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Parental Care in Invertebrates

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I. INTRODUCTION

Social behavior among invertebrates ranges from the asocial through subsocial (parent–offspring association) to the most complex of eusocial societies (overlap of generations, reproductive division of labor, cooperative brood care) (E. O. Wilson, 1971). The taxonomic, physiological, and ecological diversity provide ample material for comparative studies of behavior. Because parental behavior is widely dispersed taxonomically, the invertebrates represent numerous independent experiments in the evolution of the parental lifestyle. Comparative analyses should thus permit invertebrate biologists to address several questions that are inaccessible to vertebrate biologists. Unfortunately, our present understanding of parental care in invertebrates is limited. This has occurred both because of the overwhelming diversity of invertebrates and because subsocial behavior often was studied as a pretext for understanding advanced sociality.

The natural history and ecological correlates of invertebrate parental behavior have been adequately covered by previous reviewers. Excellent compilations of the natural history of parental care (with an emphasis on the insects) appear in E. O. Wilson (1971), Hinton (1981), Eickwort (1981), and in Preston-Mafham and Preston-Mafham (1993). Since E. O. Wilson's (1975) interest in the evolutionary prime movers of parental behavior, the ecological and behavioral correlates of parental care among invertebrates have also been reviewed extensively (R. L. Smith, 1980; Thornhill and Alcock, 1983; Tallamy, 1984; Zeh and Smith, 1985; Tallamy and Wood, 1986; Tallamy, 1994). After revisiting these prime movers, I review two additional areas: the physiological and behavioral mechanisms that control the onset, intensity, and termination of parental care; and the use of invertebrates to address parental care theory. This approach is taken to demonstrate that mechanistic studies of invertebrate parental behavior will provide insight as well as experimental tools for ecologists, to fill gaps in the coverage of invertebrates, and to reveal the potential for the use of invertebrate models in tests of parental care theory. Taxonomically, less emphasis will be given to the Hymenoptera and Isoptera because these groups have been reviewed extensively in works addressing eusociality, and to the marine taxa because of the lack of information beyond their natural history.

II. Revisiting the Prime Movers of Care

Seminal works on the social insects and social behavior by E. O. Wilson (1971, 1975) stimulated a burst of experimental studies of parental care. Wilson detailed four ecological pressures (prime movers) that select for parental care: stable and structured environments, harsh environments, scarce and specialized food resources, and predation. A consequence of the promulgation of the prime movers was that empirical studies were quickly undertaken to identify prime functions. Search for prime functions also was encouraged by the notion that the causes of parental care in noneusocial species would be straightforward. In most parental invertebrates, particularly those that nest or carry their offspring, intensive study has revealed that caregiving has multiple functions. This finding suggests that parental care involves a suite of evolutionary changes as well as the loss of adaptations suited to the nonparental lifestyle (some of these secondary changes occurring long after the origin of parental care). The identification of the prime cause of parental care, therefore, will be difficult in many cases.

Three examples will demonstrate the complex functions of care in many invertebrates. The salt-marsh beetle, *Bledius spectabalis,* often is given as an example of an organism in which parental care evolved to cope with a harsh environment. Indeed, Wyatt (1986) elegantly demonstrated that maintenance of a wine-bottle-shaped burrow prevented rapid flooding and anoxia in the intertidal environment. Subsequent investigation has revealed that parental care serves the additional functions of provisioning young with algae, keeping the burrow mold-free, and defending against carabid predators and ichneumonid wasp parasitoids (Wyatt, 1986; Wyatt and Foster, 1989a,b).

Rudolf Diesel has enumerated multiple functions of care in the Jamaican land crab, *Metopaulias depressus,* for which it is suspected that the evolutionary prime mover is an inhospitable environment. *Metopaulias* lives in water that collects in the axils of epiphytic bromeliads. A water-filled axil serves as a nursery during a 9-week developmental period (Diesel, 1989). Untended bromeliads are unsuitable for crab larvae because leaf debris both reduces dissolved O_2 and lowers pH in the nursery. The maternal *Metopaulias* regularly removes debris from leaf axils, raising dissolved O_2.

The larval environment is further modified by the addition of snail shells that raises pH and increases Ca^{2+} availability (Diesel, 1992; Diesel and Schuh, 1993). The mother also captures prey and brings it to the nursery, and protects young from spider and nymphal damselfly predators.

The prime mover of parental care in burying beetles (*Nicrophorus* spp.) is thought to be the exploitation of a scarce and valuable resource, small vertebrate carrion. In burying beetles, male–female pairs secure the carcass underground and defend it from intraspecific and interspecific competitors. Parents control the decomposition by removing hair or feathers, rounding the carcass into a ball, and applying antimicrobial secretions (Pukowski, 1933; Halffter et al., 1983). Shortly before hatching of young the female opens a small hole in the uppermost part of the carrion ball. This provides access to the carcass interior for feeding by first instar larvae. Parents supplement feeding by regurgitating liquified carrion. If the food supply is not sufficient to support the entire brood, parents will cannibalize a subset of the brood so that adequate resources remain for surviving young (Bartlett, 1987). Both parents will defend the brood against predators such as carabid beetles, and against infanticidal intruders (Scott, 1990; Trumbo, 1990a).

Each of these examples of complex care is more remarkable because each occurs in a genus with closely related asocial species. *Bledius* and *Metopaulias,* in fact, coexist with nonparental congeners. The multiple functions of parental care suggest that the initial evolution of parental care was followed by secondary parental adaptations that replaced adaptations with similar functions in the nonparental ancestor. For example, parental care in many groups has an egg care function; several authors have noted the greater vulnerability of untended eggs of parental as compared to nonparental species (Eberhard, 1975; Hinton, 1981; R. L. Smith, 1980; Tallamy, in press). This suggests that as caregiving came to include the function of facilitating hatching, resources previously devoted to egg viability in nonparental ancestors may have been employed for other purposes. The existence of a suite of adaptations, whether parental or nonparental, suggests that evolution in either direction may be impeded by having to cross a fitness valley. This is because a single environmental change is unlikely to favor every component of a parental or nonparental lifestyle. Clearly, however, natural selection has surmounted the barrier in many cases.

The complex function of care can make it more difficult to identify a single environmental prime mover. Experiments in which a parent is removed may disrupt many aspects of an organism's life history, and thus contribute little to our understanding of the origin of parental care. How then might one test the hypothesis that a prime mover such as a harsh environment has been important for the evolution of parental care? The numerous examples of the independent lineages that have evolved care provide one opportunity.

One of the earliest interspecific comparisons found that there was a relative increase in the number of marine species possessing nonpelagic larval development (associated with greater parental investment) in harsher environments (toward the poles and at greater depths) (Thorson, 1950; Mileikovsky, 1971). Environmental harshness, however, is a relative concept and will clearly depend on the taxa under consideration. Beetles utilizing marine tidal zones and crabs in terrestrial habitats may both be considered an invasion of a harsh environment. Further interspecific tests of this hypothesis will require *a priori* establishment of criteria for environmental challenge. Substantiation of the importance of this and other prime movers can perhaps be made more convincingly with invertebrates because of the large number of independent lineages thought to have evolved parental care, and the tremendous diversity in the level of sociality among closely related taxa.

Phylogenetic comparisons also have limits. The evolution of parental care, like the evolution of flight, is an adaptation that may permit subsequent radiation (but see Tallamy, in press). The cause and effect of associations such as that between parental care and environmental harshness may be difficult to resolve. Once parental care evolves, due to whichever prime mover, the protection afforded immature stages may permit invasion of an environment that was formerly not suited for juvenile development. In some cases it will be difficult to determine whether parental care evolved concurrently with invasion of the harsh environment, or whether parental care was a preadaptation. A similar caveat applies to each of the other three prime movers.

III. Physiology of Care

Behavioral ecologists are concerned primarily with functional explanations of variation in behavior. A thorough ecological examination of behavioral plasticity includes information on stimuli eliciting behavioral changes, fitness consequences of adopting alternative behaviors, and a phylogenetic analysis of differences in social behavior. Knowledge of the physiology of behavioral plasticity is helpful for exploring how plasticity is related to ecology. For instance, the ability to manipulate the physiological state of an individual provides a naturalistic way to alter behavior and thereby examine correlations and trade-offs among behavioral states (Wingfield *et al.*, 1987); fitness consequences of alternative behaviors (Ketterson and Nolan, 1992; Ketterson *et al.*, 1992); and resulting changes in the behavior, hormonal state, and fitness of social partners (Wingfield *et al.*, 1990). In addition, physiological responses can be sensitive probes to determine which environmental stimuli organisms pay selective attention to when making critical life-history decisions (Dusenberry, 1992). Despite the fact that in many ways insects are the paradigmatic group for examining social plasticity (E. O. Wilson, 1971; Thornhill and Alcock, 1983), there has been little work on the physiological basis of intraspecific and interspecific diversity of this behavior.

Students of insect parental behavior can draw upon a solid understanding of the physiology of reproduction. Endocrinologists have outlined the control of reproductive maturation and behavior in several models (Koeppe *et al.*, 1985; Hagedorn, 1985). In the protocerebrum of the insect brain, the pars intercerebralis has neural input into the corpora allata (CA), the synthesis and release site of juvenile hormone (JH) (Feyereisen, 1985) (see Fig. 1). JH is the primary gonadotrophic hormone in insects (Koeppe *et al.*, 1985), and also regulates numerous adult behaviors (Robinson, 1987; Cusson and McNeil, 1989). The brain-CA-ovary axis of insects is structurally and functionally analogous to the neuroendocrine regulation of the adenohypophysis of the pituitary by the hypothalamus in vertebrates (Scharrer, 1987).

Invertebrate parents provide extended parental care in three principal ways: carrying young internally or externally, providing resources for young within nests, and tending young that are clustered near food sources. Al-

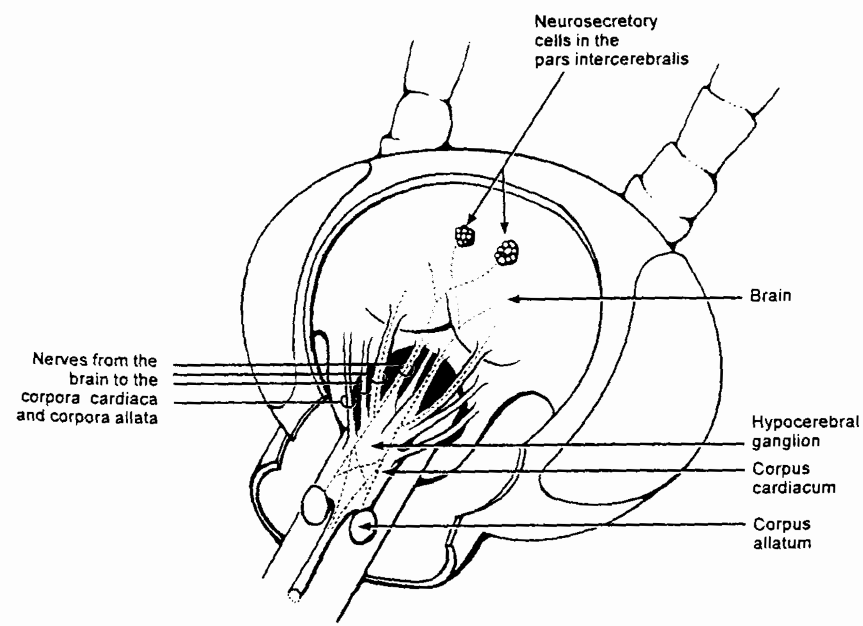

Fig. 1. Semidiagrammatic representation of the brain and endocrine tissues of insects. (Modified from Engelmann, 1970.)

though careful behavioral and ecological studies have been conducted on representatives of each of these three modes of parental care, physiological studies are limited to those that carry young and to nest builders. Here, I review the physiological correlates of reproduction and parental care in the three most intensively studied invertebrate models: the cockroach, *Diploptera punctata;* the earwigs; and the burying beetle, *Nicrophorus orbicollis.*

A. Pregnancy in the Viviparous Cockroach, *Diploptera punctata*

Cockroaches exhibit a variety of reproductive patterns including oviparity (deposition of eggs), viviparity (birth of live young), and ovoviviparity (hatching of eggs internally) (reviewed in Roth and Willis, 1960). Oviparous species with limited parental investment (e.g., *Periplaneta americana*) produce small batches of eggs continually after reaching reproductive maturity. Gonadotrophic cycles are overlapping and there is a small peak in JH synthesis prior to the onset of vitellogenesis in the first oocytes, followed by a succession of JH peaks corresponding to late vitellogenesis in basal oocytes and early vitellogenesis in penultimate oocyctes (Weaver *et al.*, 1975; Feyereisen, 1985). Viviparous and ovoviviparous cockroaches, in contrast, carry young internally and exhibit more defined parental and hormonal cycles, analogous to those in vertebrates (Scharrer, 1987).

The viviparous cockroach, *Diploptera punctata,* is the best studied example of "pregnancy" in an invertebrate. *Diploptera punctata* begins gestation about 8 days after the imaginal molt. It has a 60-day pregnancy period during which a highly nutritive milk containing 45% protein and 16–22% lipid is secreted from the walls of the brood sac (Ingram *et al.*, 1977). After the imaginal molt, neural input from the brain is thought to initially inhibit the synthesis of JH in the CA (denervation results in enhanced CA activity) (Tobe and Stay, 1980, 1985). The CA of adult *Diploptera* females are thought to be released from inhibition by mating and feeding, as the CA are in other cockroaches (Gadot *et al.*, 1989a; Aclé *et al.*, 1990). A rise in JH biosynthesis is followed by vitellogenesis (Fig. 2). Initially, developing oocytes feedback positively on the CA, but once the ovary is mature, JH synthesis is inhibited. After peaking, JH synthesis declines prior to oviposition (Rankin and Stay, 1985). Ovarian ecdysteroids also increase and then decrease prior to oviposition, the peak occurring slightly after the JH peak (Stay *et al.*, 1984). The importance of changing ecdysteroid titers for regulating the reproductive cycle is not clear.

During most of gestation, synthesis of JH remains inhibited. Basal oocytes (which give rise to the second brood) are nonvitellogenic until a few days prior to parturition of the first brood (Stay and Lin, 1981). JH treatment (implantation of active CA or topical application of JH analogs) during

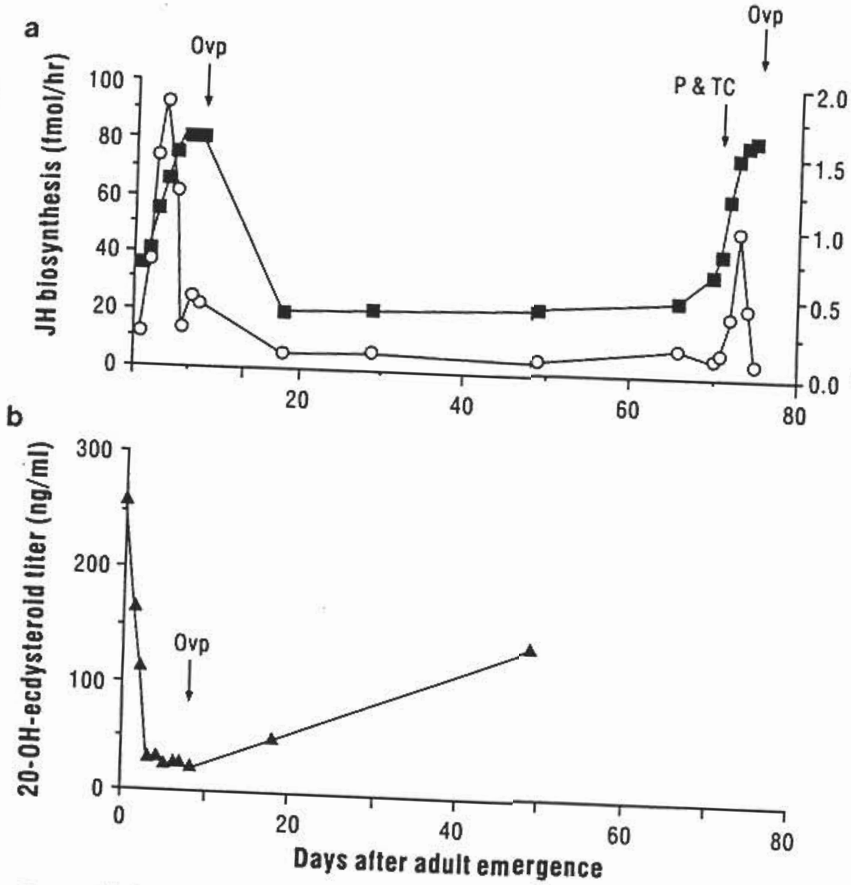

Fig. 2. (a) Changes in biosynthetic rate of juvenile hormone (JH) by the corpora allata (open circles), and length of the basal follicle (closed squares) during the pregnancy cycle of *Diploptera punctata.* Ovp = oviposition; P & TC = parturition and termination of care. (b) Blood titers of 20-OH-ecdysone during the pregnancy cycle. (Figure modified from Rankin and Stay (1985) and Stay *et al.* (1984).)

gestation causes a premature decline in protein and milk content of the brood sac (Stay and Lin, 1981), demonstrating a negative link between this hormone and parental investment. According to Rankin and Stay (1985), a low rate of JH synthesis during pregnancy is maintained by the small ovary, which cannot stimulate the CA, and by inhibition from the brain. The presence of embryos within the brood sac is apparently detected by sensory hairs and this information is relayed to the brain via the ventral nerve cord (Engelmann, 1957). Removal of embryos during late pregnancy caused CA activity to increase and accelerated the second bout of vitellogenesis and oviposition. Rankin and Stay (1985) postulated both neural and humoral inhibition of the CA, because denervation resulted in only partial release from inhibition. Neuropeptides that inhibit CA activity of *Diploptera punctata in vitro* have been isolated from both the brain and blood (Rankin and Stay, 1987; Woodhead *et al.*, 1993).

There are many variations on the mother–offspring relationship among cockroaches, only some of which have been explored at the level of physiology. The oviparous German cockroach, *Blatella germanica*, carries an egg sac externally and maintains low levels of JH synthesis during egg care in a manner similar to pregnancy in viviparous cockroaches (Gadot *et al.*, 1989b). Young of the ovoviviparous cockroach, *Leucophaea maderae*, are reported to accompany their mother on nocturnal foraging trips following parturition (Liechti and Bell, 1975). The Australian burrowing roach, *Macropanesthia rhinoceros*, and the woodroach, *Cryptocercus*, have extremely long-term familial associations (Seelinger and Seelinger, 1983; Nalepa, 1988; Ruegg and Rose, 1991; Matsumoto, 1992). Unfortunately, very little is known about the physiological correlates of these postparturition parent–offspring relationships.

B. Nest Building in Earwigs

Our most detailed account of endocrine correlates of a subsocial nest builder is of the earwigs, *Labidura riparia* and *Euborellia annulipes* (Dermaptera). Much of the research on parental behavior in this group is reported in the French literature. The account here is largely drawn from summaries and original observations contained in Lamb (1976), Baehr *et al.* (1982), Vancassel *et al.* (1984), and Rankin *et al.* (1995a,b).

There are approximately 1000 species of Dermaptera. Of the 13 species studied, all show maternal care (Lamb, 1976). After emergence as adults, females undergo a brief period of reproductive maturation and then cycle through alternating periods of ovarian development and brood care. During the sexual phase (ovaries maturing), earwigs feed (including cannibalization of young), mate, and form burrows. Ovarian development is suppressed in the parental phase, during which time the mother fasts while caring for her eggs. After hatching, the female stays with nymphs for 3–4 days, then opens the burrow, captures prey, and provisions the nest. The parental period ends when young disperse.

After emerging as an adult, the start of vitellogenesis correlates with an increase in JH titer in the blood. Neither feeding nor mating is required for this increase (Vancassel, 1973; Lamb, 1976; Vancassel *et al.*, 1984). Topical application of JH causes an earlier age of courtship but does not result in earlier mating in the ring-legged earwig, *Euborellia annulipes*

(Rankin *et al.*, 1995a). The removal of the CA prevents oviposition; CA removal accompanied by application of JH-mimics restores oviposition, demonstrating the typical role of JH in reproductive maturation (Baehr *et al.*, 1982). As in *Diploptera*, there is both a JH and ecdysteroid peak prior to oviposition. In contrast to *Diploptera*, however, *Euborellia* maintains elevated synthesis of JH at the beginning of the oviposition period, possibly because oviposition will occur over a 1- to 2-day span (Fig. 3). This suggests

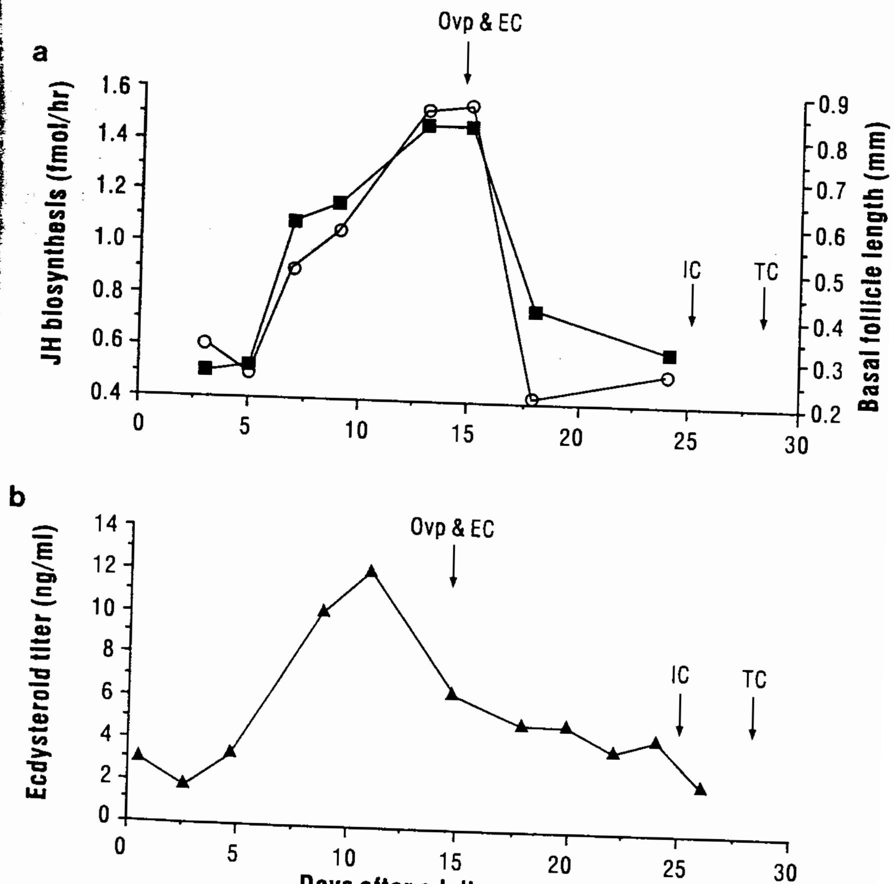

Fig. 3. (a) Changes in biosynthetic rate of juvenile hormone (JH) by the corpora allata (open circles), and length of the basal follicle (closed squares) during the parental cycle of earwigs. Ovp & EC = oviposition and egg care; IC = initiate care of nymphs; TC = terminate care. (b) Blood titers of ecdysteroids during the parental cycle. (Figure modified from Rankin *et al.* (1995) and Baehr *et al.* (1982).)

that mature ovaries do not have an immediate inhibitory effect on CA activity, as does occur in *Diploptera* (Rankin *et al.*, 1995). Topical application of JH at adult emergence results in an earlier age of first oviposition, but at the expense of a smaller clutch (Rankin *et al.*, 1995).

During parental care, blood levels of both JH and ecdysteroids decline and remain low. The ecdysone/20–hydroxyecdysone ratio changes markedly between the sexual and parental phase, but the significance of this is unclear (Vancassel *et al.*, 1991). If eggs are removed from mothers on the first day of the parental cycle, there is a short-term increase in both JH titer and oocyte size, apparently in preparation for a new sexual phase. The majority (64%) of such mothers do not accept eggs presented after a 48-h hiatus from care, and all refuse eggs after 72 h. When mothers have provided 5 days of care, however, egg removal has less dramatic effects on parental responsivity; only 11% of such mothers refused eggs after 48 h without contact (Vancassel *et al.*, 1984). It is not clear whether this difference in maternal response is caused by changes in the characteristics of maturing eggs or by the cumulative time spent providing care. Mothers normally do not hunt or eat during egg care. If food is continually provided late in the parental cycle, however, some will feed. These mothers terminate care early, have high blood levels of JH and ecdysteroids, and have premature oocyte development, all characteristic of the beginning of the next sexual phase. Conversely, enforced fasting and regular contact with young can prolong parental care (Vancassel *et al.*, 1987). Substitution of younger offspring for old also prolongs parental care (Caussanel, 1970), as occurs in parental dung beetles (Klemperer, 1983a), suggesting that offspring provide important cues that influence the endocrine state of caregivers.

In *Labidura riparia,* the parental period also can be extended by removal of the CA, presumably because a lower JH titer delays the termination of parental behavior, the reinitiation of vitellogenesis, and the onset of the next sexual phase (Pierre, 1978). In support of the role of JH in terminating parental care in *Euborellia annulipes,* Rankin *et al.* (1995a) found that topical application of JH III on the day of oviposition shortened the period of egg care, increased the probability of cannibalism, and stimulated premature ovarian maturation. Despite these findings, Baehr *et al.* (1982) do not think there is a direct connection between low levels of JH and parental care. They found that ovariectomized females had hyperactive CA and yet would accept and care for experimentally provided eggs for extended periods. Thus, they argue that parental behavior is controlled more directly by the brain. Presumably, JH treatment causes an earlier termination of care through its indirect effects on the brain via the ovaries (see Fig. 4).

Caussanel *et al.* (1978) reports neurosecretory correlates of care. Neurosecretory products of the pars lateralis and A cells in the pars intercerebralis

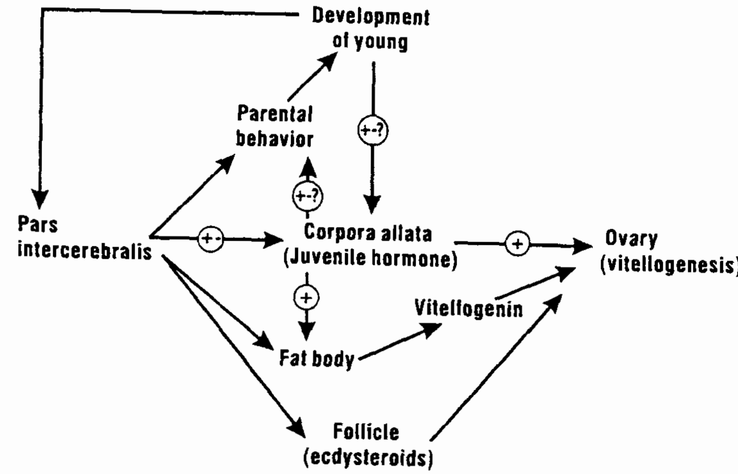

FIG. 4. Model of the regulation of reproduction and parental behavior in insects. Positive and negative influences on and from the corpora allata are shown.

decrease during the vitellogenic cycle, but are elevated during egg care. These site-specific increases in secretion occur despite an overall decrease in secretion from the pars intercerebralis during maternal care. Maternal care is also correlated with storage of neurosecretory material in the aortic walls. If the pars intercerebralis is cauterized, care is interrupted and young are cannibalized (Baehr *et al.*, 1982).

In summary, there are several similarities between pregnancy in cockroaches and brood care by earwigs. In both models, there are peaks in both JH and ecdysteroids prior to oviposition followed by inhibited CA activity and low blood levels of JH during parental care. JH synthesis and ovarian development are then stimulated during the latter part of the parental period, presumably because of changing cues from offspring. Demonstrations of direct links between changing hormonal levels and parental behavior, however, have been few. Fortunately, endocrinological techniques are available for addressing this issue. The development of fast, sensitive, and reliable radioimmunoassays for JH (Strambi *et al.*, 1984; Goodman *et al.*, 1993; Huang *et al.*, 1994) make it possible to work with the large number of individuals required for behavioral study. Classical techniques of gland removal and hormone replacement are feasible; in many cases dissected CA also can be employed *in vitro* to measure biosynthetic rates of JH. A decided advantage in behavioral experiments is that JH and JH analogs can be applied topically, allowing noninvasive manipulations with a minimum of disruption. Although JH is quickly broken down in the blood, analogs such as methoprene can be employed when a JH-like effect must be maintained for a longer period of time. It also is possible to raise JH titers in the blood by applying inhibitors of JH esterase. A number of anti-CA compounds (precocenes) have been developed to eliminate the source of JH nonsurgically; these compounds, however, do not perform equally well in all groups of insects (Bowers *et al.*, 1976). There also has been considerable recent progress, especially employing the cockroach models, in identifying allatostatins from the brain that regulate the synthetic activity of the CA (Woodhead *et al.*, 1993; Stay *et al.*, 1994). In combination, the application of these techniques should allow behavioral endocrinologists to determine whether JH has direct or indirect effects on parental care.

C. Extended Biparental Care in the Burying Beetle, *Nicrophorus orbicollis*

I initiated endocrinological studies of biparental burying beetles, which reveal several differences from the two models previously discussed. After burying beetles emerge as adults, they feed on carrion and fly larvae for 2–3 weeks until reproductive competence is attained. Females become sexually receptive shortly after emergence and will store sperm for considerable periods (Eggert, 1992). JH titers and ovarian mass increase over the first 20 days and eventually reach a resting-state plateau (see Fig. 5; Trumbo *et al.*, 1995).

Burying beetles reproduce only when they locate a small carcass, a temporally and spatially ephemeral resource. This pattern is similar to mosquitoes in which ovaries remain in a resting state until a blood meal is obtained (Edman and Lynn, 1975). After burying beetles inter a carcass, they remove hair and deposit antibiotic anal secretions to control the decomposition (Pukowski, 1933). Competition for fresh vertebrate carcasses is keen, with competitors possessing behavioral and physiological adaptations to exploit carrion quickly. Sarcophagid flies, for example, decrease the time it takes for their young to exploit carrion by larvipositioning directly on the resource (Denno and Cothran, 1976). When a female burying beetle locates a carcass, she begins a period of assessment behavior, apparently determining whether the resource is of suitable size and condition. Within 10 minutes of the discovery, JH levels have doubled. Within 18–24 h, ovarian mass increases two to three times and oviposition in the surrounding soil begins (D. S. Wilson and Knollenberg, 1984; Scott and Traniello, 1987; Trumbo *et al.*, 1995). The rapid and substantial ovarian increase is accompanied by some of the highest measured titers of JH among insects; these titers have been confirmed by qualitative analyses of JH (Fig. 5).

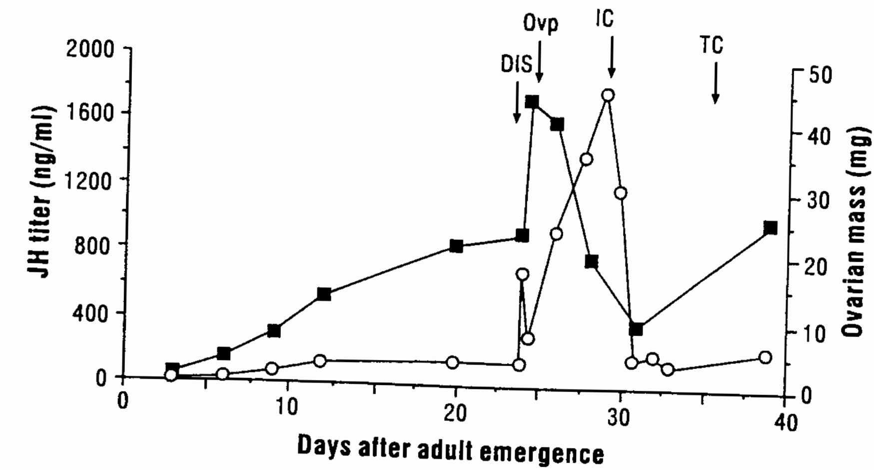

FIG. 5. Blood titers of juvenile hormone (JH) (open circles) and ovarian mass (closed squares) during the parental cycle of the burying beetle, *Nicrophorus orbicollis*. DIS = discovery of a carcass; Ovp = oviposition; IC = initiate care of larvae; TC = terminate care. (Figure modified from Trumbo *et al.* (1995) and S. T. Trumbo, unpublished data.)

Females do not feed during the initial 10 minutes following discovery, suggesting that feeding is not necessary for the initial JH surge. Substantial feeding prior to oviposition does occur, however, and may have quantitative effects on the number of eggs produced. Mating after resource discovery also does not appear to be necessary for the rapid JH increase or ovarian maturation. While a male will often aid the female and mate regularly during nest preparation, a lone female will complete the entire nesting cycle on her own if a male fails to discover the resource. Cues derived from behavioral assessment, and not from mating or feeding, are thus responsible for increases in JH and maturation of ovaries following carcass discovery. Reproduction, therefore, appears to be regulated by a complex integration of environmental, behavioral, and endocrine factors in a manner similar to many vertebrates (Lehrman, 1965; Crews, 1975).

Following oviposition, JH titers decline but still remain at levels higher than experienced prior to resource discovery. Interestingly, a second peak in JH titer occurs in both the male and female parent, coinciding with the arrival of young on the carcass (S. T. Trumbo, unpublished results; Fig. 5). The arrival of young on the carcass and the second peak in JH occur approximately 5 days after carcass discovery at a time when ovarian development is suppressed. When young arrive on the carcass, parents become extremely active, regurgitating liquified carrion and increasing nest maintenance. As young grow and become independent, parental activity subsides and care consists mainly on defense against predators (Fetherston *et al.*, 1990, 1994). Titers of JH decline during the latter part of the parental cycle, before increasing again at the time parents desert the nest (S. T. Trumbo, unpublished results). Aggression against congeneric competitors remains high during the entire parental period and does not parallel changes in blood levels of JH.

As in *Diploptera* and the earwigs, female burying beetles experience an increase in JH prior to oviposition, low levels of JH during part of the parental cycle, and an increase in JH and ovarian growth as parental care is being terminated. In burying beetles, however, there is an intriguing additional surge of JH during the early and most active phase of the parental cycle. There are at least two possible explanations for high levels of JH during the first few days of parental care. The first possibility (parental care) is that the JH peak is connected to very active caregiving (parents rarely rest during the first 2–3 days larvae are on the carcass). A second possibility (clutch replacement) is that the maintenance of elevated JH during the initial period of care coincides with the time frame in which a female will attempt to reuse the resource should a brood failure occur. Brood failure can occur because of poor hatching success or because a conspecific male takes over the resource, kills all offspring, and mates with the resident female (Trumbo, 1990a; Scott, 1990). Late in the parental cycle, the deterioration of the resource is such that females will not produce a replacement clutch in response to brood failure. Elevated titers of JH would be maintained then, as long as the female was willing to reinitiate reproduction on a carcass. Under this hypothesis, decreasing blood levels of JH late in the parental cycle would be associated with unwillingness to oviposit near a resource that can no longer support a brood. It should be noted that in dung beetles, regression of ovarian follicles during parental care is gradual, and may be associated with a gradual decline in the probability of reusing the dung resource in the event of a brood failure (Martinez and Caussanel, 1984; Sato and Immamori, 1987; Edwards and Aschenborn, 1989). Neither the parental care nor the clutch replacement hypothesis for the second JH peak in burying beetles can be supported empirically at this time.

D. Eusocial Insects

The study of the physiological regulation of simple family groups may provide insight into the evolution of sociality. This may depend, in part, on whether advanced sociality evolved through the subsocial (mother–offspring) or parasocial (sister–sister) route (Michener, 1969). In primitively

eusocial insects such as bumblebees (*Bombus*) and paper wasps (*Polistes*), the queen actively maintains her dominant position as primary egg layer by display, aggression, and egg eating. In both *Bombus* and *Polistes*, dominance is correlated with large CA, higher blood levels of JH, greater oocyte development, aggression, and more time spent egg laying (Röseler *et al.*, 1984; Larrere and Couillaud, 1993). Individuals with low JH spend more time foraging, one of the principal forms of alloparental care. In bumblebees, the dominant individual may suppress JH levels in subordinates, in part, by producing a pheromone that decreases CA activity in nest mates (van Doorn, 1987; Larrere and Couillaud, 1993). Treatment with JH analogs tends to have little effect on social hierarchies in established association in *Polistes*, and in queenright bumblebee colonies. On the other hand, JH treatment is likely to confer dominance on individuals if administered before a hierarchy is established (Röseler *et al.*, 1985), and in queenless bumblebee colonies (van Doorn, 1987; Larrere and Couillaud, 1993). These findings parallel work on dominance hierarchies in vertebrates in which the stability of the social group and timing of hormonal manipulations is critically important (Wingfield *et al.*, 1987).

In the highly eusocial honeybee (*Apis mellifera*) and in the wasp *Polybia*, JH plays the quite different role of mediating age-based division of labor among nonreproductive workers. Low levels of JH are associated with nest activities such as caring for brood, while higher levels of JH are typically found in other forms of alloparental care such as foraging (O'Donnell and Jeanne, 1993; Robinson *et al.*, 1989).

E. The Importance of Mechanistic Studies

Unfortunately, few studies of the physiological basis of reproductive behavior of invertebrates also address areas of primary concern to behavioral ecologists. A thorough understanding of the physiology of invertebrate parental behavior promises to make three contributions to behavioral ecology: (1) permit the quantification of responses to key stimuli affecting behavior; (2) provide tools for exploring the costs–benefits of life-history trade-offs; and (3) provide insight into the role of phylogeny in adaptive evolution.

It is important to identify the exact informational cues that organisms monitor to address questions about optimality, constraints and evolutionary direction (Stephens, 1989; Ryan, 1990; Stamps, 1991; Endler, 1992). Studies of sexual selection, for example, have taken important new directions subsequent to analyses of the arbitrary location of secondary sexual characteristics (Burley, 1977), pre-existing sensory biases (Basolo, 1990), and mate copying (Dugatkin, 1992). Likewise, theoretical study of decision making by parents will be stimulated when we better understand the cues to which caregivers pay selective attention. In the biparental burying beetle, a female will spend more time performing energetically demanding caregiving activities such as feeding young and maintaining the nest when forced to provide care alone (Fetherston *et al.*, 1994). Is her altered behavior dependent on stimuli associated with the condition of young, with demands by the young, with the presence–absence of her mate, or with parental effort of her mate? It is unlikely that we will understand parental care decisions and limits to adaptive responses of parents until we know what information parents selectively monitor. Physiological analyses may permit easily quantifiable, sensitive probes in experiments manipulating critical stimuli.

Hormones play a principal role in allocating organisms' internal resources to competing reproductive and nonreproductive needs (Finch and Rose, 1995). Manipulations of testosterone in free-living vertebrates have allowed the examination of the trade-offs among territory aquisition, mate attraction, caregiving, and survival (Marler and Moore, 1988; Ketterson *et al.*, 1992). Similar studies soon may be possible with invertebrates. In the dung beetle, *Onthophagus bimodis,* for instance, males that complete pupal development above a critical size pursue a parental strategy, locating dung pats and assisting females with brood care. Smaller-bodied males never provide care, however, and attempt to sneak copulations as a means of achieving reproductive success (Cook, 1990). Such size-dependent switches in life-history strategy are thought to be selected in response to strong intrasexual competition along with a highly variable feeding environment for larvae (Eberhard, 1982). Unfortunately, very little is known of the hormonal control of adult male behavior in *Onthophagus.* Manipulations of larvae that alter the strict body size–reproductive strategy relationship may provide powerful tests of adaptive explanations of alternative life histories.

Mechanistic studies also may contribute to comparative studies of invertebrate parental behavior. The multiple origins of parental and social systems among so many distinct phylogenetic groups of insects, regulated by similar endocrine systems, begs for interspecific comparisons. In particular, the evolutionary potential of organisms' reproductive physiology might be addressed. Comparative approaches to the evolution of parental care physiology among vertebrates is limited. Little is known about the physiological changes that occurred as the ancestors of birds and mammals evolved parental care. Because key components of parental care likely evolved but once (e.g., lactation) we cannot know whether alternative physiological routes might have evolved to control the same trait. The multiple origins of parental behavior within the insects will allow for two types of tests. First, broad phylogenetic comparisons can be made to examine whether

convergent behavior is necessarily based on convergent physiology. Second, comparisons of closely related species within groups in which both parental and nonparental lifestyles are represented will permit the testing of specific hypotheses of how evolution proceeds from one adaptive peak to another. Even with the limited knowledge presently available, it is clear that parental and social behavior is not regulated in exactly the same manner among independent lineages. Whether anatomy and physiology are extremely malleable in the hands of selection, or whether they impose formidable constraints on the evolution of behavior, will not be understood until functional and mechanistic studies are integrated.

IV. Parental Care Theory and Invertebrates

A. The Regulation of Brood Number

The number and size of offspring that will be raised are primary life-history variables. The trade-off between number and size of offspring is predicted to result in an optimal brood size that maximizes total fitness of the parent (C. C. Smith and Fretwell, 1974; Godfray, 1987; K. Wilson and Lessels, 1994). The optimal brood number is generally less than the maximum brood number that could be raised because body size of offspring affects their subsequent reproductive success. Small-bodied individuals experience greater mortality (J. Mappes and T. Mappes, personal communication), are less competitive for resources (Otronen, 1988), and produce fewer offspring (Tyndale-Biscoe, 1984; Cook, 1988; Bartlett and Ashworth, 1988). The production of undersized offspring can be especially disadvantageous when offspring must compete for limited resources (Brockelman, 1975; Lloyd, 1987). Females of the solitary wasp, *Euodynerus foraminatus,* for example, provide more food to offspring that are likely to engage in frequent contests for mates or nest sites (clumped nests) than when competition among offspring is expected to be less severe (Cowan, 1981). The ability to partition resources among offspring efficiently is especially critical when fitness of offspring is related to body size in a logistic fashion, in which young without adequate resources are not competitive, and young receive diminishing returns for superabundant resources (e.g., see Tyndale-Biscoe, 1984).

Theoretical and empirical tests have demonstrated that optimal clutch size can be affected by larval competition, costs of reproduction, brood parasitism, and search time for suitable locations to oviposit (K. Wilson and Lessels, 1994). Less attention has been given to constraints imposed by parents' ability to gather accurate information concerning resource avail ability and number of young. These constraints will not come to light until the cues that parents employ to monitor their environment are known. Brood size adjustments also may be limited by parents' ability to provide care. A number of folivorous insects, for example, shield young under their body. Eggs on the outside of an egg cluster are highly vulnerable to predation and parasitism (Odhiambo, 1959). Using the parent bug, *Elasmucha grisea,* Mappes and Kaitala (1994) demonstrated that females of different body size produce a clutch that is appropriate to the area that a female can cover and therefore defend. Small females that were experimentally provided an enlarged clutch lost all additional eggs. Interestingly, *Elasmucha* lays the largest eggs in the central, safest part of the egg mass, confirming that unequal care within a brood is expected when prospects for offspring vary (Mappes *et al.,* in press). This study nicely demonstrates that components of life history cannot be considered in isolation (Hinde, 1975). Obviously, an adequate understanding of clutch size in *Elasmucha* would require detailed examination of all ecological factors that have had a significant effect on the evolution of female body size.

The evolution of parental care allowed species to adjust brood size in ways not possible in nonparental species. Continued contact with young permits greater investment per offspring; repeated assessment of resource availability; and, when young fail, recouping of investment and redirection of resources. Parental care may thus permit a finer degree of control over brood number and hence body size of offspring. This prediction is supported by less variation in body size among wood-feeding species with parental care as compared with those without care (Haack and Slansky, 1987). Because parents often act as a buffer between the environment and their offspring, resource availability to young is often less variable than resource availability to the parent. Among a number of taxa, females of small size produce offspring of equivalent size to large-bodied females by producing fewer young per reproductive attempt (Tyndale-Biscoe, 1984; Schmidt and Smith, 1987; McLay and Hayward, 1987; but see Lee and Peng, 1981).

An understanding of the stimuli that parents monitor to assess both resource availability and number of brood will permit a more complete accounting of clutch–brood size decisions. The simplest mechanism to adjust brood number to available resources is to gather food until a single offspring can be supported, oviposit an egg into the provision, and repeat until resources are exhausted. This strategy is employed by many caregiving dung beetles, which exploit an easily divided resource (e.g., Sato and Immamori, 1987).

When food is less malleable, there is less flexibility in securing the appropriate amount of food per offspring. Many solitary wasps capture discrete prey items for their developing young. Size of offspring at adult emergence

is related to the quantity of stored food. The digger wasp, *Ammophila sabulosa,* adjusts provisioning according to the size of prey items (caterpillars) captured. If the initial prey item placed in an egg cell has a mass >200 mg, the cell is usually permanently closed. If the initial caterpillar is less than this critical size, additional small prey items (<200 mg) are brought to the cell (Field, 1992). Field suggests that when a cell is multiply provisioned, second and subsequent prey items are generally small because the additional burdens of capturing and transporting large caterpillars will not be compensated for by commensurate benefits for offspring receiving a superabundant provision.

When large and indivisible resources are exploited, brood size adjustments must be made solely by altering the number of young. The parasitoid wasp, *Trichogramma,* lays a clutch that is proportional to the value of its host (insect eggs). Volume is estimated by the time interval required to traverse the host (Schmidt and Smith, 1987). Burying beetles, which exploit a wide size range of vertebrate carcasses (2–75 g for *Nicrophorus vespilloides,* Müller *et al.,* 1990a), likewise have elaborate mechanisms to adjust brood number. On very small carcasses, females oviposit a reduced clutch (Müller *et al.,* 1990a). Clutch size adjustments are crude, however, and alone cannot account for the fine ability to match brood number to food supply. The male or female working together, or either parent working alone, can regulate brood size by cannibalizing day-old larvae that make their way to the prepared brood ball (Bartlett, 1987; Trumbo and Fernandez, 1995). On carcasses that cannot support the clutch that has been oviposited, parents reduce brood number such that surviving larvae on a wide range of carcass sizes will disperse from the resource at an equivalent mass (D. S. Wilson and Fudge, 1984; Trumbo, 1990b; Scott and Traniello, 1990). The critical stimulus that parents assess appears to be volume of the brood ball during the postoviposition, prehatching period (Trumbo and Fernandez, 1995; C. Creighton, personal communication). Experimental removal of parents after oviposition results in scramble competition for resources among undersized young (Trumbo, 1990b).

When caregiving is extended over a long period of time, parents can alter brood size in response to changing conditions. Parents of many species cannibalize young if disturbed or if prospects otherwise deteriorate (e.g., Lamb, 1976; Rollo, 1984). Recycling of investment may be especially critical in species utilizing low-nitrogen food sources such as wood (Nalepa and Mullins, 1992). Burying beetles raise fewer young on carcasses that are infested with carrion fly larvae, but the mechanism for this adjustment is unknown (Trumbo, 1992). When juvenile mortality is high, but the environment remains otherwise favorable, females may lay replacement clutches (Edwards and Aschenborn, 1989). Females of the burying beetle, *Nicropho-*

rus vespilloides, will sometimes lay a replacement clutch in response to partial loss of brood, if the surviving number is well below the capacity that the carrion resource can support (Müller, 1987). When mortality occurs among larval dung beetles, the female will reallocate dung to brood balls of healthy young (Montieth and Storey, 1981; Tyndale-Biscoe, 1984), and form additional balls for oviposition (Klemperer, 1983a).

The cues parents use to assess brood number are poorly understood. Complete removal of the brood stimulates oviposition in many taxa (Tallamy and Denno, 1981; Vancassel *et al.,* 1987), but quantitative inhibition of increasing brood number and the importance of critical stimuli have rarely been demonstrated. Females of the dung beetle, *Onticellus cinctus,* appear to assess a correlate of the number of brood balls. Higher concentrations of a possible brood pheromone presumably inhibit further oviposition (Klemperer, 1983a,b). An understanding of the cues parents employ to assess brood number will likely provide important tools for investigating conflicts between parents and offspring over the optimal number of young, and conflicts over the appropriate investment in each offspring. Excluding the eusocial taxa, invertebrates have rarely been employed to examine such issues. Parent–offspring conflict is expected to be more pronounced when the number of brood is few, as occurs in many dung beetles. The consequences for parents and offspring when parents are manipulated to raise varying number of young can be revealed by experimentally varying signals from offspring (e.g., brood pheromone in *Onticellus* and *Copris* (Klemperer, 1983a), or auditory signals from *Cephalodesmius* (Montieth and Storey, 1981)). The investigation of the cues involved in parent–offspring conflict also may be examined by presenting parents with congeneric young with different developmental needs than parents' own young. Such manipulations are possible because many parental insects are poor discriminators of young that are experimentally presented under the appropriate conditions (Melber and Schmidt, 1975; Klemperer, 1982; Kudô, 1990; Radl and Linsenmair, 1991; Trumbo and Wilson, 1993; Kight, 1995). For example, burying beetles will raise any congeneric young that are placed in the nest at the time the parents own young are to hatch (Müller and Eggert, 1990). If burying beetle parents monitor regurgitation demands, then parents might be expected to raise broods of different size when provided young of species with different nutritional needs.

Parental investment is an attractive resource for nonparental individuals to exploit. Brood parasitism can have clear costs for parents (Tallamy and Horton, 1990; Müller *et al.,* 1990b; Trumbo, 1994). Parental care in the generally nonparental parasitoid wasps is thought to have evolved to prevent additional parasitoids from ovipositing in the same host (Hardy and Blackburn, 1991). When brood parasitism is common, reduced clutch sizes

are predicted because fewer resources will be available per young, resulting in undersized offspring of both parent and the brood parasite (Andersson and Eriksson, 1982; also see K. Wilson and Lessels, 1994). When brood size is regulated by parental infanticide, however, a different outcome might be expected. To dilute the contribution of a parasite before indiscriminate brood reduction occurs, one might expect an increase in clutch size when parasitism is likely. This hypothesis is yet to be tested in a species exhibiting filial brood size regulation.

B. Facilitating Feeding of Offspring

Many caregiving invertebrates provide offspring with nutritive resources beyond those stored in the egg. The continued presence of a parent allows the food-gathering advantages of adults (faster location of food sources, processing of food, less vulnerability while foraging, and storage of larger reserves) to benefit young. Invertebrate parents provide extended care by: (1) carrying young internally or externally; (2) tending eggs–nymphs that are clustered near food sources; or (3) providing resources for young within nests. For each parental lifestyle there is a continuum of care from transient protection with no provisioning, to long-term care persisting until the completion of immature development.

Investment by carrying young can range from short-term protection of offspring to the provision of nutritive milk to incubating young (Ingram *et al.,* 1977) to the extreme exhibited by mites *Sitergites* and *Acarophenax,* which harbor young until they burst out of the maternal corpse (Hamilton, 1967). The tsetse fly, *Glossina,* makes perhaps the greatest relative investment in an embryo, giving birth to a single large offspring (Buxton, 1955).

Invertebrates that lay eggs in exposed environments can offer protection to the brood by remaining after oviposition. Parental care ranges from transient hovering over a newly laid clutch to long-term protection of immature stages. In the leaf-feeding tortoise beetle, *Acromis sparsa,* the mother protects eggs, nymphs, and pupae against parasitoids and predators, and terminates care only when her adult offspring complete ecolysis (Windsor, 1987). Other plant feeders take an active role in guarding the brood as they move through the environment. The lace bug, *Coryuca hewitti,* communicates to young by rapidly vibrating her abdomen and possibly providing an aggregating pheromone (Faeth, 1989) as the mother "herds" the brood toward new leaves. The membracid bug, *Umbonia crassicornis,* facilitates feeding more directly, cutting a series of spiral slits in the bark with her ovipositor prior to hatching. The mother then remains with nymphs until they reach adulthood, maintaining feeding aggregations by stroking nymphs on their backs with her forelegs (Wood, 1974). In leaf feeders, facilitation of feeding is thought to be a secondary parental adaptation, subsequent to selection for protection of exposed young.

Among nest and web builders, the simplest form of provisioning is to tolerate young at a site where the adult normally stores food for its own use (Buskirk, 1981). Tolerance of young and inhibition of long-distance movements by adults also facilitates transfer of digestive symbionts to offspring, especially in taxa specialized to feed on resources of low quality. Many wood-feeding insects have evolved extended familial associations, including complex parent–offspring communication (Schuster and Schuster, 1985; Nalepa, 1994). In other species, special food resources are provided to young in the form of trophic eggs (West and Alexander, 1963), prepared dung balls (Halffter, 1977), regurgitated carrion (Pukowski, 1933), and paralyzed prey (many subsocial Hymenopteria; Pratte and Jeanne, 1984). In earwigs, parents both bring food to the nest and regurgitate to young (Shepard *et al.,* 1973; Lamb, 1976), although they normally do not ingest food themselves.

Complex provisioning behavior in nest builders is thought to have evolved by the addition of steps onto an established behavioral sequence. Dung beetle nesting habits, for example, have been categorized into five types (Halffter, 1977). Types I–III are variations on burying food within previously prepared galleries at the site of the dung source. More "advanced" ball-rollers (IV and V) move food away from the source prior to burial and nest construction, either making single balls and nests and providing limited care (IV), or making multiple balls and providing highly developed care (V). Such classifications can be overly rigid when applied to individual species. For example, the Australian dung beetle, *Cephalodesmius,* has been classified as Type III because it forms multiple balls in a previously excavated nest. *Cephalodesmius,* however, synthesizes dung from readily available leaf litter and is not dependent on the temporally and spatially ephemeral dung resource. Thus, Montieth and Storey (1981) argue that there is no ecological necessity to delay nest building until a food source is located, and therefore it is inappropriate to include this group among the more primitive nesting dung beetles.

In a similar way, nesting patterns of subsocial wasps have been categorized according to apparent behavioral complexity without full regard for foraging ecology. The simplest nesting sequence is to provide a single large prey item for the larva, while complex nesting can entail multiple nests, monitoring of larval food requirements, sophisticated orientation abilities, and progressive provisioning (a *Microstigmus* wasp is recorded to have brought 171 captured thrips to a brood cell (Matthews, 1970)). Behaviors associated with multiple provisioning are thought to be prerequisites of social behavior in the Hymenoptera. Attempts to develop a hierarchy of

nesting complexity among the Hymenoptera (Evans, 1958; Atkins, 1980) clearly do not fit other taxonomies. Many anomalous nesting habits within a phylogenetic taxon likely are due to ecological differences in the distribution, availability, and size of food resources. Phylogenies of behavior may provide insight only when comparing closely related species. The tendency to view complex nesting behavior across taxa within a single classification system may be borrowed from theories of chained responses (see Hinde, 1970) in which complex behavior was explained as programmed sequences of linked mechanical steps. The classification of nesting patterns is one area in which ecological insights need to be more fully integrated with established mechanistic interpretations of behavior.

C. Protecting Young

Defending young against predators and parasites is thought to be one of the prime movers in the evolution of parental care (E. O. Wilson, 1975), especially for nonnesting species in which young are exposed in the environment (Tallamy and Wood, 1986). The significance of defense for the maintenance of the parental life history is easily demonstrated. In many folivores, mortality approaches 100% if the parent is removed (Tallamy and Denno, 1981; Windsor, 1987; Edgerly, 1987; Choe, 1989). Although parental care in many species typically has multiple functions, avoiding detection by predators (Mappes and Kaitala, 1995) and active defense of young against predators often appear to be at least secondary adaptations (Rosenheim, 1987; Wyatt and Foster, 1989a; Diesel, 1992).

Nonparental species have evolved numerous adaptations to reduce predation and parasitism of eggs. Eggs are generally dispersed singly or in small clumps in protected places (but see Stamp, 1980). Eggs may be further protected by incorporation of toxins, possession of hard shells (Eberhard, 1975), covering with waxlike compounds (Wood, 1974), or by hiding in shell-like secretions (Miller, 1971). A completely different suite of adaptations are present in species with parental care. Once parental behavior takes over the function of egg protection, resources previously devoted to counter predation and parasitism may be better invested elsewhere. Unguarded eggs of parental species tend to be more vulnerable to predation and parasitism than eggs of nonparental species. Likewise, young of species with care may be less sclerotized than those of closely related nonparental groups (Anderson, 1982). Other coadaptations may follow the evolution of parental care. To facilitate care, eggs of parental species are often laid in one tightly clustered clump (Eberhard, 1975; Tallamy, 1984). When young become mobile, they tend to remain aggregated even in the absence of a parent (Eberhard, 1975; Sites and McPherson, 1982; Nafus and Schreiner, 1988; Windsor and Choe, 1994), although in a few species, parents actively maintain family groups (Kearns and Yamamoto, 1981). In *Elasmucha grisea,* larvae release trail pheromones that both siblings and mothers can follow (Maschwitz and Gutmann, 1979). Injured young may produce an alarm pheromone that stimulates maternal aggression (Wood, 1976; Kudô, 1990; Maschwitz and Gutmann, 1979). Among folivorous species with care, it is not surprising that removal of a parent results in nearly complete mortality. A conspicuously large grouping of eggs or immatures, absent the protective mechanisms of nonparental species, make unguarded young extremely vulnerable.

The evolution of novel defense mechanisms can entail new ecological risks. Plants that employ secondary compounds to deter generalist predators may be exploited by specialists that take their cue from these same compounds. Likewise, parental adaptations may deter some predators or parasitoids but allow specialists to cue in on an abundant and easily located resource. A number of parasitoid wasps selectively exploit young of parental species (Eberhard, 1975; Nafus and Schreiner, 1988; Wyatt and Foster, 1989b; Kudô, 1996; Edgerly, in press). In a revealing set of experiments, Eberhard (1975) demonstrated that in the pentatomid bug, *Antiteuchus tripterus,* the presence of a guarding mother increased the chance that the specialist wasp, *Phanuropsis semiflaviventris,* would parasitize eggs of *Antiteuchus.* This occurred despite antiparasitoid defensive behaviors that mothers specifically employed against the wasp (shielding the egg mass, leaning toward the wasp, antennating, shaking the body, and kicking). Eberhard suggested that *Phanuropsis* uses the parent to orient to its host, something that the parasitoid finds difficult to do when the parent is removed experimentally. The net effect of care in *Antiteuchus* is still positive, largely due to reduction in losses to generalist predators. Eberhard suggested that this species may be in an evolutionary trap, in which selection for thin egg shells and clumped oviposition, which accompanied the evolution of care, may prevent movement toward a nonparental adaptive peak. It is conceivable that the success of a specialist predator or parasitoid might be sufficient to move a parental species toward a new adaptive peak not involving care. The likelihood of this scenario would depend on the cues specialists employ (cues from parent, young, or habitat?), as well as whether care involves multiple functions.

Douglas Tallamy (in press) has pointed out that the comparative effectiveness of alternative nonparental life histories (e.g., hiding small numbers of eggs in scattered locations) cannot be tested by simple removal of parents. Obviously, nonparental ancestors of extant species with care did better than the 100% juvenile mortality that is often the outcome of parental removal experiments. Tallamy argues that parental care is pleisiomorphic within certain clades of Homoptera and the true bugs (Heteroptera), is often less successful than nonparental options, and that the subsocial "advancement" has been lost in numerous taxa because of the substantial costs of care. Under this scenario, the pentatomid hemipterans are derived from a parental ground-nesting ancestor with a lifestyle similar to that exhibited by present-day cydnid bugs (Sites and McPherson, 1982; Filippi-Tsukamoto *et al.,* 1995). Parental care has been retained (or occasionally re-evolved) when host plant seasonality allows but one reproductive attempt, reducing the costs of high parental investment (Tashikawa and Schaefer, 1985), or when care has taken on additional functions such as facilitating feeding.

The intensity of parental defense has been used to measure changes in parental effort, especially as it relates to changing reproductive value of the parent or of offspring. In general, parental effort regarding the brood on hand is predicted to be greater with increasing reproductive value of the brood, and with decreasing reproductive value of the parent. Brood defense makes an especially effective assay of parental intensity. Because many young of parental species are defenseless against predators throughout development, the need for protection will remain constant over sufficient time to conduct experimental tests. This may not be the case with provisioning, where needs of immatures change quickly. Tallamy (1982) found that younger *Gargaphia solani* mothers (greater reproductive value of parent) were less likely to defend offspring aggressively than older mothers. Females with high reproductive potential also attempted to reduce the costs of care by dumping eggs more frequently in egg masses of other females (Tallamy, 1986). Caregiving females also increased defense intensity (more wing fanning, ramming, and chasing of a simulated predator) as the reproductive value of maturing nymphs increased (Tallamy, 1982). Crespi (1990) found that the thrips *Elaphrothrips tuberculatus* were more aggressive when defending larger clutches. Unfortunately, the number of empirical studies of reproductive value theory employing parental defense is rather limited, despite the ease with which defense can be quantified, the short life span of invertebrates that causes reproductive value of parents and offspring to change quickly, and the ability to alter brood size experimentally.

D. Terminating Care

Because parental care is costly, parents are expected to re-evaluate the decision to provide care during the parental period. Parental care is terminated when young mature and become less dependent on parental attention, or when prospects for successfully rearing the brood diminish to the point that parents abandon their young prematurely. Although parent–offspring conflict theory predicts that parents generally end the familial association, in some cases care simply ends when young disperse (Vancassel *et al.,* 1987;

Ruttan, 1990). More often among invertebrates, the parent abandons the clutch or brood. The timing of desertion may not be distributed continuously, but may occur at specific stages in the development of young. Thus a maternal mosquito, *Trichoprosopon digitatum,* leaves at the time eggs hatch (Lounibos and Machado-Allison, 1986); the pentatomid bug, *Parastrachia japonensis,* stays with second instars, but deserts third instars (Tachikawa and Schaefer, 1985); and the tortoise beetle, *Acromis sparsa,* leaves when its adult offspring emerge (Windsor, 1987). Manipulation experiments, in which young of one stage are switched with those of a different stage, demonstrate that parents are monitoring the development of offspring. The duration of care can be extended by substituting young offspring for old in earwigs, dung beetles, and cydnid bugs (Caussanel, 1970; Klemperer, 1983a; S. L. Kight, personal communication). Klemperer (1982) has demonstrated that care is mediated by a chemical signal from brood; mothers typically abandon brood balls without young, but will maintain, repair, and keep empty brood balls upright if they are treated with dichloromethane extracts from viable brood. Communication between offspring and parent may also maintain care in the dung beetle, *Cephalodesmius,* in which larvae stridulate by scraping their "chin" along their "tail" (Montieth and Storey, 1981). The importance of communication of brood to caregivers has been nicely demonstrated in the honeybee, *Apis mellifera.* Workers can differentiate among brood cells of well-fed and hungry larvae (Huang and Otis, 1991), and among young and old brood (LeConte *et al.,* 1994). Changing proportions of fatty acid esters on the cuticle of maturing larvae apparently induce adult workers to terminate feeding and to begin capping brood cells (LeConte *et al.,* 1994).

The termination of care may occur at discrete points in the circadian cycle. The tsetse fly, *Glossina,* generally gives birth to her single offspring in the midafternoon (Buxton, 1955), and male burying beetles abandon their brood in the first few hours after sunset, corresponding to the activity period during nonparental phases of adult life (Trumbo, 1991).

Different species regulate the duration of caregiving by monitoring various combinations of internal and external cues. The mosquito, *Trichoprosopon digitatum,* tends eggs for approximately 30 h (at which time eggs hatch) on floating rafts within water-holding fruit husks. This parental behavior, highly unusual among the Diptera, may keep eggs from being washed from the container habitat during heavy rainfall (Lounibos and Machado-Allison, 1986). When eggs were taken from brooding females and replaced with eggs that were 12 h older, females nevertheless guarded rafts until 12 h after hatching. Conversely, brooding females that were given eggs 12 h younger, inappropriately abandoned rafts 12 h prior to hatching. Thus, the mechanism for terminating care in this species seems to be entirely internal, and is not affected by the state of the young (Lounibos and Machado-Allison, 1986).

In an elegant set of experiments, Kight (in submission) demonstrated that the duration of care in the ground-nesting *Sehirus* is controlled by both internal and external cues. *Sehirus* parents guard eggs until they hatch (approximately 10 days), and then guard and provision young for 1–3 days posthatching. Kight assayed parental responsiveness by measuring reaction to tactile disturbance. Females experimentally given older eggs in place of younger ones showed a decrease in responsiveness shortly after hatching, suggesting that mothers were affected by the experience of hatching, and that the condition of offspring was monitored. The reduction in response occurred at a time when aggression would have been high had no experimental manipulation been made. Conversely, females given younger eggs in place of older ones extended brooding for up to 6 additional days, but no longer. Thus, when hatching fails to occur, an internal process eventually terminates care, independent of the condition of the young. Kight suggests that bracketing maternal responsivity with both experiential and endogenous factors may ensure maternal care of appropriate duration.

The maintenance of care sometimes depends on mutual feedback between parent and offspring. Crayfish mothers produce a brood pheromone that is attractive to early-stage larvae (Little, 1976). Continued production of the brood pheromone is dependent on contact with larvae. When larvae reach the fourth larval stage, they are less responsive to brood pheromone. The decrease in mother–offspring contact, in turn, leads to decreased pheromone production and the cessation of maternal responsiveness (females become cannibalistic toward larval crayfish) (Little, 1976).

Prospects for both the parent and offspring can change following oviposition, prior to normal termination of care. Among iteroparous species (more than one breeding attempt per lifetime), parents often monitor environmental conditions when deciding whether to continue care or to abandon the brood. In both a staphylinid beetle that utilizes decaying mushrooms as a resource and in carrion-feeding burying beetles, parents will abandon young if the resource deteriorates prematurely (Ashe, 1987; S. T. Trumbo, personal observation). In both cases, the young are known to have rapid development in comparison to closely related nonparental genera, presumably to minimize the possibility that the resource deteriorates before young mature.

The time invested in parental care, the risk of predation, and the decreased ability to forage are often fixed costs that must be incurred regardless of the number of young being reared. Thus, it is not unexpected that parents sometimes desert or cannibalize small broods (Eberhard, 1986; Müller, 1987; Olmstead and Wood, 1990). Abandoning small broods is expected when the diminished benefits derived from caring are not matched by diminished costs. Kight and Kruse (1992) demonstrated that both clutch size and time invested affect termination of care in the back-brooding water bug, *Belostoma*. Experimentally reduced clutches were discarded by males more often than normal clutches, but the probability of desertion also depended on the length of prior investment. Males that have less time left until hatching of eggs were more likely to continue brooding than males that had just begun the parental period. In this case, past investment provides a reliable measure of the rate of return for future investment (expected benefits ÷ time remaining until hatching).

Parental care theory predicts that in semelparous (one breeding attempt per lifetime) species, parents are expected to invest maximally in their one brood. In a comparative study, A. Kaitala and J. Mappes (personal communication) demonstrated that iteroparous shield bugs (*Elasmucha* spp.) will abandon clutches if disturbed. Semelparous congeners, however, never abandon their clutches. If forcefully dislodged, mothers will spray distasteful chemicals over their young as a last resort. One of the more bizarre forms of terminal investment is found in the tick, *Ixodes kopsteini*, which dies shortly after formation of eggs. This species does not have the ability to oviposit externally. Instead, the young hatch inside the dead body of their mother, the corpse acting as a protective sanctuary.

Parental care theory predicts that parents and offspring may disagree when caregiving should terminate (Trivers, 1974). Examination of the cues that parents use to make decisions should provide insight into how parent–offspring conflict evolves. It will be of particular interest to know how cues that parents employ to terminate care may affect offspring's ability to manipulate care. Evolutionarily, offspring may have enhanced possibilities of manipulating the level of care when parents have been selected to monitor cues derived directly from young, rather than selected to monitor indirect cues that may signal the appropriate time to desert.

E. The Costs of Parental Care

Organisms have limited physiological resources that they can devote to growth, survival, production of gametes, and care of offspring (Calow, 1979). If organisms devote more to one life-history component, such as care for the brood on hand, then fewer resources are available for competing needs. Thus, parental care is assumed to have costs (Trivers, 1972).

A misleading accounting of the costs of care may be obtained by comparing the subsequent reproductive performance of formerly parental and nonparental individuals. Individuals of greater vigor may be able to devote more resources to all components of fitness, obscuring the trade-offs that

are assumed to exist among parental care, survival, and future reproductive ability (van Noordwijk and de Jong, 1986). Tallamy and Denno (1982), for example, found that females of *Gargaphia solani* with larger clutches and greater parental investment early in life were the same individuals that produced larger clutches late in life, despite the expected negative relationship if all things (genetics, juvenile environment, adult feeding) were equal. To circumvent the confounding effects of differential vigor on allocation of resources among life-history components, experimental manipulations are often employed. Removal of brood from a caregiver can shorten the time to the next oviposition (Vancassel, 1977; Müller, 1987; Nalepa, 1988) and increase lifetime egg production (Tallamy and Denno, 1982; Fink, 1986).

Observations of caregivers suggest that the principal costs of care are reduced foraging and increased risk of predation. Parents often spend less time feeding themselves than nonparental individuals (Edgerly, 1987), and may experience a decrease in fat reserves (Eberhard, 1975). The reduced mobility of caregivers is especially costly for predators that must pursue prey (Odhiambo, 1959; R. L. Smith, 1976, in press; Crowl and Alexander, 1989; Kight *et al.*, 1995). Decreased mobility, either because of attendance of sedentary juvenile stages or because of the encumbrance of carrying young, can also increase predation risk (Smith, 1976; Tallamy and Horton, 1990). In many species that shield young on exposed vegetation, the tendency to run, fly, or drop to the ground when disturbed is suppressed during care (Eberhard, 1975; Tallamy, in press). Among insects in which care is provided while guarding a bonanza resource such as dung or carrion, individuals may gain substantial weight during care, and the costs of care may be primarily in the form of predation risk and time that cannot be spent searching for additional resources. Because hormones mediate numerous critical life-history decisions (Finch and Rose, 1995), endocrinological manipulations are likely to become increasingly important in revealing trade-offs among components of fitness.

The substantial costs of providing care have undoubtedly contributed to the evolution of mechanisms to reduce such costs. Young of the treehopper, *Publilia reticulata*, receive protection either from their mother or from ant mutualists. The presence of ant caretakers apparently acts as a cue for the mother to desert the brood, a behavioral response that transfers the costs of care from the mother to the ants (Bristow, 1983). Because subsocial insects generally have weak mechanisms to discriminate among conspecific young, egg dumping also is effective for minimizing the costs of care. Egg dumpers of *Polyglypta* are faster to oviposit a second clutch (Eberhard, 1986), and *Gargaphia* egg dumpers have greater lifetime fecundity than conventional caregivers (Tallamy and Horton, 1990). Tallamy (in press) further suggests that viviparity (which frees the mother from providing care in one place) and paternal behavior may have evolved to reduce the costs of maternal care.

In the woodroach, *Cryptocercus*, the costs of long-term care (3+ years) while utilizing nitrogen-poor wood, are sufficient to induce semelparity in the field (Nalepa, 1988). Pairs typically can produce a replacement brood only if the original brood is lost early in its development. Nalepa (1994) suggests that in the ancestors of termites, the transfer of some of the costs of care to latter-stage instars (which are nutritionally independent of the parents in *Cryptocercus*) may have been a critical point in the evolution of eusociality in termites. The transfer of caregiving costs from mother to older offspring sets the stage for satisfying all three conditions for eusociality (overlap of generations, brood care by workers, and nonreproductive castes). When latter-stage instars provide care, the mother can reserve her own physiological resources for survival and further egg production. The availability of younger siblings for older siblings to care for may prolong the mother–offspring association. While alloparenting provides an avenue for pre-reproductive individuals to increase their inclusive fitness, it also diminishes the possibility that the physiological resources necessary for independent reproduction will ever be accumulated. In several cockroaches, feeding and a positive energy balance are necessary to stimulate ovarian maturation (Engelmann, 1957; Stay and Coop, 1973). Clearly, hormonal studies of feeding, reproduction, and caregiving in subsocial cockroaches, and of the subsocial stage of colony founding in termites, is likely to provide insight into the evolution of eusociality in this group.

The commitment to provide parental care often entails staying in one place, greater exposure to predators, reduced feeding opportunities, and lost time searching for additional mates or valuable resources. Many of these costs are incurred whether the parent provides care for one offspring or for many. One might predict that larger clutches would evolve when there are positive economies of scale, in order to reduce the per offspring costs of care. Nonparental species are predicted to have greater lifetime fecundity, but accomplish this by dispersing many clutches of fewer eggs over a longer period of oviposition. Interspecific comparisons support the prediction of fewer but larger clutches in species providing the greatest investment (Schreiner and Nafus, 1991; Tallamy, in press; J. Mappes, personal communication).

Providing care for a larger clutch may diminish the possibility of further reproduction by more thoroughly depleting fat reserves, as well as by interfering with feeding. Selection for production of a larger clutch may establish a positive feedback whereby increased clutch size reduces subsequent reproduction, and thus selects for an increased tendency toward semelparity and a large one-time investment in young. This selective reinforcement of the parental lifestyle may keep species in a parental "bind" (Tallamy, in press). After the primary evolutionary event that initiates the parental lifestyle, subsequent secondary adaptations to reduce the costs of care are expected. The ecological avenues available to reduce the costs of care will, in large part, determine whether further selection will diminish or enhance the parental tendency. The potential for egg dumping, transfer of care to mutualists, or uniparental male care will select for reduced maternal care, while oviparity or production of a large clutch will reinforce a maternal life history of caregiving.

V. Paternal Care: Uniparental Male versus Biparental Care

Postzygotic care by males is rare among invertebrates. Its rarity has stimulated study of the selective forces that push a species toward a paternal lifestyle. Our understanding of the physiological and behavioral mechanisms that regulate paternal behavior is extremely limited. Therefore, I confine the discussion to a behavioral and ecological comparison of uniparental male versus biparental care.

Exclusive male care apparently evolves under a very different set of circumstances than biparental care. Uniparental male care is associated with all three basic patterns of postzygotic care: carrying eggs (King and Jarvis, 1970; R. L. Smith, 1976), tending young exposed in the environment (Odhiambo, 1959; Ralston, 1977; Ichikawa, 1988; R. L. Smith and Larsen, 1993), and nesting (Kaestner, 1968; Mora, 1990). Nest building generally is not elaborate and often occurs out in the open. Complexity and exclusivity of nests utilized by uniparental males may be constrained by the need to permit easy female visitation. In contrast, biparental care is usually associated with nests. The nest may represent a substantial investment and be occupied for long periods of time. These differences are related to differences in courtship and the nature of resources exploited.

A. Courtship

Both uniparental male care and biparental care are associated with high certainty of paternity. In uniparental care, the mechanism of paternity assurance is usually repeated copulation just prior to oviposition (King and Jarvis, 1970; R. L. Smith, 1979; Mora, 1990). A female may court a male to induce him to accept her eggs, presumably because male care is a valuable resource that increases her lifetime fecundity (Mora, 1990; R. L.

Smith and Larsen, 1993; Tallamy, in press). When males can guard eggs of several females simultaneously, there is the potential for polygyny (Odhiambo, 1959; King and Jarvis, 1970; Ralston, 1977; Mora, 1990). Males may be able to increase their access to females via caregiving when females actively discriminate against males without eggs or a nest, as occurs in the harvestman, *Zygopachylus albomarginus* (Mora, 1990). A preference for males that are guarding eggs is the equivalent of females copying the mate choice of other females. If searching for a male entails costs, a male already caring for eggs might be attractive because he has demonstrated both his ability to stimulate a previous female to oviposit and his willingness to provide care. (If adding her clutch to the nest of a caring male overextends his parental ability, however, a female may first destroy eggs before ovipositing her own (Ichikawa, 1995).) In the hemipteran *Rhinocoris*, hatching success of eggs increases with the number of eggs tended (up to a point), suggesting that locating males with egg batches may be a good female strategy (L. Thomas, personal communication). In vertebrate mating systems, mate copying in species without male care may reduce the costs of female choice and result in the selection of higher-quality mates (Dugatkin, 1992). It is possible, but not yet tested, that mate copying may promote polygyny in invertebrates with exclusive male care.

It would also be of interest to search for a connection between egg dumping by females and the evolution of uniparental male care. Among egg dumpers, females prefer to leave their eggs with females already tending a clutch. The evolution of a paternal tendency in such species might immediately be associated with females leaving eggs with caring males, female preference for males already tending eggs, and thus the potential for polygyny. Groups that exhibit both uniparental male and uniparental female care, such as *Rhinocoris* (Hemiptera) would be ideal for investigating a relationship between egg dumping and uniparental male care.

Patterns of copulation vary among biparental invertebrates. The frequency of copulation may be related to the exclusivity of the pairing. When pairs mate within an excavated nest or gallery, such as occurs in termites, the bark beetle, *Ips*, and the dung beetle *Phaneaus*, copulation may occur infrequently (Schmitz, 1972; Halffter and Lopez, 1977; Nalepa and Jones, 1991). In burying beetles, on the other hand, where visitations by rivals are common during burial of a carcass, copulations are frequent and ensure that the resident male sires most of the brood (Müller and Eggert, 1989).

Elaborate courtship might be expected in monogamous species with biparental care. Courtship can coordinate reproduction and nesting behavior of the two sexes, and can ensure that substantial investment is not wasted on a partner that is inferior or one encumbered with another mate. Although this reasoning may apply to birds (Lehrman, 1965; Wittenberger and Tilson, 1980), courtship is surprisingly cursory among most biparental invertebrates (Pukowski, 1933; Kirkendall, 1983; Nalepa and Jones, 1991; Ruegg and Rose, 1991; but see Linsenmair, 1987). Biparental care within invertebrates has generally evolved in groups that exploit a critical, contested resource such as food or shelter. Among many biparental invertebrates, each sex engages in intrasexual fights (Pukowski, 1933; Schuster and Schuster, 1985; Sato and Hiramatsu, 1993; Shellman-Reeve, 1990). Mate choice thus may be largely passive, and pairing the indirect result of both sexes excluding rivals. In fact, in many cases the adults search for the critical resource independently and will begin to nest immediately while the resource is usable, even before a partner arrives. After pairing is established, individuals may become aggressive toward intruders of either sex (Pukowski, 1933; Kirkendall, 1983; Schuster and Schuster, 1985; Linsenmair, 1987; Nalepa and Jones, 1991).

Burying beetles demonstrate a revealing change in aggressiveness as nesting ensues. Initially, only same-sex conspecifics and heterospecifics are excluded. After the nest is formed and oviposition begins, residents become aggressive toward opposite-sex intruders because successful intruders will cannibalize the entire brood (Trumbo, 1990a). Even so, residents with brood attack same-sex intruders more vigorously than opposite-sex intruders (S. T. Trumbo, unpublished results). Differential aggressiveness likely occurs because individuals expelled by a same-sex rival will receive no reproductive benefit from the carrion resource. On the other hand, expulsion of one's mate, followed by infanticide and pairing with the intruder, often results in a replacement brood (Trumbo, 1990b). The cost of replacement by an opposite-sex intruder, therefore, can be considerably less than the cost of replacement by a same-sex intruder. Less aggression toward opposite-sex intruders might therefore be expected, despite the certainty of infanticide following a takeover.

Restrictions on male promiscuity, either through the withholding of copulations or via female synchrony of sexual receptivity, have been proposed as mechanisms promoting paternal investment in biparental species (Thornhill and Alcock, 1983; Zeh and Smith, 1985). Among invertebrates, however, the association of biparental care with a bonanza, contested resource suggests that restrictions on male promiscuity may play a less important role in the evolution of biparental care than resource ecology.

The potential for polygyny is generally not as great among species with biparental care as with exclusive male care. Extended paternal care can severely limit male access to additional females (Eggert, 1992; Reid and Roitberg, 1994) and, in some cases, males may reject supernumerary females. Polygyny and biparental care, however, are compatible in some species. Where resource availability varies, males may assess resource quality and then reject or accept additional females accordingly. In the bark beetle, *Ips confusus*, males usually accept up to three females but often reject the fourth, presumably because of the negative effects of crowding within galleries (Borden, 1967). In the burying beetle, *Nicrophorus defodiens*, males that locate a suitable carcass release a sex pheromone if a female is not present. After a female discovers the resource, the male normally terminates advertisement (Pukowski, 1933). When exploiting a large carcass (>40 g) that can support the brood of more than one female, however, males will often continue advertising after the initial pairing. Release of sex pheromone is inhibited once additional females are attracted to the carcass (Trumbo and Eggert, 1995). Males, then, take into account both the quality of the resource as well as the number of females present, when deciding whether to continue releasing pheromone. Polygyny enhances the male's but not the females' reproductive success. Paired females may attempt to interfere with male advertisement by pursuing, pushing, and climbing on top of a male that continues to advertise (Eggert and Sakaluk, 1995; Eggert and Müller, in press).

B. Resources

Uniparental male care among invertebrates rarely occurs in proximity to a discrete food resource. Tallamy (in press) points out that of seven arthropod taxa that evolved exclusive male care, six consist entirely of predators that hunt, and one feeds on scattered detritus. Both of these foraging strategies require mobility, and predation further necessitates agility. Thus parental care, whether involving carrying young or occurring at one site, is in direct conflict with the needs of mobile, agile foragers. The costs associated with reduced foraging may not be borne equally by females and males because poor nutrition diminishes egg production more than sperm production (Tallamy, 1994; R. L. Smith, in press). This was demonstrated using the giant water bug, *Belostoma flumineum;* fecundity of females, but not number of offspring sired by males, was reduced by a poor diet during the adult stage (R. L. Smith and D. W. Tallamy, unpublished results). When there is selection for parental care in active foragers, males may be able to bear the costs of care more easily than females ("enhanced fecundity" of female hypothesis, Tallamy, 1994, in press).

The function of male care in uniparental species has been addressed by removing the male from his brood. In each case in which it has been investigated, uniparental male care reduces predation and/or parasitism (Odhiambo, 1959; Ralston, 1977; Mora, 1990). In aquatic species in which males carry eggs, paternal care serves the additional function of facilitating hatching (King and Jarvis, 1970; R. L. Smith, 1976).

Biparental care occurs, for the most part, in species nesting in or in proximity to a critical, discrete resource that has the potential to support the nutritional or shelter needs of a large number of brood (the major exception being found among the biparental Hymenoptera). The pattern of resources utilized by species with uniparental male versus biparental care is thus quite different. Emlen and Oring (1977) suggested that uniparental male care may evolve from the ancestral state of biparental care by female desertion of caring males. Among invertebrates, however, uniparental male and biparental care exhibit little overlap in either phylogeny or the type of resource exploited, suggesting that uniparental male care rarely evolved from biparental care.

Among invertebrates with biparental care, removal of the male parent always results in reduced brood production in experimental manipulations (Peckham, 1977; Cook, 1990; Trumbo, 1991; Amman and Bartos, 1991; Nalepa, 1994; Tallamy, 1994). Where biparental care occurs among the Hymenoptera, male nest guarding is thought to have evolved from territorial behavior (maintaining access to females returning to the nest) (Alcock, 1975). The presence of the male near the nest while the female is foraging reduces attacks by predators and parasites (Hook and Matthews, 1980; Coville and Coville, 1980). In some *Polistes,* the additional task of brood care has evolved (Hunt and Noonan, 1979; Cameron, 1986). Among other biparental species, male care often serves many functions and may involve resource procurement, nest preparation, and provisioning of offspring (see Zeh and Smith, 1985; Tallamy and Wood, 1986). The function of male care varies with the type of resource. Where species exploit resources with a high nitrogen content such as carrion or dung, males help secure the resource from intraspecific and interspecific competitors (Halffter *et al.*, 1974; Trumbo, 1994; Scott, 1994). Where paternal care is extended, males aid in provisioning young (Halffter and Edmonds, 1982; Fetherston *et al.*, 1994). In species that exploit low-quality resources such as wood or leaves, preparing the nest and enhancing the nutritional value of the resource may be just as important as defense (Montieth and Storey, 1981; Kirkendall, 1983; Schuster and Schuster, 1985; Nalepa and Jones, 1991; Matsumoto, 1992; Tallamy, 1994).

The most complex forms of biparental care are sometimes thought to involve strict division of labor by the sexes (Zeh and Smith, 1985). In most examples of sexual division of labor, however, male care is a simple extension of nest–mate guarding, and male participation is usually limited to the oviposition and nest initiation stages, as is found in Hymenoptera and in many dung beetles (Peckham, 1977; Halffter, 1977; Sato and Immamori, 1988). Zeh and Smith cite the example of biparental *Hemilepistus* as having complex care and division of labor. Task specialization in this species is not pronounced, however, since males and females have similar parental repertoires and simply take turns foraging and guarding (Linsenmair, 1987). Similar high levels of paternal care are found in other biparental species with little division of labor, including those with the longest familial associations. In such species, each sex can take the duties of the other; specialization may be limited to quantitative differences in behavioral tendencies (Fetherston *et al.,* 1990). This pattern of biparental care is found in *Cryptocercus* (Seelinger and Seelinger, 1983), termites (Nalepa and Jones, 1991), passalid beetles (Valenzuela-González, 1993; Schuster and Schuster, 1985), and burying beetles (Fetherston *et al.,* 1990, 1994). Notably, in these species males and females often search for resources independently and the male may initiate nesting without the female in order to quickly exploit the resource (Pukowski, 1933; Schuster and Schuster, 1985; Nalepa and Jones, 1991).

The effectiveness of flexible parental repertoires versus strict sexual division of labor is demonstrated by mate compensation in species with complex care. When the dampwood termite, *Zootermopsis nevadensis,* is fed a nitrogen-poor diet, females restrict their activity, presumably to retain energy for egg production. Males, however, sustain high activity during colony initiation. This shifts the costs of nest initiation from the female to the male at a time when poor nutrition has a significant impact on female fecundity (Shellman-Reeve, 1990). Mate compensation has been demonstrated most convincingly in the burying beetle, *Nicrophorus orbicollis.* When his mate is absent, the male parent adjusts by staying 4 days longer with the brood (ensuring that one parent is present until the brood disperses), and also by increasing active forms of parental care such as feeding the larvae and maintaining the nest (Trumbo, 1991; Fetherston *et al.,* 1994). When care is limited to two individuals, rigid task specialization results in little room for error. Even in biparental species such as the leaf-gathering dung beetles, *Lethrus,* and *Cephalodesmius,* in which males forage while females manufacture brood balls, females are fully competent to forage on their own if partners no longer return with provisions.

C. Future Ecological Studies of Paternal Care

Patterns of copulation suggest that when there is exclusive male care in invertebrates, females often are quite willing to mate with males that demonstrate evidence of caregiving. Studies that examine the cues that females use to assess males (presence of eggs, quality of nest, quality of male) will provide insight into the evolution of uniparental male care. In particular, it will be interesting to establish whether mate copying is related to the potential for polygyny, and thus has been important in the evolution

of uniparental male care. Physiological studies will provide needed information on the extent to which uniparental male care shifts the costs of reproduction from the female to the male.

There has been considerable debate whether females withhold copulation to elicit male assistance in biparental species. In many cases, copulations occur frequently and prior to procurement and preparation of the resource. Physiological assays may allow for sensitive analyses of whether cues from the female, the resource, or from the brood stimulate males to initiate care. Such studies will enlighten the discussion of whether female coercion, the potential for polygyny, or resource ecology is most significant for shaping patterns of paternal investment.

VI. Summary

Ecological and physiological analyses of invertebrate parental care need to be integrated. Consideration of phylogeny provides one starting point. R. L. Smith (in press) and Tallamy (in press) have provided detailed phylogenetic and ecological comparisons of the evolution of parental care among closely related taxa. There are no formidable barriers to extending the analysis in these and other groups to the level of physiology. Burying beetles (*Nicrophorus* spp.), for example, are thought to be derived from the nonparental *Ptomascopus* (tribe Nicrophorini). *Ptomascopus* utilizes a small carcass as a breeding resource as does *Nicrophorus,* but does not build a nest or stay with the offspring following oviposition (Peck, 1982). Endocrine analyses of both genera will provide information on how the novel adaptation of parental care was inserted within the reproductive cycle of a nonparental ancestor. In some cases, the endocrinology necessary for comparative studies with closely related nonparental species has already been done. The hormonal regulation of the reproductive behavior and physiology of mosquitoes has been worked out in detail, largely because of the importance of this group as vectors for disease. The maternal mosquito, *Trichoprosopon digitatum,* (Lounibos and Machado-Allison, 1986) would provide an excellent subject for an investigation of the comparative physiology of care.

Broad phylogenetic comparisons have the potential to address how physiology constrains the expression of parental care. Parental care in numerous independent phylogenetic lines of insects, for example, is regulated by the same neural and endocrine structures. Are the importance of the various neural and endocrine factors similar in all groups, or has phylogeny and/or ecology affected the evolution of physiological regulation? Do the types of sensory cues employed to stimulate care in a particular group affect the direction that evolution has taken, the possibility of parent–offspring conflict, or mate compensation in biparental species?

For many reasons, invertebrates will be used to address these questions, not the least being the ability to perform ecological and physiological manipulations on large numbers of individuals in a short period of time. Some of the advantages of invertebrates as experimental subjects have not been exploited in studies of parental care. Breeding experiments to select for high and low lines of caregiving will prove useful for uncovering the genetic basis of care. Genetic effects on parental care among invertebrates have rarely been established (but see Tallamy and Dingle, 1986; Robinson *et al.*, 1989). Individuals from selected genetic lines can be employed to examine the physiological differences between individuals with varying tendencies to express parental behavior; genetic lines also will be useful in field experiments investigating the ecological trade-offs of adopting alternative patterns of investment. The effects of development on the expression of care have been neglected as well. The ease with which the developmental environment of many immature invertebrates can be manipulated suggests that the lack of understanding is caused by neglect and not by experimental barriers.

The study of parental care among invertebrates will be renewed by the discovery of new species, the discovery of caregiving among previously described species, and the discovery of new functions of care in those known to be parental. The challenge of explaining the known diversity of care is formidable in its own right. The inclusion of further empirical studies as well as theoretical insights promise to make the investigation of parental care among invertebrates a paradigmatic study of how parallel social adaptations evolve among diverse taxa.

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