Concaveation and Maintenance of Maternal Behavior in a Burrower Bug (Sehirus cinctus): A Comparative Perspective

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This study investigates 2 patterns of maternal behavior typical of mammals, using a heteropteran insect as the study animal. *Sehirus cinctus*, a burrower bug (Heteroptera: Cydnidae), exhibits relatively well-developed maternal behavior that includes guarding eggs and provisioning offspring. Mothers remained maternally responsive to stimulus eggs for 24-48 hr following removal of their own eggs, but the response grew weaker with longer separation times. A proportion of nulliparous females also exhibited maternal responsiveness when presented with stimulus eggs. Males, however, never responded parentally to eggs. The results of this study highlight similarities in general female responsiveness to stimulus young and differences in male responsiveness to stimulus young among certain invertebrates and vertebrates.


Physiological and experiential aspects of parental behavior have been studied almost exclusively in vertebrate animals, primarily rodents. For example, a number of studies have examined changes in reproductive physiology and the disappearance of maternal behavior following the separation of pups and dams (Hammons, Velasco, & Rothchild, 1973; Lee, Haisenleder, Marshall, & Smith, 1989a, 1989b; Moffat, Suh, & Fleming, 1993; Rosenblatt & Lehrman, 1963; M. Smith & Reinhart, 1993; Taya & Sasamoto, 1989). Other studies have investigated proximate factors underlying maternal concaveation—the appearance of parental behavior among nulliparous individuals following exposure to pups (Clark, Spencer, & Galef, 1986; Fleming, Korsmit, & Deller, 1994; Izquierdo, Collado, Segovia, Guillamon, & Del Cerro, 1992; Rosenblatt, 1967; Stern, 1991).

Although these effects are well documented in mammals, it is presently uncertain to what extent such behavioral patterns occur in other animal groups. Several avian species have been used to model the hormonal and behavioral consequences of withdrawing egg stimuli during incubation (El Halawani, Burke, & Dennison, 1980; Goldsmith, Burke, & Prosser, 1984; Lea & Sharp, 1991; Lea, Vowles, & Dick, 1986; Silver & Gibson, 1980), but similar experiments on other vertebrate and invertebrate groups are virtually nonexistent.

To better understand the influences of evolutionary history and physiological constraints on behavioral mechanisms, it is useful to compare species of markedly different phylogenetic descent. This study examines two well-documented mammalian processes in the distinctly nonmammalian context of a heteropteran insect: the maintenance of maternal responsivity through stimuli from offspring and the induction of maternal behavior in nulliparous individuals.

Parental care occurs in a number of insect families (reviewed by Kaitala & Mappes, 1992; Tallamy, 1984; Tallamy & Wood, 1986) and may be manifested as uniparental female (Kight, 1995a; Tallamy, 1982), uniparental male (Kight & Kruse, 1992; R. Smith, 1974), or biparental care (Trumbo, 1992; Wilson, 1971). The subject of the present study, *Sehirus cinctus* (Heteroptera: Cydnidae), is a burrower bug in which females excavate shallow burrows, oviposit a clutch of eggs, guard the eggs until hatching (Figure 1), provision recently hatched young with food, and remain to guard for several days thereafter (Sites & McPherson, 1982; Southwood & Hine, 1950). The relatively well-developed maternal behavior of this species therefore provides a useful model system for investigating mother–offspring interactions for comparison with maternal vertebrates.

**Method**

*Sehirus cinctus* is the only cydnid in the Western Hemisphere known to exhibit parental behavior (Freeschner, 1960). Different
populations specialize on various species of mint (Labiaceae), and in Indiana appear to feed exclusively on the fruits of *Prunella vulgaris*, a mint commonly found in early spring (Kight, 1995a). Individuals overwinter as adults (Blatchley, 1926) and emerge in mid to late April when host plants become available. Although females mate prior to reproductive diapause (personal observation), they do not lay eggs until spring (Sites & McPherson, 1982). After feeding on developing *Prunella* fruits, females dig shallow burrows into which they oviposit a cluster of 120–150 eggs. Mothers maintain continuous physical contact with eggs throughout embryogenesis (8–10 days under laboratory conditions) and respond defensively when disturbed (Sites & McPherson, 1982) by turning toward and placing themselves between their eggs and the source of disturbance. Under natural circumstances, such behavior may deter egg predators and parasites. Additional elements of care (fanning, warming, etc.) are not reported for this species. When eggs hatch, mothers immediately forage for *Prunella* fruits to provision the brood. After several days, nymphs disperse and maternal care comes to an end.

Subjects were first-generation laboratory-reared offspring of adult *Sehirus cinctus* captured in April 1994 at roadside locations in Monroe County, Indiana. Rearing was accomplished by isolating brooding females with their eggs in ventilated plastic petri dishes (50 × 15 mm) containing moist sand and food. At the 2nd instar, nymphs from multiple broods were transferred to large group-rearing containers. Following eclosion, adults were kept at 5 °C for 3 months to experience winter diapause and synchronize their reproductive behavior. Animals were subsequently kept in mixed-sex groups of 20 at room temperature (25 °C) under a 18L:6D photoperiod in large ventilated petri dishes (100 × 15 mm) containing moist sand and food. Experimental animals began ovipositing within 3 weeks of emergence from diapause, and brooding females and eggs were transferred to smaller individual dishes for experimental purposes.

To assess maternal responsiveness, I devised a behavioral assay based on an egg-guarding female’s response to disturbance. Each testing day, subjects were observed for 2 min during which they were lightly touched posterolaterally with a dissecting probe at 30-s intervals. Bugs could respond in one of three ways: defense, no movement toward the probe, movement away from the probe, or movement. Each subject thus received a total of 5 light touches within a given focal period. Each defensive response received a score of +1, each movement away from the probe a score of −1, and each neutral response a score of 0. Therefore, an individual received a total response score ranging from −5 to +5 per daily focal period. Previous observations indicate that mothers respond defensively throughout the normal brooding cycle but that nonreproductive individuals without eggs flee when disturbed (Kight, 1995b).

As an additional index of maternal responsiveness, I recorded whether females were in contact with eggs on each testing day. Previous observations (Kight, 1995b) indicate that maternal response scores are positively correlated with maternal contact with eggs and nymphs.

### Maintenance of Maternal Responsiveness

To assess the decay of maternal response in the absence of eggs, brooding females were removed from their eggs 48 hr after oviposition and isolated in novel enclosures. After 24 hr, females in one group were transferred to petri dishes containing recently oviposited stimulus eggs obtained from the nest of another female. Under novel conditions, females do not discriminate their own from strange eggs but do prefer recently brooded eggs (Kight, 1995a). Hence, subjects were given the opportunity to resume brooding after a 24-hr interruption. Maternal responsiveness was assayed immediately (a) after initial egg removal, (b) immediately before egg replacement, (c) 2 hr after egg replacement, and (d) 24-hr after egg replacement.

To assess the effects of longer periods of separation, a second group of females was treated in a similar fashion, but individuals were separated from eggs for 48 hr. A third group, in which eggs were never returned to subjects, were tested once daily after egg-removal and served as a control for both experimental treatments.

### Response of Nonparental Individuals to Eggs

To assess the response of nonparents to eggs, randomly chosen adult males and nulliparous adult females (females given the opportunity to mate but that had not yet oviposited) were isolated and confined with freshly laid stimulus eggs for 24 hr in the bottom of small test tubes. This was accomplished by placing a barrier of cotton near the bottom of each tube such that bugs had only about 1 cm² to move about. Hence, individuals were forced into constant contact with eggs. After 24 hr, these subjects were released into petri dish test arenas containing freshly oviposited stimulus eggs, given 24 hr to acclimate, then assayed for maternal responsibility.

Because confinement with eggs is unlikely to occur under natural conditions, a control group was prepared in which nulliparous control females were confined in the previously described manner, but without stimulus eggs. Subjects were then placed into petri dish test arenas containing freshly oviposited stimulus eggs and treated in the previously described manner.

Data analysis included two-tailed nonparametric procedures for independent samples with $\alpha = 0.05$ (Siegel & Castellan, 1988). Ranges in subject age and time since diapause were never greater than 2 weeks. All treatment groups contained 20 individuals.

### Results

#### Maintenance of Maternal Responsiveness

Control mothers ($N = 20$) exhibited high response scores immediately following removal from eggs (Figures 2–3).
The responsivity scores of both groups of females, however, were higher than those of males (Kruskal-Wallis: KW = 9.5106, $p = .0086$; multiple comparisons: egg-exposed ♀♀ > ♂♂, non egg-exposed ♀♀ > ♂♂, $p < .05$) but did not differ from each other (multiple comparisons: egg-exposed ♀♀ ≠ non egg-exposed ♀♀, $p > .05$). When all bugs found in contact with test arena eggs were compared with all bugs not in contact, the former exhibited higher responsivity scores (Kruskal-Wallis: KW = 31.90, $p < .0001$).

Note that the single male found in contact with eggs had a response score of −4 and may have been at the eggs by chance. When males were excluded from analysis, however, the result was the same, with responsivity scores higher in brooding females than nonbrooding females (Kruskal-Wallis: pooled, KW = 22.07, $p < .0001$). The same was true within treatment groups (Kruskal-Wallis: egg-exposed ♀♀, brooders > nonbrooders, KW = 13.24, $p = .0003$; non egg-exposed ♀♀, brooders > nonbrooders, KW = 8.4776, $p = .0036$), although response scores among brooders varied considerably. It appears that females, even when not in reproductive condition, possess the capability of exhibiting maternal behavior.

**Discussion**

Early studies with laboratory rats demonstrated that when pup-removal occurred at birth, mothers would not nurse or retrieve stimulus pups on subsequent days (Rosenblatt & Lehrman, 1963). Later in the litter period, however, when pups were removed for several days, a high proportion of dams behaved maternally toward stimulus pups. The authors concluded that maternal responsivity was more likely to be maintained after becoming well established through

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**Response of Nonparental Individuals to Eggs**

Of the 20 experimental nulliparous females confined with eggs, 7 were observed in contact with test arena stimulus eggs after a 24-hr acclimation period (Figure 4). Only 1 out of 20 males was found in contact with eggs. Experimental females were thus more likely than experimental males to be found in contact with eggs (Fisher exact test: $p = .0436$). Experimental females, however, did not differ from control females, in which 5 out of 20 brooded despite the lack of close confinement with eggs in the pretrial enclosures (Fisher exact test: $p = .7311$). Control females also did not differ from males in the probability of contacting eggs in the test arena (Fisher exact test: $p = .1818$).
experience. Subsequent studies have demonstrated that 1 hr of experience within the first few days of delivery is sufficient to establish and maintain maternal responsiveness (Bridges, 1975; Cohen & Bridges, 1981), long after the period when maternal behavior is hormonally mediated (Fleming & Sarker, 1990; Orpen & Fleming, 1987; Orpen, Furman, Wong, & Fleming, 1987).

Although my study did not examine the effects of removing eggs immediately following oviposition, female burrower bugs separated from eggs after 2 brooding days immediately displayed maternal behavior toward stimulus eggs following a 24-hr separation. The response was delayed in females separated from eggs for 48 hr, but a significant proportion eventually exhibited a maternal response. These results indicate that maternal responsiveness gradually wanes in the absence of tactile or chemical stimuli from eggs.

Diminishing maternal responsiveness is probably associated with changes in physiological state—a state normally maintained by stimuli from offspring. Numerous studies have documented hormonal changes following the removal of offspring in rodents (Lee et al., 1989a; Lux-Lantos, Hockl, Tesone, & Libertun, 1994; Orpen et al., 1987; Taya & Sasamoto, 1989) and birds (El Halawani et al., 1980; Goldsmith et al., 1984; Ramsey, Goldsmith, & Silver, 1985; Hall, 1987; Lea & Sharp, 1989, 1991; LeBoucher, Richard-Yris, Guemene, & Chadwick, 1993). The few studies of hormonal correlates of insect parental behavior indicate that circulating levels of juvenile hormone (JH) may be associated with transitions in maternal behavior (Caussanel, Brézuet, & Karlinsky, 1978; Trumbo, Huang, Borst, & Robinson, in press; Vancassel, Foraste, Strambi, & Strambi, 1984). Although the endocrine systems of insects and vertebrates use completely distinct suites of hormones, maternal behavior is correlated with endocrine factors in both groups. For example, pup removal is associated with changes in levels of serum luteinizing hormone in rat dams (Hammons et al., 1973); nest removal is associated with changes in levels of serum prolactin in female turkeys (El Halawani et al., 1980); and egg removal is associated with changes in juvenile hormone levels in maternal earwigs (Vancassel et al., 1984).

The sensory mechanisms triggering such behavioral and physiological changes in insects are varied but often share features similar to those found in mammals. For example, photoperiod (reviewed by Saunders, 1982) influences gonadal development and reproductive behavior in numerous insect species and, among mammals, can affect the onset of puberty (Silver, 1992) and duration of pregnancy (Mitchell & Yochim, 1970). Insect vitellogenesis and oviposition may also be induced by stretch receptors in the gut (Schlein & Warburg, 1985) or genitalia (Sugawara, 1979) after the female feeds or copulates. Tactile stimulation from copulation is also known to induce ovulation in several mammalian species (Carter, 1992). In sylphid burying beetles, juvenile hormone levels rise almost immediately after females encounter and handle a carrion resource (Trumbo et al., in press). Lone male burying beetles, after discovering a carcass, often release a pheromone that attracts females (Bartlett, 1987; Trumbo & Eggert, 1994). Reproductive pheromones are also well documented in a number of mammalian species (reviewed by Vandenberghe, 1988).

The stimuli maintaining maternal responsiveness in Sehinurus appear to be tactile and olfactory. Kight (1995a) found that primiparous mothers brooded eggs that had been isolated for 24 hr but preferred eggs recently removed from a brooding female. Mothers presumably deposit a pheromone on the eggs and nest while brooding. Although tactile cues from eggs isolated for 24 hr will elicit a maternal response, recently brooded eggs from which the putative pheromone has not dissipated elicit a stronger response.

Initial studies on nonpregnant rats (Rosenblatt, 1967) found that exposure to pups elicited maternal responsiveness in nulliparous adult rats, including ovariectomized females, hypophysectomized females, and males. The author concluded that all rats maintain the potential to exhibit maternal behavior and that the response is not necessarily under hormonal control. Subsequent studies used this response to control for effects of pregnancy and parturition on physiological factors associated with maternal behavior (Clark et al., 1986; Insel, 1990; Numan, Numan, & English, 1993).

In my study, maternal behavior in nulliparous burrower bugs occurred almost exclusively among females. In addition, confinement with stimulus eggs may have facilitated the response, but it was not necessary because a number of nulliparous females exhibited maternal behavior on encountering eggs only in the test arena. Hence nulliparous females, but not males, bear the potential for maternal behavior. However, less than half of nulliparous females responded, whereas primiparous females in the egg-removal experiments were always maternally responsive during the period immediately following oviposition (see also Kight, 1995a).
1995a). Moreover, response scores of those nulliparous females found in contact with eggs were varied and often weaker than those of primiparous egg brooders. Perhaps experiential and physiological cues associated with oviposition act to lower the threshold at which females respond to eggs. That nulliparous females varied in both incidence and strength of response to stimulus eggs may reflect variation in this threshold.

Male burrower bugs do not exhibit maternal responsiveness, but male rodents can be induced to do so (Rosenblatt, 1967). Male care among mammals is typically associated with monogamous mating and is generally assumed to be necessary for offspring survival (reviewed by Clutton-Brock, 1991). Similar assumptions may be made for biparental insects, such as sylphid burying beetles, in which male and female must cooperate to secure valuable carrion resources from competitors (Scott & Tranelli, 1990). The resources used by Sehirus cinctus, however, can be secured by one parent and there may be little selective pressure for male care.

The capacity for male parental responsiveness in rats (which do not normally provide care) may be a reflection of phylogenetic descent, as several related species exhibit biparental care (Gubernick & Alberts, 1989; Oliveras & Novak, 1986). Apparently nulliparous males and females of certain beetle species also exhibit parental behavior (Valenzuela-Gonzalez, 1993), but these species are characterized by an evolutionary history of male parental behavior. Among burrower bugs (family Cydnidae), however, there is no evidence that males of any species have ever provided care. The capacity for males of certain mammalian and insect species to exhibit parental responsiveness, as well as the absence of this capacity in the present species, may therefore be a consequence of genetic or developmental constraints, or both, on its evolution.

Parental responsiveness among vertebrates and invertebrates could potentially arise in response to common selective pressures. Wilson (1975) described several ecological factors that might favor the evolution of care, including harsh environmental conditions, predation, and spatially or temporally limited resources. For example, the eggs of belostomatid water bugs, Belostoma flumineum, are extremely sensitive to desiccation and will only hatch if egg-bearing males keep them at the water surface to provide both ventilation and moisture (R. Smith, 1976). In other insect species, parental presence is necessary to minimize damage done to eggs by fungi (Lamb, 1976; West & Alexander, 1963). Guarding behavior in nymphalid butterflies (Nafus & Schreiner, 1988), grapsid crabs (Diesel, 1989), reedvuid assassin bugs (Ralston, 1977), and pentatomid stink bugs (Eberhard, 1975) reduces the number of eggs lost to predation and parasitism. Similar ecological factors may also have influenced the evolution of egg care for Prunella, and the food source rapidly disappears. The need to secure ephemeral resources may have strongly influenced the evolution of care in Sehirus cinctus. This reproductive synchrony between insect and host plant may also explain the lack of selection against the potential for concaveation. Because most females lay their eggs at approximately the same time, they should rarely encounter strange eggs when nulliparous.

Insects like Sehirus cinctus are useful for comparative studies of animal behavior. This study demonstrates that animals with markedly different physiologies and phylogenies can exhibit remarkably similar behavioral patterns. In both rats and burrower bugs, maternal responsiveness is maintained through stimuli from eggs and young but decays rapidly when such stimuli are removed. Stimuli from eggs and young can also induce maternal responsiveness in nulliparous individuals in both groups. Further studies on the parental behavior of diverse organisms will help resolve whether such behavior has similar proximate foundations and ultimate consequences.

References
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