animal lineages (30, 62, 73, 125, 157, 159, 168). In the insects, parental behavior lies at the core of all levels of insect sociality and has arisen independently in at least 13 different orders (33).

Wilson (172) has identified four environmental "prime movers" that create conditions favorable to the evolution of parental care: stable or structured environments, physically stressful environments, rich and ephemeral resources, and predation. He proposed that in different ways each prime mover produces demographic consequences that promote parental care. There is little doubt that reproductive losses from predation, competition, or physical harshness can be reduced by subsocial interactions between parents and their young.

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The extent to which insects encounter such adversity, however, is largely a function of the persistence, dispersion, accessibility, and nutritional richness of the food resources on which they depend. If the evolutionary problems imposed by specific combinations of resource traits are consistent, convergence in life history solutions to these problems is expected. In this review we present evidence that this, in fact, is the case among subsocial insects. Clear patterns of behavioral convergence are evident when food resources are viewed in terms of their spatial, temporal, physical, and ecological characteristics.

LIFE HISTORY PREADAPTATIONS

Subsociality is only one of several life history alternatives that minimize adverse conditions associated with a given resource. Maternal defense in the lace bug *Gargaphia solani,* for instance, reduces nymphal losses from predation sevenfold (151). Yet the overwhelming majority of lace bugs are asocial and successfully avoid predators by concealing eggs within plant tissue and/or spreading reproduction over time and space (152). Which reproductive pattern evolves in response to a particular set of selection pressures is a complex function of many interacting factors (145) including phylogenetic inertia, morphological and physiological characteristics of the taxon, and the presence or absence of critical behavioral preadaptations.

Even the most primitive parent-offspring interactions cannot occur in the absence of certain preadaptations. Foremost is the need to confine reproduction to specific periods and places. It is physically impossible to defend or otherwise care for offspring that are dispersed through time and space. Subsociality also requires considerable adult longevity. Parents must not only survive to oviposit, but also live long enough to benefit one or more clutches of offspring. This is particularly true in temperate regions (178, 180, 183; K. L. Olmstead, T. K. Wood, manuscript in preparation) or in highly seasonal areas of the tropics (D. M. Windsor, W. Nentwig, manuscript in preparation) where insects must pass several months before climatic changes encourage reproduction. Most subsocial species do not have the option of weathering unfavorable periods in the egg stage; they must enter favorable seasons fully or nearly mature so that they may breed and begin providing for offspring immediately. Finally, the asocial behavior patterns of adults must contain basic elements from which natural selection can mold parental behaviors that encourage offspring survival. Specific parental behaviors such as defensive posturing, aggression, and nest building are often simple extensions of behaviors exhibited by asocial relatives (1, 171). For example, asocial female *Corythucha* lace bugs discourage persistent males from uninvited sexual advances by fanning their wings and aggressively ramming males (D. W. Tallamy, unpublished observation). These same behaviors form the basis of anti-predator maternal defense in subsocial *Gargaphia* lace bugs (37, 64, 151).

The extent to which subsocial preadaptations integrate to form parental care may be influenced by the costs they impose on insects. Parents that actively defend their young from predators, for example, risk costly physical injury or even death. A less obvious problem may arise when care is provided for offspring clustered in one spot. Insect eggs or prey of any sort that are concentrated in one area may be more attractive to predators and parasites than isolated eggs (50). Thus, subsociality may actually increase the probability that eggs will be detected by predators. A third and potentially serious cost of parental behavior stems from the evolutionary decision to invest much time and energy in a few progeny rather than minimal amounts in many progeny (158). Insects that provide care for one group of offspring forfeit the chance to produce additional offspring, at least until the first group has reached self-sufficiency. This loss of fecundity is adaptive only if young that receive care reach reproductive maturity in greater numbers and/or more quickly than young that do not (151, 153). There is growing evidence that much of the intraspecific variation currently recognized in insect parental behavior may be the result of mechanisms to reduce parental costs (147–149; W. G. Eberhard, manuscript in preparation).

THE RESOURCE HYPOTHESIS

Once essential preadaptations are in place, conditions that impede the survival and development of immature insects can promote subsocial interactions. It is our contention that all such conditions arise as a direct consequence of an insect's association with a particular class of nutritional resources. Food resources generate some of the most powerful selective forces shaping insect life history traits (108, 112, 126, 145). The nutritional quality, persistence, and dispersion of food can influence the rate and location at which an insect feeds and thus the extent to which it is exposed to predators and parasites or competition within its guild (100). Physical characteristics of food resources determine the ease with which they are consumed and assimilated. In essence, resources are paramount in regulating when, where, and how insects feed; consequently, they can be implicated in the evolution of reproductive patterns. It is therefore useful to interpret patterns of convergence within evolutionary alternatives such as subsociality in terms of the resources on which insects depend. In the following sections we discuss subsocial adaptations to the ecological and physiological challenges imposed by the temporal and spatial distribution, nutritional quality, accessibility, and opportunities for refuge that characterize the principle food resources, i.e. plant parts (foliage, wood, detritus), living animals, carrion, and dung.

Foliage

Foliage and plant sap are abundant, readily obtainable resources that in spite of seasonal variation in quality and availability are relatively persistent. Although

a great many insects take advantage of these benefits, foliage offers surface-feeding herbivores few opportunities for refuge from predators and parasites. Many of these "folivores" reduce their vulnerability through mechanisms such as crypsis, noxious defenses, or mutualistic interactions with ants (34, 119, 180). To further reduce losses during reproduction, other species complement these defenses with parental protection of their young (53, 99, 176, 179, 180).

Parental defense of offspring is universal among subsocial folivores. When hymenopteran parasites are important sources of egg mortality, the adult folivore straddles eggs to shield them physically. This behavior is especially common among phytophagous Hemiptera (7, 60, 78, 88), Membracidae, and Aetalionidae (16, 51, 55, 175, 178, 184) but also occurs among neotropical Chrysomelidae (162, 173; D. M. Windsor, W. Nentwig, manuscript in preparation) and numerous sawflies (28, 29). The pentatomid *Antiteuchus tripterus limbativentris*, for example, exhibits defensive postures that discourage generalist predators and restrict parasitism by scelionid wasps to the perimeter of the egg mass (31). While guarding eggs, females of the coreid *Physomeris grossipes* deter predators with chemicals discharged from anal glands (53, 99). In one of the few known cases of egg-guarding among Diptera, tabanid *Goniops chrysacoma* females straddle egg masses deposited on leaf surfaces until eggs hatch and larvae fall to the ground (96).

A second more dynamic defense directed against invertebrate predators is exhibited by other folivores. Female *Gargaphia* lace bugs (25, 131, 151), for instance, rarely sit on eggs but position themselves to intercept predators before they reach the eggs. Unlike most subsocial Hemiptera, these insects do not end parental defense when eggs hatch. Instead, females remain with and protect offspring until they mature. In *Gargaphia* (64) and several species of treehoppers (177) maternal defensive behavior is triggered by visual cues and/or alarm pheromone(s) released by disturbed or injured nymphs. In other treehoppers alarm pheromones cause both mother and young to disperse from the site of danger and reaggregate elsewhere on the plant (86, 179, 185).

When parental protection is extended beyond the egg stage in leaf-feeding insects, the family unit may become mobile in search of fresh resources. If a parent is to protect its offspring, selection should favor gregarious behavior in offspring and also parental behaviors that maintain aggregations. Such "herding" is, in fact, commonplace among subsocial folivores (28, 29, 64, 75; D. M. Windsor, W. Nentwig, manuscript in preparation). When transferring from one host leaf to another without their mother to guide them, aggregations of *G. solani* nymphs often divide if faced with a choice of paths. When the mother is present she moves ahead of her nymphs and stands at the leaf axils, blocking all but one route. By maintaining the cohesion of the aggregation, she is able to guard it as a single group (64). For similar reasons branch-feeding membracids also maintain nymphal aggregations although they may have a continuous

supply of nutrients and need never leave the branch where eggs are deposited (175, 178, 181, 185).

Embiopteran webspinners are largely tropical insects that live within silken galleries constructed among the mosses, algae, or lichens on which they feed (11, 113). Though not foliage per se, these resources are ubiquitous and persistent in the tropics. Insects cannot easily harvest them without exposure to enemies. All webspinner species are communal but the extent to which females care for young has been examined in relatively few species. Webspinner galleries provide several benefits including waterproof housing and possible protection from predators (J. S. Edgerly, manuscript in preparation). Silk, however, does not protect eggs from hymenopteran parasites. As a result, female *Clothoda urichi* cover eggs with many layers of macerated bark, feces, and silk and guard them until they near hatching. At hatching, females must remove this covering or the nymphs are unable to emerge.

Ant mutualism may be a major factor in the development of subsociality among the Membracidae (180, 182, 185). Ants collect honeydew from treehoppers and in turn significantly reduce predation on these membracids. Thus, it is critical for females brooding eggs to establish mutualistic relations with ants. In the presence of ants, *Publilia reticulata* females can safely desert initial broods to deposit smaller second clutches on the same or a nearby host (14). In contrast, overwintering *Entylia bactriana* females aggregate and thus increase the probability of being located by ants. Females oviposit eggs over a number of days, depositing larger clutches and remaining longer when attended by ants. If ants fail to locate an ovipositing female, she will desert her developing egg mass and move to a larger treehopper aggregation. Due to heavy predation very few deserted eggs hatch and even fewer nymphs survive past the first instar (179; K. L. Olmstead, T. K. Wood, manuscript in preparation).

In addition to warding off predators, a few folivores have developed maternal behaviors that facilitate offspring feeding. Some membracid females cut a series of spiral slits with their ovipositor in the bark or leaf petioles of their host (175, 178, 185). After eclosion, first instar nymphs feed within these slits. Such behavior certainly increases the accessibility of nutrients, but it may also improve the nutritional quality of sap by creating a nutrient sink near the wounded area (65, 164). Other treehopper females that oviposit in the midrib of host leaves repeatedly wound the midrib between the leaf petiole and the eggs with their ovipositor (180, 185). By blocking the plant's vascular system, this behavior may trap mobile nutrients within the leaf and/or prevent the influx of inducible host defenses into the feeding site (150). Phloeid bugs have gone one step further to assist feeding (63, 81, 165). Gravid females place eight to ten eggs in bark crevices and then press their cryptic, lichen-covered bodies over the crevice. When eggs hatch, nymphs cling to the underside of their mother. It

is not clear how nymphs obtain nutrition but it has been suggested that the bark of the host plant is too thick for first instars to penetrate (7). Instead they apparently obtain food from their mother, either from salivary or anal secretions or by piercing her digestive track directly through abdominal intersegmental membranes (57).

In most folivore families with subsocial members, maternal care has developed in relatively few genera. In the Membracidae, however, powerful selective pressures have led to the polyphyletic development of subsocial behavior throughout the geographic range of the group. It is possible that mutualistic associations between ants and treehoppers favor maternal behaviors that increase the probability that offspring will be attended by ants when eggs hatch (182, 185).

Wood

Woody resources are abundant in many habitats, are even more persistent than foliage, and provide some refuge from enemies and rapid fluctuations in temperature and humidity. Insects that capitalize on these benefits, however, must overcome significant disadvantages. Wood is a tough, relatively inaccessible resource that can be difficult for immature insects with small or weak mandibles to penetrate or manipulate (49). The extent to which males of subsocial wood-feeding specialists assist their mates in gallery construction suggests that efficient woodworking warrants the cooperative efforts of both parents. Furthermore, wood is typically low in nitrogenous compounds and the cellulose and lignin of its fibers are difficult to digest and assimilate. Insects can only utilize such resources (a) through obligate symbiotic relationships with cellulose-digesting protozoans, (b) by feeding indirectly on cultivated or naturally occurring fungi, and/or (c) if the organism can tolerate slow growth and development. Subsociality can reduce these physical and nutritional limitations in several ways.

Interactions between nymphs and both parents in *Cryptocercus* roaches help temper the physical and nutritional disadvantages of their woody diet (20, 84, 85, 87, 110, 117, 130; C. A. Nalepa, manuscript in preparation). *Cryptocercus* adults pair for life and chew a series of horizontal galleries interspersed with large rearing chambers in rotting logs. Unlike their termite relatives, only young nymphs require the transmission of intestinal flagellates, which they receive through proctodeal trophallaxis with their parents. Nymphal growth is extremely slow (five years). Early in this prolonged development the nymphal diet is enhanced by products obtained from parental hindgut fluids and fecal pellets. In fact, parents provide a significant source of food for nymphs during their first year of development.

Among the most common beetles specializing on decaying wood are the Passalidae, which use it for both food and shelter (106, 107, 128). Passalids are

monogamous and cooperate in the construction and defense of interconnected galleries (127). Larvae of various species may differ in their ability to prepare wood as food and to construct galleries. Larval *Odontotaenius disjunctus* can chew and survive on wood directly, but grow more rapidly if they feed on wood that has been previously converted into frass by adults (76, 95). Larvae of *Heliscus tropicus,* on the other hand, can neither chew nor tunnel through wood without the aid of their parents (49). In both cases larvae depend to some extent on the woodworking abilities of their parents; this dependence has apparently resulted in subsocial interactions of unusual complexity. Recent studies suggest that the social structure of passalid colonies is characterized by overlapping generations and some degree of cooperative brood care. Colonizing adults commonly share their galleries with offspring at all stages of development, including first generation nonreproductive adults. Young adults are known to assist parents in the construction and repair of sibling pupal cases, and may cooperate in other social tasks as well (129).

Perhaps the most advanced level of subsociality in insects that utilize wood is that of scolytid bark beetles. These beetles exploit trees through mutualistic interactions with fungi (4, 5). Many scolytid genera aggregate as adults and reproduce in communal brood chambers (59), but true subsocial interactions are restricted to three genera. In *Ips* (123) and *Gnathotrichus* (122), a male constructs a small entrance hole through the bark of its host and releases a pheromone to attract females. Females cannot gain entrance to his tunnel without first mating, whereupon each female prepares her own brood galleries. Throughout larval development the male remains to guard the entrance tunnel from predators and cleptoparasites (171).

Males and females of *Minarthrum* bark beetles cooperate to excavate brood galleries and rear young (59). Females deposit single eggs in short "cradle" pits and then pack the pits with wood chips supporting active fungal hyphae. When eggs hatch, larvae consume their individual fungal plugs, which are periodically replenished by the female. Females also maintain hygiene in the galleries by moving larval feces to fungal gardens or by pushing waste from the galleries altogether. Similar patterns of parental attendance have been reported in the neotropical tenebrionid *Phrenaptes bennetti* (89).

Detritus

For the purposes of this discussion detritus will be defined as any of various plant parts, including seeds, fruits, and leaves, that are separated from the plant. Detritus can be abundant, but is often fragmented and dispersed through time and space. Locating sufficient quantities of detritus demands considerable energy and time and may increase exposure to enemies. If insect detritivores are to protect offspring from enemies, their parental options are limited: They can (a) confine protection of young to the egg stage and guard without foraging for

food, (b) carry or accompany offspring while foraging, or (c) bring detritus to young at a central location.

The best examples of detritivores that carry or accompany their offspring while foraging are found among the cockroaches. These insects exhibit a continuum of maternal foraging investment (115, 116). Species such as *Eurycotis floridana* and *Supella supellectilium* briefly carry their eggs in an extruded ootheca as they travel. *Ectobius panzeri* also carries oothecae while foraging, but for a much longer period; various *Blattella* and *Blaberus* spp. carry their oothecae until eggs hatch. Many cockroaches extend foraging protection beyond the egg stage. First instars of the ovoviviparous *Byrsotria fumigata* track their mother by a pheromone and aggregate under her body or in areas between the wings (72). *Leucophaea maderae* females forage actively with their nymphs throughout the first two instars (174). The tegmena of *Phlebonotus pullens* females are arched over the surface of the abdomen, forming a specialized transport chamber where nymphs remain while their mother forages (102). Young nymphs of *Perisphaerus semilunatus* lack eyes, cling to the underside of their mother, and have atypical elongate mouthparts that may be specialized for feeding on maternal secretions (114). Perhaps the most specialized maternal investment is seen in *Diploptera punctata,* where brood care is completely internalized (55, 61, 142–144). Eggs hatch within an abdominal brood sac where the nymphs remain and absorb nutrients for approximately 60 days. This evolutionary breakthrough allows female *Diploptera* to forage freely without exposing their young to predation.

Predation on young may also be reduced by maintaining offspring and their nutrient reserves in subterranean chambers. Such caches can be located close to detritus sources to reduce foraging costs, but moving beneath the soil creates new problems. Reduced air exchange and high humidity favor the proliferation of fungi that can destroy eggs and provisions. Although fungal growth on eggs and pollen can be chemically controlled in some insects (18), species without such defenses must remain in brood chambers to remove fungal spores and hyphae until their young are self-sufficient.

Burrowing behavior is well developed in subsocial Dermaptera (8, 23, 43, 71, 132, 160). Female *Forficula auricularia,* for instance, excavate a subterranean burrow in autumn and share it with males. After oviposition the following spring, the female aggressively ejects the male from the burrow and prevents his return. Females may regulate egg temperature by moving the clutch higher or lower within their vertical brood chambers (71). They also regularly manipulate each egg in their mandibles, presumably to remove fungal spores and hyphae. In the absence of parent females, eggs of *Labidura riparia* quickly succumb to common soil fungi (19). After *F. auricularia* eggs hatch, nymphs are fed by their mother with regurgitated detritus until they complete the first instar.

Orthopteran detritivores have also developed advanced subsocial nesting and provisioning. Female *Anurogryllus muticus* seal themselves within underground brood chambers, deposit eggs, defend the chamber, and maintain hygiene by removing excess feces (167). When eggs hatch, females provide young with detritus, which they periodically enrich with trophic eggs. Females of some gryllotalpid mole crickets (45, 52) and the gryllid *Brachytrupes achatinus* (39) also remain with their eggs and young nymphs in subterranean burrows. Although similarities are probable, the extent to which maternal behavior in these species parallels that of *A. muticus* is unknown.

Subsocial hemipteran detritivores have converged on similar behavior patterns: Young are typically protected within subterranean chambers. Such maternal care abounds in certain cydnid burrower bugs. Though most species have only been observed feeding directly on the roots and lower stems of plants (40, 94, 140, 155, 186), recent evidence suggests that seeds constitute a major part of their diet (133). *Sehirus bicolor* females dig a shallow brood chamber under leaf litter and there they deposit and defend a clutch of eggs. When eggs hatch, mother and nymphs search together for suitable food until nymphs reach the second instar. Brooding behavior in *S. cinctus* is similar but, while guarding eggs, females periodically leave their chamber and forage for mint seeds to feed nymphs (133). If necessary, cydnids can move their egg cluster (78, 94, 155). Female *Tritomegas bicolor* carry their egg clusters impaled on the beak and supported by the forelegs. The pentatomoid *Parastrachia japonensis* provisions shallow brood cavities with small drupes impaled on her stylets (44, 146). Maternal care is unusually specialized in *Brachypelta aterrima* (120, 121, 124). As in other subsocial cydnids, females protect egg clusters within subterranean brood chambers. However, unlike most hemipterans, first instars acquire digestive symbionts not from the egg but directly from maternal rectal secretions.

There are fewer known cases of subsociality among Coleopteran detritivores. Nevertheless, there is remarkable convergence between these beetles and other detritivores. Similar to the subsocial cockroaches, *Helochares lividus* (56) and *Spercheus emarginatus* (3) carry eggs while foraging. *Bledius spectabilis* inhabits the intertidal zone of European beaches where it forages for algae (15). Attacks by carabid predators and ichneumonid parasites are reduced when females rear their young in sand tunnels specialized to promote ventilation when high tides reduce oxygen levels (38). Larvae depend on the mother for protection and also for algae, which is provided on a regular basis. The seed-eating carabid *Carterus calydonius* also rears its young in underground chambers. Each brood chamber is provisioned with enough seeds to bring offspring to pupation (12, 154). In certain *Cephalodesmius* spp. (33, 46, 83), males and females pair-bond for life and cooperate extensively while rearing larvae. Division of labor is distinct: The female excavates a large brood

chamber while the male guards the entrance. The male then forages for detritus, which includes leaves, flowers, and fruits, and passes these to the female in the chamber. After adding a generous supply of her own feces, the female shapes the detritus into a large ball and allows it to ferment for two weeks. The ball is then divided into several cakes, each large enough to nourish a single larva. The male continues to provision the nest for several weeks while the larvae feed and grow. As their young near pupation, both parents seal themselves with the larvae inside the chamber.

Living Animals

Insect predators and parasites (hereafter collectively called predators) exploit a relatively dispersed, disjunct, and often mobile resource. Like insect folivores and detritivores, predators are themselves vulnerable to predation and parasitism during reproduction (21, 91, 98, 105). Reproductive patterns that minimize these losses are therefore favored. Predation is a consumer tactic that generally does not favor subsocial interactions. Most predators receive only a fraction of their nutritional and energetic requirements from a single prey item and therefore must capture prey at frequent intervals, particularly while procuring energy for reproduction. In most cases, the time, energy, and mobility necessary for repeated foraging conflict with the demands of parental care. When prey capture is linked to predator mobility, parental care can only evolve if the benefits to offspring outweigh the costs of lowered mobility to parents. In fact, subsociality has developed in relatively few insect predators; spreading reproduction over time and space is a more common life history pattern.

There are four subsocial alternatives for predatory insects: Following oviposition, (a) females can forego feeding and remain to guard eggs; (b) females can carry young while foraging but may sacrifice some mobility, capture efficiency, and/or clutch size; (c) highly mobile females can forage from a central location where young are protected and fed; or (d) males can assume parental responsibilities, allowing females to resume the hunt and increase their reproductive potential.

Predation and parasitism of eggs are so destructive to certain tropical reduviid bugs (7, 32, 92) and mantids (36) that it is profitable for females to forego their own nutritional requirements and stand guard over eggs. Data are not available, but it is likely that this subsocial sacrifice of time and feeding reduces future reproductive capabilities. Similar behavior is rare among hymenopteran parasites but occurs in the braconid *Cedria paradoxa* (6) and several of the Bethyliidae (reviewed by 41). Female bethyliids immobilize their prey with stings and feed on host hemolymph as their eggs develop. After ovipositing on the host, mother wasps remain to guard their eggs and larvae from hyperparasites. Such behavior represents a substantial time investment in one

clutch, but maternal costs from reduced feeding may be minimized if females also feed on paralyzed prey.

A second parental option is exhibited by *Chilianella* reduviids (7). These predatory females retain their ability to hunt by transporting nymphs on their abdomen. Presumably the young feed on prey captured by their parent. Though clutch size is reduced to one or two offspring, females can protect and feed young while building nutritional stores for future reproduction. Several blood-feeding ectoparasites of vertebrates provide similar maternal benefits to their young. Dermapteran parasites of bats (Arixeniidae) and rodents (Hemimeridae), and hemipteran bat parasites (Polyctenidae) are viviparous, depositing first instar nymphs directly on their victims (2, 74). For the pupiparous tsetse flies (*Glossina* spp.), louse flies (Hippoboscidae), and bat flies (Streblidae and Nycteribiidae) blood is a rich and nutritionally complete resource but would be unavailable to their vermiform larvae if not for advanced maternal adaptations (90). Females produce eggs that are individually retained in the uterus. Upon hatching, the larva is nourished with materials derived from blood meals by specialized maternal glands (26). The larva completes its development within the safety of the uterus, passes from its mother, and pupates. Fecundity is reduced, but vivipary and pupipary allow offspring to capitalize on their mother's ability to track and exploit a highly nutritious resource, combining the maternal benefits of nourishment with protection.

The greatest proliferation of subsociality among predators has occurred in the highly mobile aculeate Hymenoptera, particularly the Pompilidae, Sphecidae, Eumenidae, and the primitive Vespidae, Halictidae, and Anthophoridae (reviewed by 33, 80). Although they are not predaceous by definition, we consider subsocial bees (Halictidae and Anthophoridae) behaviorally analagous to predatory wasps because of similarities in the persistence, dispersion, accessibility, and nutritional richness of pollen and prey. Subsocial Hymenoptera rear their offspring within the protective confines of various enclosures. Here larvae are more easily guarded, but they are also isolated from prey and must be fed by an adult. Once a nest is provisioned, females of most species enclose the egg within the nest and repeat the process elsewhere. Social and physical parasitism can be so intense, however, that females of some species remain in the nest to guard young. In *Oxybelus, Tachytes*, and *Trypoxylon* sphecids, males inadvertently play an important role in nest defense (21, 91, 97, 98). As females hunt for provisions, males compete for dominance of a nest site in order to guarantee mating rights with the returning female. While defending against intruders, males significantly reduce offspring mortality from cleptoparasites (58, 97). Defense is more deliberate in *Trypargilum superbum folvipes*: Males continue to guard the nest from predatory ants until the larvae pupate within a tough cocoon (22). In other species, females progressively provision their nests

with prey as their larvae grow. As with nest guarding, provisioning results in prolonged associations with a particular nest and its occupants. Progressive provisioning may reduce the threat from parasites and predators, but not without tradeoffs in fecundity; time invested in one larva is time that cannot be invested in additional offspring (158).

A few Carabidae oviposit in soil depressions and guard their eggs until hatching (reviewed by 154). Females take no food while functioning in this capacity, but they do prevent the growth of fungi by frequently cleaning the eggs. Progressive provisioning has not developed in predatory carabids; the larvae disperse immediately upon hatching.

The fourth and most intriguing subsocial alternative for predatory insects involves a parental role-reversal between males and females. In certain *Rhinocoris* and *Zelus* reduviids the male guards the eggs while the female continues to hunt (88, 105). This behavior bears distinct advantages for both sexes. The benefits to females are obvious: Paternal care permits females to continue harvesting resources for future reproduction efforts by allowing them to avoid a 15-day investment in egg-guarding. The benefits to males are quite different and clearly outweigh the possible disadvantages of paternal care. Benefits to male fitness in terms of the increased survival of offspring are significant. Survivorship of *Zelus* eggs improves 34% when males protect them from parasites (105). But males receive an additional bonus for their paternal investments. Shortly before oviposition, gravid females seek a brooding male and for the price of a mating are permitted to add their eggs to his clutch. Thus, by protecting eggs a male gains access to a pool of females he may otherwise not encounter and, more importantly, guarantees his paternity over the eggs produced by those females.

For similar reasons paternal care has also evolved in six genera of Belostomatidae (24, 134–136, 161). In these aquatic predators, females deposit eggs on the dorsa of receptive males. The male frequently interrupts oviposition to copulate and may copulate with and receive eggs from several females before his back is completely occupied. With his paternity assured, the male actively aerates his brood by various pumping and stroking motions until they hatch.

Dung and Carrion

Although dung and carrion have different origins, they impose similar benefits and constraints. Wilson (171) has called them "bonanza" resources since they are extremely rich in nitrogenous compounds and usually provide more than enough nutrients for larval development. But such resources are widely dispersed and ephemeral, and are suitable for only short periods before they desiccate or are claimed by competitors. To exploit dung or carrion, insects have become specialized at locating and dominating sources quickly.

One mechanism that has arisen independently in the Staphylinidae (54),

Scarabaeidae (48, 68), and Silphidae (82, 103) involves sealing the resource in a subterranean chamber. In this way predators and competitors are excluded while moisture is retained. Reviews of this behavior (47, 55, 68, 162, 171) suggest that it is an effective but labor-intensive solution that often requires the cooperative efforts of male-female pairs. Parental efforts are most critical and demanding during the resource acquisition phase of reproduction. If silphid beetles, *Nicrophorus,* for instance, do not locate and bury a small vertebrate soon after its death, the carcass will be devoured by fly larvae (82, 103, 104, 141). When males cooperate with their mates in this effort, carrion is buried significantly faster than when females work alone (169). Pairs must also protect their find from other silphids, and battles for possession of a carcass are common (170). When the prize is secured underground the male in most species mates with the female and then abandons the site. Females remain in the chamber, for the selective pressures favoring prolonged subsocial interactions in subterranean detritivores also act on *Nicrophorus*: The carcass is still an attractive resource that must be protected from competitors, predators, and the proliferation of fungi (170). Females are also important in facilitating larval feeding (103, 104). For a short time following each molt, the female feeds larvae regurgitated carrion.

Necrophagous sarcophagid flesh flies lack the morphological tools for burying carcasses; they compete for ephemeral carrion sources in a different way. Many species are ovoviviparous, retaining eggs in the uterus prior to eclosion (90). When a female locates a carcass, she can immediately deposit first instar larvae. Subsocial ovoviviparity not only avoids the mortality risk associated with free-living eggs, but also promotes rapid resource utilization through larviposition (27).

Subsociality in the scarabaeid dung beetles has converged on similar parental patterns (17, 47, 67–69). Utilization of dung as a larval resource occurs throughout the Scarabaeinae, Aphodiinae, and Geotrupinae, but subsocial interactions are developed only in the scarabaeine Coprini. In *Copris* and *Synapsis,* males assist females in excavating subterranean brood chambers and in preparing the larval dung cake. Males then abandon the females or remain inactive, leaving females to repair defects in the brood balls and to remove developing fungi (111, 158a, 162). Several species of cleptoparasitic dung beetles *(Aphodius)* regularly attempt to usurp the brood chambers of Coprini females, further necessitating maternal defense of the chamber (66, 118).

MATERNAL VS PATERNAL INVESTMENT

In the overwhelming majority of subsocial insects it is the female rather than the male that interacts with offspring. The rarity of significant paternal investment among insects has been attributed to several factors (reviewed by 101, 109,

138, 187), most notably paternity assurance. Females can always be certain that they are directly related to their offspring, whereas males cannot. Successful sperm transfer by no means assures a male of paternity. Multiple matings and sperm competition are common among insects; in many cases most eggs are fertilized by sperm received from the final mate (9, 93, 101, 137, 139, 163). Rather than risk investing time and energy in unrelated offspring, males of most species begin and end their paternal investment with copulation.

This argument has been challenged, however, on the basis of its generality (187). There is growing evidence that the expression of paternal behavior does not depend on the certainty of paternity when future opportunities for promiscuous matings are limited (42, 77, 166). Instead, paternity influences the evolution of paternal care only when a male must sacrifice future promiscuity for investment in offspring (166). In the only verified cases of postcopulatory uniparental care by male insects, there may be no loss of male promiscuity. Belostomatid and reduviid males may actually enhance promiscuity through paternal care, as guardian males are actively sought by gravid females (88, 105, 137). By leaving eggs with males, females maintain their ability to capture prey without a lapse in reproduction.

Paternal investment also increases when reproduction on a particular resource requires substantial investments in labor and territorial defense. The efficient exploitation of certain resources often requires the cooperative efforts of both parents and favors monogamous pair-bonding during reproduction (35, 156, 169). The colonization, manipulation, and protection of wood, for instance, has favored paternal involvement in cryptocercids, passalids, and scolytids. Male dung and carrion beetles also assist their mates in nest construction, provisioning, and territorial defense. With this involvement males prevent insemination of their mates by other males and also contribute to the survival of their offspring. Since the territorial defense of mates and resources greatly reduces opportunities for promiscuity, males that abandon females not only risk losing these benefits but also have little chance of securing additional matings (70, 83, 187). Thus, when resources impose labor demands, paternity assurance may be the result rather than the cause of paternal investment.

CONCLUSION

Selection should favor the evolution of life history patterns that maximize the benefits and minimize the costs associated with the exploitation of any given resource. The prevalence of subsocial behavior in insects reflects its significance as an evolutionary alternative for minimizing such costs. Insects exploiting foliage, wood, detritus, carrion, dung, or living animals are necessarily exposed to primary costs from predation, competition, and/or nutritional limitations. Subsocial mechanisms to minimize primary costs, however, can

create new secondary parental demands: Insects that avoid predators or competitors by reproducing in subterranean chambers, for example, are often forced to invest additional time and energy in provisioning and hygienic activities.

Although our knowledge of insect subsociality is incomplete, some evolutionary patterns are clear. The type of parental care and the degree to which males and females invest in their young appears related to the utilization of food resources: Insects sharing the same resource class have frequently converged on similar subsocial solutions to resource-related problems. Because their food provides relatively little shelter, folivores are exposed to heavy predation and parasitism. Consequently subsocial folivores guard their young to varying degrees, but (with the exception of Embiidina) do so without the benefits of a nest. Reproduction occurs directly on the resource, ensuring abundant and accessible food for offspring without additional parental investments. Two subsocial patterns emerge from insects exploiting woody hosts. Selection has repeatedly favored parental behavior that (a) transforms wood into an effective shelter for offspring and (b) facilitates feeding in immature insects, either by supplementing a nutrient-poor diet or by overcoming the inherent physical barriers that hinder feeding. Insects can rear their young on fragmented detritus if they guard them while foraging or, perhaps even better, minimize foraging risks by gathering food themselves and provisioning offspring within concealed brood chambers. The richness and ephemerality of carrion and dung promote adaptations that minimize exposure to desiccation and competition. Subsocial specialists on these resources either bury their cache and reproduce in the seclusion of a subterranean chamber or enhance the competitive abilities of their young by internalizing the vulnerable egg stage and depositing active first instar larvae. The subsocial activities of most predatory insects are constrained by the need for mobility. In the highly mobile aculeate Hymenoptera, young are reared and progressively fed within protective cavities. Less mobile subsocial predators must reproduce near sources of prey; these species guard exposed eggs at the oviposition site or carry them along while foraging.

In this review we have attempted to explain patterns of convergence in the evolution of insect subsociality through the selective forces associated with food resource utilization. Our arguments, however, are no stronger than the data on which they depend. In spite of recent advances, knowledge of subsocial behavior has advanced beyond anthropomorphic descriptions in only a few cases. To further our understanding of the ecology, genetics, and evolutionary biology of insect parental behavior we must use the tools of comparison and manipulation in a variety of insect taxa. Without such an approach we cannot hope to understand why some insects care for young while others do not, or, more importantly, what the evolutionary relationships are between primitive

forms of sociality and the more advanced eusocial behavior of the Hymenoptera and Isoptera.

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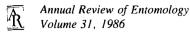
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