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The reproductive biology of *Ptomascopus morio*, a brood parasite of *Nicrophorus*

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Abstract

Nicrophorine beetles (*Nicrophorus* and *Ptomascopus* spp.) use small carcasses as a food source for young, a breeding ecology distinct from other silphid beetles. While adaptations to the use of small carcasses are well known for *Nicrophorus* (emitting sex pheromone, burying, rounding and removing hair from carcasses, regulating brood size, regurgitating to young, and preventing predation), there is little information regarding its sister group, *Ptomascopus*. Like *Nicrophorus*, *Ptomascopus morio* males emit pheromone to attract females. In the absence of carrion competitors *Ptomascopus morio* parents were found to stay with a carcass and their brood for up to 10 days. We tested six hypotheses to examine whether young benefit from this long period of parent–offspring contact. (1) There was no evidence that parents buried or otherwise pre-empted carcasses to reduce competitive pressure. (2) We found no evidence that parents influenced the decomposition of the carcass. This was supported by experimental manipulations in which brood production (number of larvae and total brood mass) was no greater on carcasses on which parents were present than on carcasses not 'prepared' by parents. In addition, the carcass was not rounded and little hair was removed by the adults. (3) The presence of parents benefited the brood by reducing the negative effects of competition with carrion fly larvae. This likely resulted from predatory feeding by adult beetles. (4) Females adjusted clutch size to the size of the carcass. Parents, however, did not make a second adjustment in brood size after young reached the larval stage (filial cannibalism), as occurs in *Nicrophorus*. (5) Although parents were observed to open feeding holes in the carcass, this was not necessary for normal larval growth and survival. Parents were not observed to feed young directly by regurgitation. (6) Lastly, parents did not reduce predation on their brood when a conspecific intruder was present. These findings suggest that after the female parent adjusts clutch size to the size of the resource, the only parental benefit is clearing the carcass of fly larvae. Other differences with *Nicrophorus* include an extended period of oviposition (5 days) and less pronounced changes in ovarian mass and juvenile hormone titers in response to discovery of a carcass. In a field experiment in Kyoto, Japan, 17 of 21 broods of *N. concolor* during August contained larvae of *P. morio*. Mixed *Nicrophorus–Ptomascopus* broods were less common at other times of the year and when *N. quadripunctatus* occupied carcasses. In the laboratory, *P. morio* was able to parasitize 19 of 20 broods of *N. concolor*. The pattern of oviposition, the absence of explicit parental behaviours, and the interactions with *N. concolor* in the field suggest that *Ptomascopus morio* is a brood parasite of *Nicrophorus*.

Key words: brood parasitism, *Nicrophorus*, *Ptomascopus*, parental care, reproduction

INTRODUCTION

The evolution of complex parental and social behaviour has been a defining area of inquiry of sociobiology (Wilson, 1975). Although behavioural ecological approaches currently predominate, comparative work has a long history in evolutionary studies correlating variation in behaviour with variation in other aspects of the biology of organisms (Darwin, 1859, 1872). One reason for the limited number of comparative studies of parental behaviour is that the two most well-studied groups, birds and mammals, are possibly derived from a single ancestor already possessing complex parental behaviour. It is therefore difficult to associate the origin

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of parental behaviour with any particular ecological or physiological variable. Among insects, however, parental care has evolved independently in numerous lineages, at least 17 within the beetles (Wilson, 1971; Kûdo, 1994). This parallels the numerous independent evolutions of eusocial behaviour among insects (Wilson, 1971). The ability to examine closely related species that differ widely in social behaviour can be of tremendous value in testing hypotheses on the environmental contributors and physiological constraints on the evolution of social behaviour (Trumbo, 1999).

Among the insects, sister groups that differ in parental/social behaviour may exhibit a number of ecological relationships. The less social species may be outcompeted and become extinct (Cambefort, 1991). Less social species may persist in environments not favourable to care-giving (Tallamy & Schaefer, 1997). In this case, the less social species may reveal stages in the development of more derived complex behaviour (Evans, 1958; Wilson, 1971; Halffter & Edmonds, 1982). Finally, less social species may become brood parasites of more advanced species. These competitive outcomes have been documented among many insect groups including the bees, wasps and dung beetles (Wilson, 1971; Halffter & Edmonds, 1982; Hanski & Cambefort, 1991; Ross & Matthews, 1991).

Burying beetles (Silphidae, *Nicrophorus* F.) have been one of the most intensely studied parental insects by behavioural ecologists (reviews in Trumbo, 1996; Eggert & Müller, 1997; Scott, 1998), in part, because of the ease of performing experimental manipulations and measuring reproductive output. There have been few comparative studies of nicrophorines, however, because all *Nicrophorus* species studied possess similar types of parental behaviour (cf. Peck, 1982 and because the closest relatives of *Nicrophorus* are rarely encountered Asian species of the genus *Ptomascopus* Kraatz (three extant species).

The purpose of the present study is to add a comparative perspective to behavioural research on nicrophorines by reporting a broad spectrum of work on *Ptomascopus morio* Kraatz. *Ptomascopus* and *Nicrophorus* are thought to form a monophyletic group (subfamily Nicrophorinae) based on the following synapomorphies, among others: paired stridulatory files on tergite 5, antennal segments 2 and 3 fused to form a 10–segmented antenna, a notched radial hinge on the wings, larvae with one pair of stemmata, larvae with reduced sclerotization, female valvifer of genitalia with claw, and having 12 autosomes and a XO sex determination system (opposed to 26 autosomes and a Xyp sex determination system of the Silphinae) (Smith, 1953; Peck, 1982; Ratcliffe, 1996; D. Sikes, pers. obs.). Most non-nicrophorine silphids exploit larger carcasses, have no parent–offspring association, and possess larval morphology and behaviour adapted for hunting dipteran larvae (Ratcliffe, 1996). Exploitation of small, fresh carcasses by nicrophorines presents many ecological problems generally not confronted by other silphids. The carcass must be discovered and used before flies and other carrion competitors become established, the carcass must be hidden or defended from other carrion competitors, a conspecific mate may not discover a small carcass, it might not be advantageous to oviposit the maximum clutch on a limited resource, larvae must be able to survive solely on carrion, and larvae adapted to burrowing within a carcass are less sclerotized and therefore vulnerable to predation. *Nicrophorus* possesses many highly derived adaptations for exploiting small carcasses (Pukowski, 1933). The reproductive biology of *Ptomascopus*, however, is largely unknown.

Natural history of nicrophorines

The behaviour of burying beetles (*Nicrophorus* spp.) has been well researched. Burying beetles exploit small carcasses as a food resource for their young. A carcass which is discovered in a location unsuitable for burial will be transported over the surface by one or more beetles (Milne & Milne, 1944; Fabre, 1949; Milne & Milne, 1976). If a male discovers a carcass before a female, the male will emit pheromone in a highly characteristic manner with his abdomen pointed up (Pukowski, 1933; Bartlett, 1987*a*; Eggert & Müller, 1989*b*; Eggert & Müller, 1992, see cover of issue). A single female or male–female pair prepares a small mammal carcass by burying, rounding it into a ball and removing hair (Pukowski, 1933). After a female discovers a carcass there is a rapid increase in both ovarian mass and titers of juvenile hormone (Scott & Traniello, 1987; Trumbo, Borst & Robinson, 1995). Females typically oviposit in nearby soil within 24 h, adjusting clutch size to the size of the carcass (Müller, Eggert & Furlkroger, 1990*b*). Even so, many more eggs often are oviposited than will mature to third instar larvae, which disperse from the carcass. A second adjustment of brood number occurs by filial cannibalism during the first 48 h larvae are on the carcass (Bartlett, 1987*b*; Trumbo, 1990*b*; Trumbo & Fernandez, 1995). Parental care in *Nicrophorus* is known to benefit young in at least four important ways. Care reduces deterioration of the resource (Pukowski, 1933), increases the rate of larval development (Trumbo, 1991; Eggert, Reinking & Müller, 1998), adjusts brood number to the size of the resource (Bartlett, 1987*b*), and protects young from predators and congeneric intruders (Scott, 1990; Trumbo, 1990*c*; Trumbo, 1991).

There has been but one small study of *Ptomascopus* behaviour. Peck (1982), found that *Ptomascopus morio* that were given small (2 g) cubes of chicken spent 1–3 days near the resource. Like *Nicrophorus*, a reduced clutch was oviposited in the soil and the developmental period of larvae was shortened compared to silphines. Unlike *Nicrophorus*, there was no nest preparation, resource manipulation or parent–offspring contact reported.

In the present study of *Ptomascopus morio* we found that parents will stay with a carcass for 10 days in the absence of competitors. We examined six hypotheses to explain this duration of contact. Do adult *Ptomascopus* help to: (1) bury or otherwise pre-empt the resource from competitors?; (2) influence the decomposition?; (3) reduce competition from carrion flies?; (4) regulate the size of the brood, either at oviposition or larval stages?; (5) facilitate feeding of young by opening holes in the carcass or by regurgitation?; (6) reduce predation on young? Additional aspects of *Ptomascopus* biology, including ovarian development, changes in titers of juvenile hormone, the duration of oviposition, and pheromone-emitting behaviour, are reported. Field and laboratory studies on species abundance, phenology and brood parasitism are reported on the nicrophorine community from Kyoto, Japan.

METHODS

A colony of *P. morio* was established using beetles caught in carrion-baited traps in the wild from Otaru, Hokkaido, Japan during June, 1998. Except where noted, experiments were conducted in the laboratory with beetles maintained on a diet of small pieces (< 2 g) of chicken liver and kept in mixed sex groups in containers ($17 \times 31 \times 8$ cm) without soil at 22–25°C, 15L:9D. In experiments measuring reproductive output, the mass of adult females was equal across treatments as an experimental control (see Bartlett & Ashworth, 1988). Unless otherwise indicated, beetles were bred in cylindrical containers (10 cm diameter, 12 cm depth) filled with soil to within 2 cm of the top, and covered with a translucent plastic cup. In experiments in which parents were removed on the day that first instar larvae arrived on the carcass, this was typically day 4 at standard laboratory temperatures. When measuring reproductive output, only third instars were included (a few first and second instar larvae were sometimes seen on depleted carcasses but these were not counted because it is unlikely that such young would develop successfully and reproduce as adults). Adults used in reproductive experiments were at least 20 days post-emergence (reproduction occurs as early as 8 days post-emergence in *P. morio*, pers. obs.). All carcasses were laboratory *Mus musculus* that were frozen shortly after death and thawed before experiments.

Patterns of pheromone release

To examine the diurnality of pheromone release by male *P. morio*, 14 males were placed into containers ($17 \times 31 \times 8$ cm) half filled with soil. A carcass (10–15 g) and a rock (provided as a perch) also were placed into each container. Containers were placed into an insectary on 10 May in Cheshire, Connecticut, USA and exposed to natural light. Each container was inspected briefly every 2 h over a 24-h period (17 May). Males in the pheromone-emitting posture (hind legs extended and the tip of abdomen pointed and lifted; Pukowski, 1933; Eggert & Müller, 1989*a*) were noted.

As a follow-up, the same 14 males were provided a new carcass 5 days later and monitored every 30 min during the evening activity period (18:00–22:30). Five days later these 14 males were again monitored for pheromone emitting behaviour during the evening activity period, only this time without a carcass.

Duration of parental contact and preparation of the carcass

Eleven male–female pairs were provided a 12–14 g carcass in covered containers ($17 \times 31 \times 8$ cm) half-filled with soil. The temperature was kept cool (17–20 °C) to extend the period of development and thereby permit a greater number of observations. A small pile of shredded leaves was placed 5 cm from the carcass. The first observation (Day 1) was made 12 h after the carcass was placed into the set-up. Brief inspections (the carcass was lifted off the ground) were made 3 times each day (2 during photophase and 1 during scotophase) for 10 days to determine whether the adults were on or within 3 cm of the carcass. Burial depth and movement of the carcass were noted. On Day 5 the carcass was examined to determine whether hair had been removed and whether holes had been opened in the carcass.

Do parents adjust brood size to the size of the resource?

To determine whether the number or mass of larvae produced on a carcass varies with size of the resource, male–female pairs were provided a small (4–5 g, $n = 11$), medium (7–8 g, $n = 12$) or large (14–15 g, $n = 12$) carcass in cylindrical breeding containers. Larvae were cleaned, counted and weighed on the day they dispersed from the carcass.

Clutch size adjustments

To determine whether clutch size varies with carcass size, male–female pairs were provided either a small (5–6 g, $n = 15$) or large (12–13 g, $n = 15$) carcass in cylindrical containers filled with soil. On day 4 (when first instar larvae began to arrive on the carcass), the parents and carcasses were removed, first instars were counted and removed (maximum of 8), and small pieces of chicken liver were placed on top of the soil to attract eclosing larvae. Over the next 4 days, additional larvae were removed twice a day from the chicken liver and counted.

Behavioural observations

Eight male–female pairs were provided a 10–12 g carcass and established in covered observation chambers ($32 \times 26 \times 10$ cm) half-filled with soil. On the first day larvae arrived on the carcass, the containers were placed in the dark and adult activity was observed under dim red light. The carcass was turned on its side to facilitate observation as larvae had previously congregated on the underside of the carcass while exposed to normal laboratory light. To induce possible filial cannibalism, 10 additional first instars were placed on each carcass. Each pair was observed for 3 h over the subsequent 24-h period.

Do parents enhance or reduce brood number after oviposition?

To determine whether parents enhance or reduce brood number during the period after larvae eclose, male–female pairs were provided 7–8 g carcasses. On the first day on which larvae arrived on the carcass, both parents were either removed ($n = 13$) or allowed to remain ($n = 13$) on the carcass. Preliminary results had indicated that a female will oviposit more viable eggs (27.1 ± 4.8) than third instar larvae that will survive (14.0 ± 3.2) on a resource of 7–8 g. Larvae were cleaned, counted and weighed after they dispersed from the carcass.

Oviposition patterns and brood production

The pattern of oviposition (spread over a number of days rather than all on 1 day) might allow a passive regulation of brood number by starving late-arriving first instars which eclose after the resource is exhausted. To examine this possibility, male–female pairs were provided 6–7 g carcasses. At the time first instars arrived on the carcass the parents were removed and 3 treatments were established. In treatment 1 (Control, $n = 10$), the carcass was left in the original breeding container with the eggs (and any first instars that had eclosed) produced by the female. In treatments 2 and 3 the carcass was transferred to a new breeding container without eggs. In treatment 2 ($n = 10$), 8 first instars were placed on the carcass each day for 4 days, simulating a female that had spread her oviposition evenly over 4 days. In treatment 3 ($n = 10$), 32 first instars were immediately placed on the carcass, simulating a female that had oviposited her entire clutch 3–4 days earlier. Dispersing larvae were cleaned, counted and weighed.

Do parents facilitate feeding?

To test the hypothesis that *Ptomascopus* parents facilitate feeding of their young, male–female pairs were provided 12.5–14.5 g carcasses. On the first day that larvae arrived on the carcass, the parents were removed. The eclosing first instars were then provided either the original carcass ($n = 12$) on which parents had previously opened holes, or a freshly thawed carcass ($n = 12$) that had not been exposed to adult *Ptomascopus* and which had not opened experimentally (such carcasses may be difficult for *Nicrophorus* to exploit; see Eggert *et al*., 1998). Dispersing larvae were cleaned, counted and weighed.

Do parents prevent resource deterioration?

Preventing the degradation of larval food resources may be important for carrion feeders. This hypothesis was tested by providing 24 male–female pairs with fresh 15–16 g carcasses. At the beginning of the experiment, 12 additional carcasses in the same size range were exposed to decomposition by placing them on moist soil next to a screened window of an insectary (78 h). This prevented fly oviposition but exposed the carcasses to airborne bacterial and fungal microbes. On the day that first instar larvae arrived on the carcass, the parents were removed. In 12 trials the original carcass prepared by the parents was provided to the young. In 12 additional trials, the original carcass was removed and replaced with a carcass that had been exposed to microbe colonization. Dispersing larvae were cleaned, counted and weighed.

Do parents reduce competition from carrion flies?

To examine whether *Ptomascopus* parents affect competition with carrion flies, 36 carcasses (9–10 g) were kept at room temperature for 24 h and then exposed in a sunny location to carrion flies for 8 h. Carcasses were then brought into the laboratory for 2 h until the beginning of *Ptomascopus'* evening active period. Twenty-four of these carcasses were then presented to male–female pairs in cylindrical breeding containers (the other 12 carcasses were placed in cylindrical containers without beetles and put to the side for 4 days). Four days later, when first instar larvae began to arrive on the carcasses, the parents were removed. In 1 treatment, the original carcass (exposed to carrion flies and then *Ptomascopus* adults) was presented to larvae. In the second treatment, each brood was provided 1 of the 12 carcasses that had been exposed to carrion flies and put to the side for 4 days (no exposure to *Ptomascopus* adults). Dispersing larvae were cleaned, counted and weighed.

Do parents prevent predation?

To examine whether parents protect young from conspecific predators, male–female pairs were provided 7–9 g carcasses. On the day larvae began to arrive on the carcass, carcasses were placed into new breeding containers without eggs. Fifteen first instars were placed on each carcass. Parents were then either removed ($n = 19$) or allowed to remain ($n = 19$) with their carcass. A male and female conspecific of reproductive age were then introduced into each breeding container. The carcass was inspected 48 h later, and surviving larvae were counted.

The parents that were removed from breeding containers were used to examine possible parental aggression toward conspecifics. Nine of these pairs were each placed in a small circular arena (9 cm diameter) with a thin dirt flooring. An additional male–female pair was then introduced into each arena and behaviour was observed for 10 minutes.

One additional assay of parental defense was performed. Ten male–female pairs were established in larger breeding containers ($17 \times 31 \times 9$ cm). Two days after larvae were first observed on the carcass, a non-breeding male was held with forceps and held next to each parent to observe the parental response.

Ovarian mass and juvenile hormone titer in adult females

Nicrophorus females experience a dramatic ovarian and hormonal response to the discovery of a carcass suitable for reproduction. To examine possible changes in *P. morio*, females were sampled at the following times: 5 days after adult emergence, 15 days post-emergence, 6 h after being presented a carcass (16-day-old females), 12 h after being presented a carcass (16-day-old females), on the day larvae arrived on the carcass (19-day-old females) and on the second day after larvae arrived on the carcass (20-day-old females). To collect haemolymph the 4 hindmost legs were severed and haemolymph was collected into acetonitrile and preserved at $-80\,^{\circ}$C. Because individual *P. morio* do not yield as much haemolymph as *Nicrophorus*, haemolymph samples from 5–8 individuals were pooled for analysis. Titres of juvenile hormone were assayed as detailed in Trumbo *et al.* (1995). At the time of haemolymph collection, females were frozen and kept at 0°C. At a later time, the pronotal width was measured and ovaries were dissected to obtain the wet weight (Trumbo *et al.*, 1995).

Field and laboratory studies in Kyoto

The community of nicrophorine beetles in forested mountainous habitats in Kyoto, Japan was assessed by placing pitfall traps baited with chicken (40 g) from 29 May until 13 October, 1988. Every 7 days all beetles were removed and the traps were restocked with new bait.

To examine reproduction of *P. morio* in the field, 147 pieces of chicken (30–40 g, thawed for 24 h) were placed on the floor of a secondary forest in Kyoto during the period from 1 July to 30 September, 1988. The carrion was tied to a stake to facilitate relocating the carrion after concealment by *Nicrophorus*. After 10 days the carrion was inspected and 4 possible outcomes were recorded: (1) won by *N. quadripunctatus*; (2) won by *N. concolor*; (3) scavenged by vertebrates (carrion removed from site); (4) won by other insects (no *Nicrophorus* or *Ptomascopus* adults or larvae and remains of carcass on site). When adults of *N. quadripunctatus* or *N. concolor* were in possession of the carrion, the number and species of nicrophorine larvae were recorded.

To examine brood parasitism of *N. concolor* hosts by *P. morio* under more controlled conditions, three experimental treatments were established in the laboratory: single male–female pairs of *N. concolor* ($n = 15$); single male–female pairs of *P. morio* ($n = 8$); pairs of *N. concolor* and *P. morio* breeding together ($n = 20$). Sections of chicken (20 g) were provided. Dispersing larvae were counted and weighed.

To investigate egg production by *P. morio*, male–female pairs were provided a 20 g section of chicken either in the presence of *N. concolor* ($n = 18$) or in *N. concolor*'s absence ($n = 14$). Eggs were counted after 3 days.

Statistical analyses

Measures of reproductive output (number of larvae, mass of larvae, and total brood mass) were normally distributed in most trials and were analysed using ANOVA or ANCOVA (General Linear Methods, Wilkinson, 1989). Non-parametric tests were used in trials in which the dependent variable was not normally distributed. Associations between discrete variables were tested using contingency tests (Wilkinson, 1989).

RESULTS

Patterns of pheromone release

There were two distinct pheromone emitting periods by *P. morio* males, one associated with sunrise and one with sunset (Fig. 1a). A more detailed examination of the evening activity period demonstrated that males were more likely to emit pheromone (with or without a carcass) during the period leading up to sunset than in the period following sunset (Fig. 1b). Adoption of the pheromone-emitting posture did occur without a carcass, but not until the end of the activity period and less often than with a carcass (2×2 contingency test, $G = 177$, $P < 0.001$).

Duration of parental contact and preparation of the carcass

Both male and female parents had extensive contact with the carcass throughout the reproductive attempt. The presence of adults near the carcass did not vary with time of day; observations were therefore grouped by day (three observations/day × 11 pairs = 33 total observations/day). The sexes differed in their pattern of association with the carcass, males were more often on or near the carcass during the period before larvae eclosed, and females were more often on or near the carcass on subsequent days (Fig. 2; 2×10 contingency

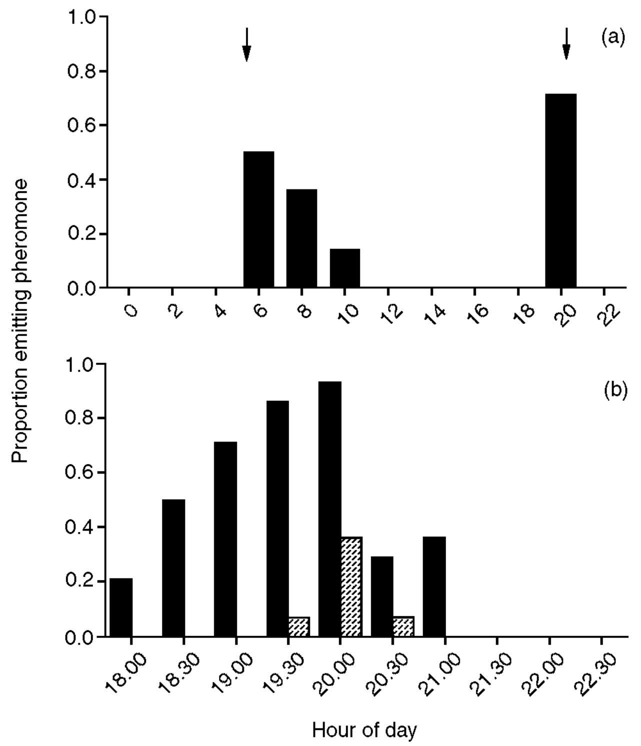

Fig. 1. The proportion of 14 male *Ptomascopus morio* adopting the pheromone-emitting posture over (a) a 24-h period (observations every 2 h) and (b) during the evening activity period (observations every 30 min). Males that were provided a carcass, are represented by solid bars, males without a carcass, by dashed bars. Arrows indicate sunrise and sunset on 17 May.

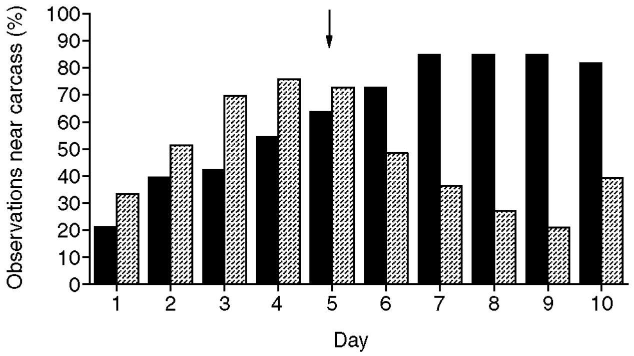

Fig. 2. The percentage of observations (33/day) in which female (solid bars) and male (dashed bars) *Ptomascopus morio* parents were on or within 3 cm of the carcass for each day of the trial. The arrow indicates the day that first instar larvae arrived on the carcass (10 of 11 trials).

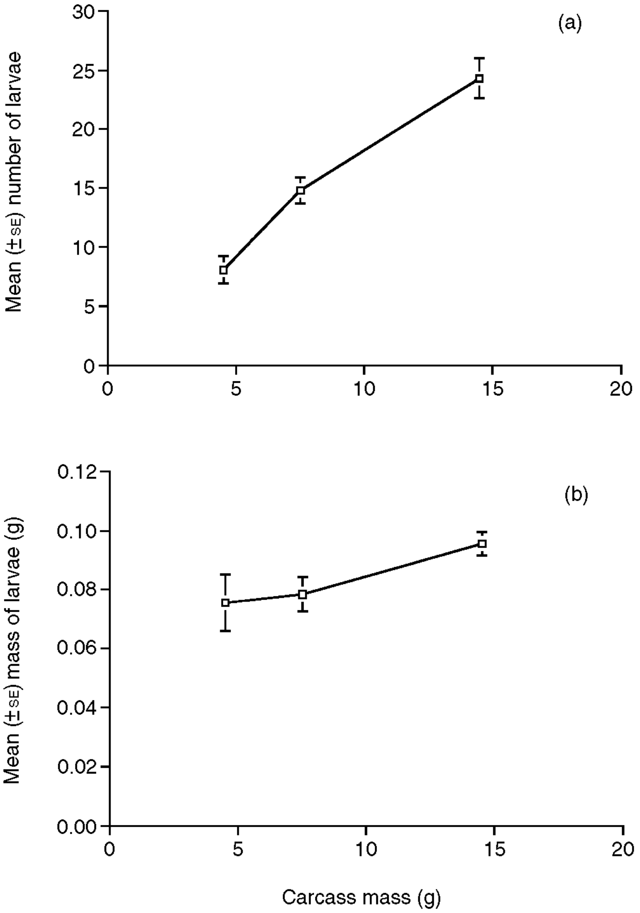

Fig. 3. The mean (± SE) (a) number of larvae and (b) mass of larvae of *Ptomascopus morio* on small (4–5 g), medium (7–8 g) and large (14–15 g) carcasses.

test, $G = 33.74$, $P < 0.001$). During the time when larvae were on the carcass, at least one parent was present on 94% of observations.

There was minimal preparation of the resource. Carcasses were never moved more than 3 cm by adults. In no trial was the carcass displaced toward the leaf pile and leaves were not used to cover the carcass. Carcasses were not buried, but adult activity beneath the carcass caused it to settle slightly (< 1 cm) into the soil. In all trials, tunnels were observed underneath the carcass and adults often moved to the tunnels during inspections. No carcass was rounded into a ball. By day 5, hair was absent from 15–40% of the surface of carcasses. It was not clear if this occurred because of feeding and inspection activity of adults or by specific hair removal behaviour. One or two holes were opened on each carcass where adults fed.

Do parents adjust brood size to the size of the carcass?

Carcass size affected reproductive output. A greater number of young ($F_{2,32} = 36.22$, $P < 0.001$) and a heavier total brood ($F_{2,32} = 98.08$, $P < 0.001$) were produced on larger carcasses. The mean mass of individual larvae did not differ among treatments (Fig. 3; $F_{2,32} = 2.72$, $P = 0.08$). *Post hoc* comparisons suggested that larvae on small and medium carcasses did not differ in mass ($P > 0.20$) but that larvae were 23% heavier on large carcasses ($F_{1,33} = 5.50$, $P = 0.02$). There was a tradeoff between brood number and mean mass of larvae. When

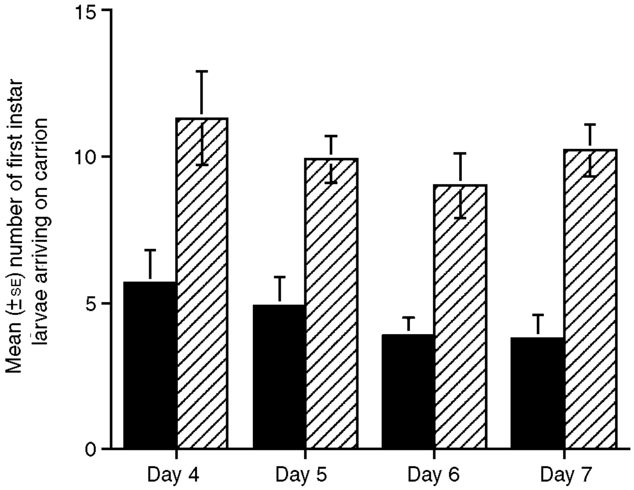

Fig. 4. The mean (± SE) number of *Ptomascopus morio* larvae arriving at carrion on each day of the trial beginning on the first day that larvae arrived (day 4) on 5–6 g (solid bars) and 12–13 g carcasses (dashed bars).

the mean mass of larvae was regressed against brood number within a carcass size treatment, there was a significant negative relationship for all three sizes of carcass ($P < 0.01$; Simple regression).

Clutch size adjustments

Females clearly adjusted the size of the clutch to the size of the resource (Fig. 4). Females produced over twice as many viable eggs over a 4-day period (44.9 ± 2.6 *vs.* 20.2 ± 2.0) on large (12–13 g) as compared to small (5–6 g) carcasses. The effect of carcass size was highly significant ($F_{1,28} = 51.46$. $P < 0.001$) while female body mass was not ($F_{1,28} = 1.00$, $P = 0.33$, ANCOVA). Because total clutch size on 12–13 g carcasses (Fig. 4) exceeds the number of young that disperse from 15 g carcasses (Fig. 3), it is clear that not all young are surviving on carcasses in this size range.

The pattern of oviposition (as indicated by time when first instar larvae arrived on carrion) was quite different from *Nicrophorus*. The arrival of larvae was spread evenly over the 4-day period (Fig. 4). Since the female was removed when the initial larvae began to arrive on the carcass, clutch size may have been underestimated. This underestimation is likely to be slight since mating behaviour and female time away from the carcass (indicating oviposition) falls off markedly on the second day larvae are on the carcass.

Behavioural observations

During 24 h of observation (3 h for each of eight pairs), no case of infanticide was observed. There also was no clear case of an adult feeding young. There were three head to head contacts between parent and young that persisted for more than 3 s. In none of these cases, however, was there evidence of feeding (the larva was not supported or lifted off the substrate, the interaction did not attract additional first instars, and no begging behaviour by larvae was observed as occurs during regurgitation by *Nicrophorus*) (Pukowski, 1933; Rauter & Moore, 1999). Over 90% of observations of *Ptomascopus* were devoted to two behaviours – standing or walking over the carcass. Walking over the carcass was associated with a fine pumping motion of the abdomen; no audible sounds accompanied this behaviour. *Ptomascopus* was not observed to drag its abdomen over the surface of the carcass. One striking difference with *Nicrophorus* was that a total of 14 copulations were observed while larvae were on the carcass (six of eight pairs). Each copulation was followed by apparent mate-guarding in which the male rode or followed the female for 2–29 min. In three of the eight pairs, the female was observed to chase the male as sometimes occurs in *Nicrophorus* near the time the male deserts the nest.

Do parents enhance or reduce brood number after oviposition?

The continued presence of parents after larvae eclose had no significant effect on three measures of reproductive output on carcasses. The number of third instar larvae ($F_{1,25} = 0.78$, $P > 0.20$), mean mass of larvae ($F_{1,25} = 3.79$, $P = 0.06$), and total mass of the brood ($F_{1,25} = 0.01$, $P > 0.20$) were not different for trials in which parents remained on the carcass as compared to trials in which parents were removed (Fig. 5). Note that when parents were present the trend was toward a greater number of larvae of slightly lower mass. Clearly there was no evidence of active brood reduction by parents.

Oviposition patterns and brood production

The simulated patterns of oviposition (placing eight larvae on the carcass over 4 days *vs.* 32 larvae on 1 day) affected brood number. In treatment 2 (eight larvae × 4 days), reproductive output was similar to the control (treatment 1) (Fig. 6; number of larvae: $F_{1,18} = 0.12$, $P > 0.20$; mean mass of larvae: $F_{1,18} = 0.05$, $P > 0.20$; total mass of brood: $F_{1,18} = 0.05$, $P > 0.20$). In treatment 3 (32 larvae × 1 day), significantly more larvae ($F_{1,27} = 18.46$, $P < 0.001$) and heavier broods ($F_{1,27} = 7.10$, $P = 0.01$) were produced than in either treatments 1 or 2 (Fig. 6). Despite the larger broods, however, the mean mass of dispersing larvae in treatment 3 was not significantly less than the mass of larvae in treatments 1 and 2 ($F_{1,27} = 0.86$, $P > 0.20$).

Do parents facilitate feeding?

Carcasses that had been opened by feeding activity of parents did not produce more young than fresh car-

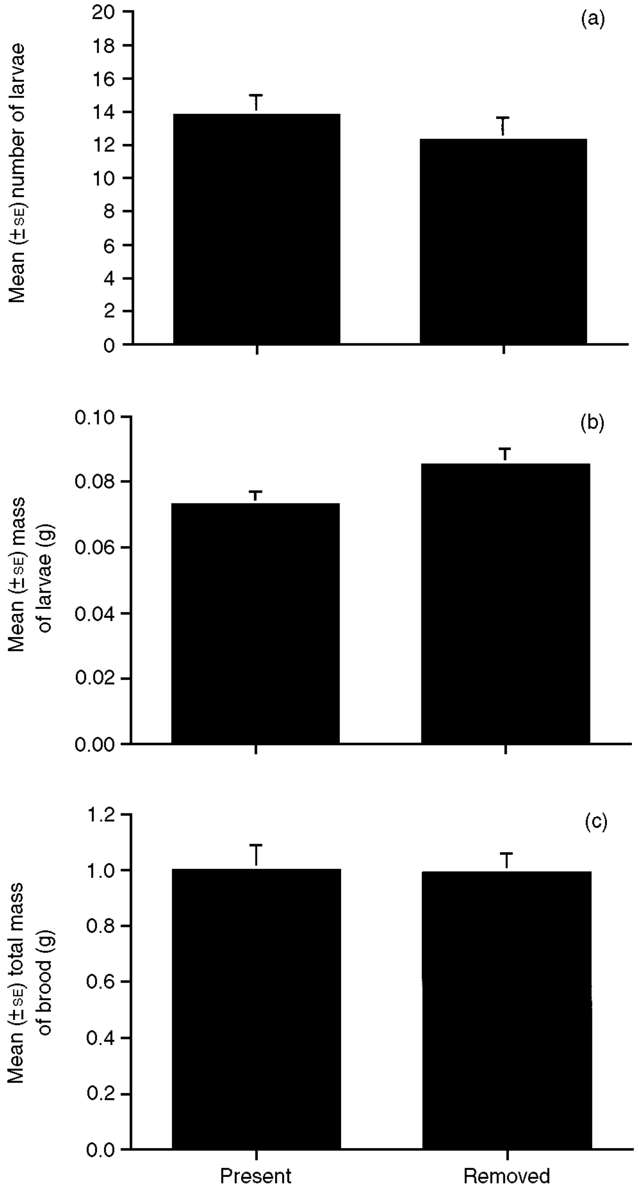

Fig. 5. Reproductive output (mean ± SE). (a) Number of larvae, (b) mean mass of larvae and (c) total mass of brood of *Ptomascopus morio* on 7–8 g carcasses with parents present and parents removed at the time first instars arrived on the carcass.

casses which had no points for larval entry created by beetles or the experimenter (Fig. 7; $F_{1,22} = 0.69$, $P > 0.20$). Interestingly, the unopened carcasses produced individual larvae of greater mass ($F_{1,22} = 32.42$, $P < 0.001$) and broods of greater total mass ($F_{1,22} = 8.53$, $P = 0.01$) than carcasses prepared by parents.

Do parents prevent resource deterioration?

We found no evidence that adult *P. morio* affected the decomposition of the carcass. Carcasses 'prepared' by parents for 4 days produced broods which were no greater in number ($F_{1,22} = 0.05$, $P > 0.20$), mass of individual larvae ($F_{1,22} = 0.62$, $P > 0.20$) or total mass ($F_{1,22} = 0.03$, $P > 0.20$) than unprepared carcasses that were exposed to microbial colonization for 4 days (Fig. 8).

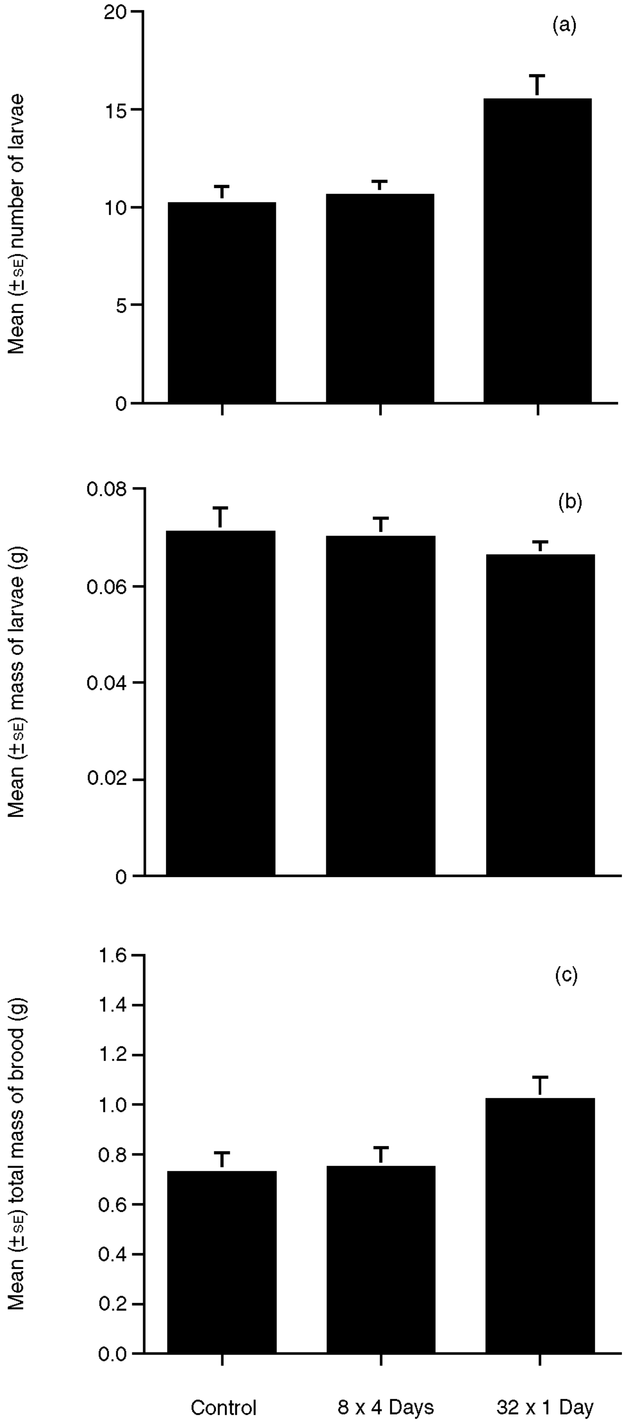

Fig. 6. Reproductive output (mean ± SE). (a) Number of larvae, (b) mean mass of larvae, and (c) total mass of brood of *Ptomascopus morio* under simulated patterns of oviposition of eight eggs produced on 4 successive days or 32 eggs produced on 1 day.

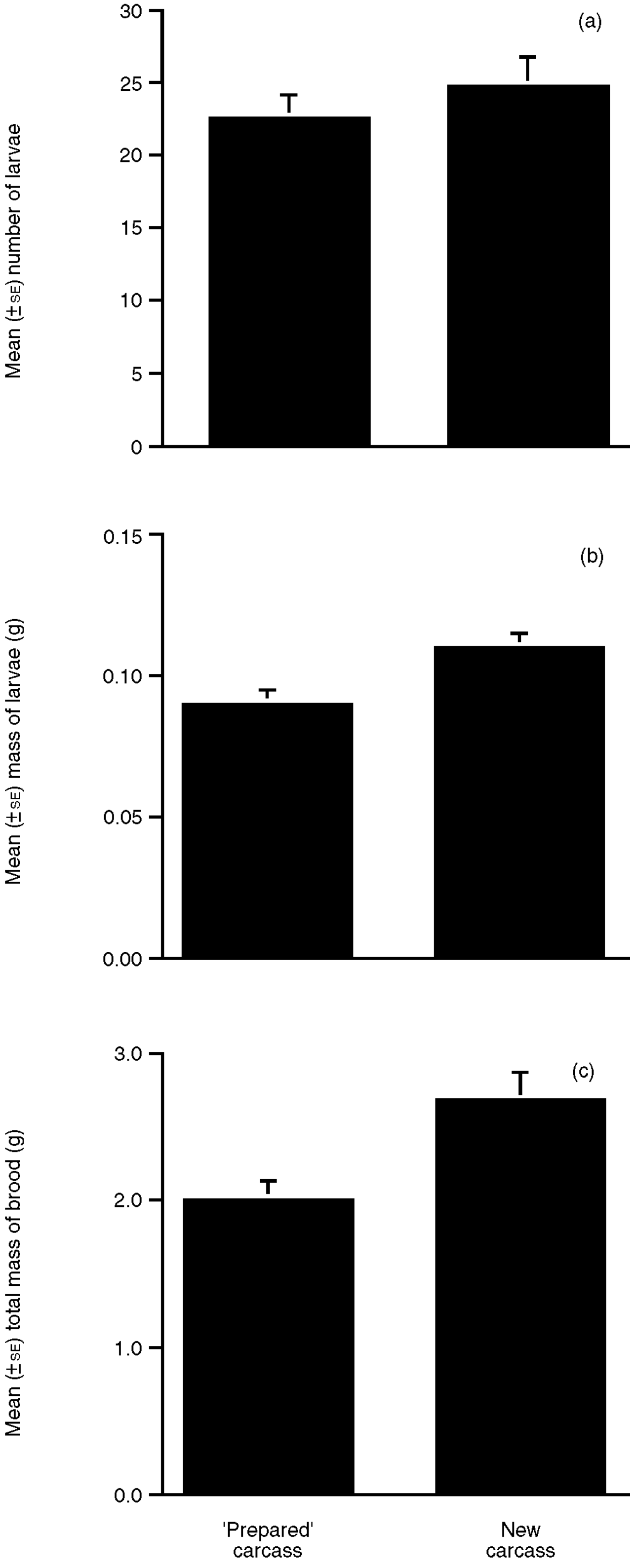

Fig. 7. Reproductive output (mean ± SE). (a) Number of larvae, (b) mean mass of larvae, and (c) total mass of brood of *Ptomascopus morio* on carcasses prepared by parents and on new carcasses which had not been opened for larval access.

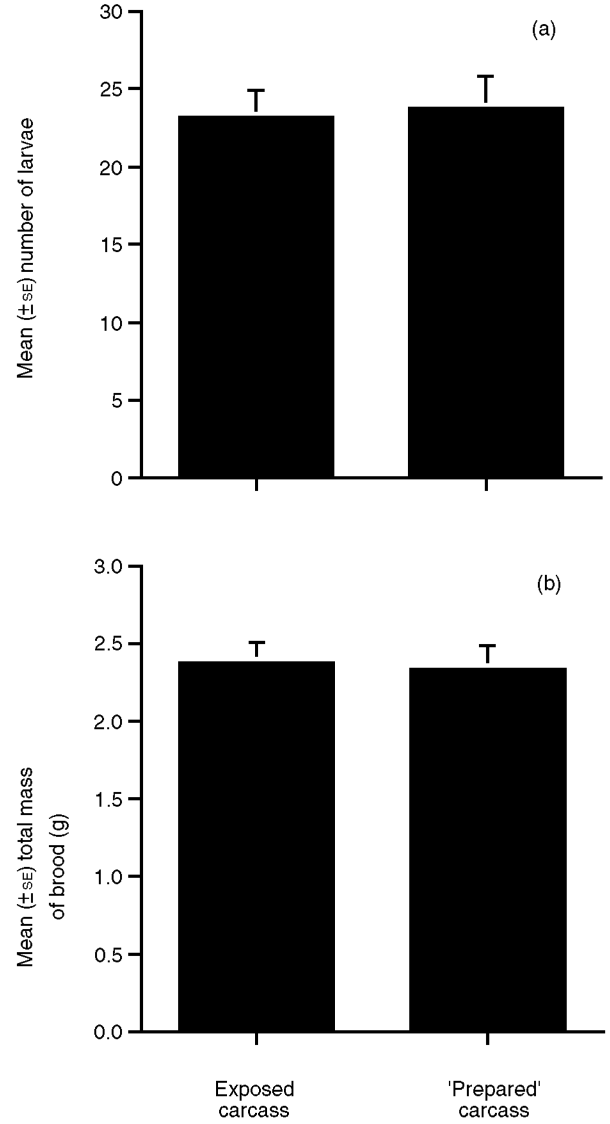

Fig. 8. The mean (± SE) (a) number of larvae and (b) total brood mass of *Ptomascopus morio* on carcasses exposed to microbes (with or without preparation by parents) and then presented to young.

Do parents reduce competition from carrion flies?

Adult *P. morio* reduced the negative effects of carrion fly larvae. The number of *P. morio* larvae ($U = 126$, $P = 0.002$, Mann–Whitney U test), the mass of larvae ($F_{1,22} = 13.5$, $P = 0.001$), and total mass of the brood ($F_{1,22} = 37.6$, $P < 0.001$) were greater on carcasses exposed to fly oviposition which had been handled by parents compared to carcasses not handled by parents (Fig. 9).

Do parents prevent predation?

Broods of 15 larvae exposed to predation risk did not fare differently whether protected or unprotected by parents. The mean number of surviving brood did not

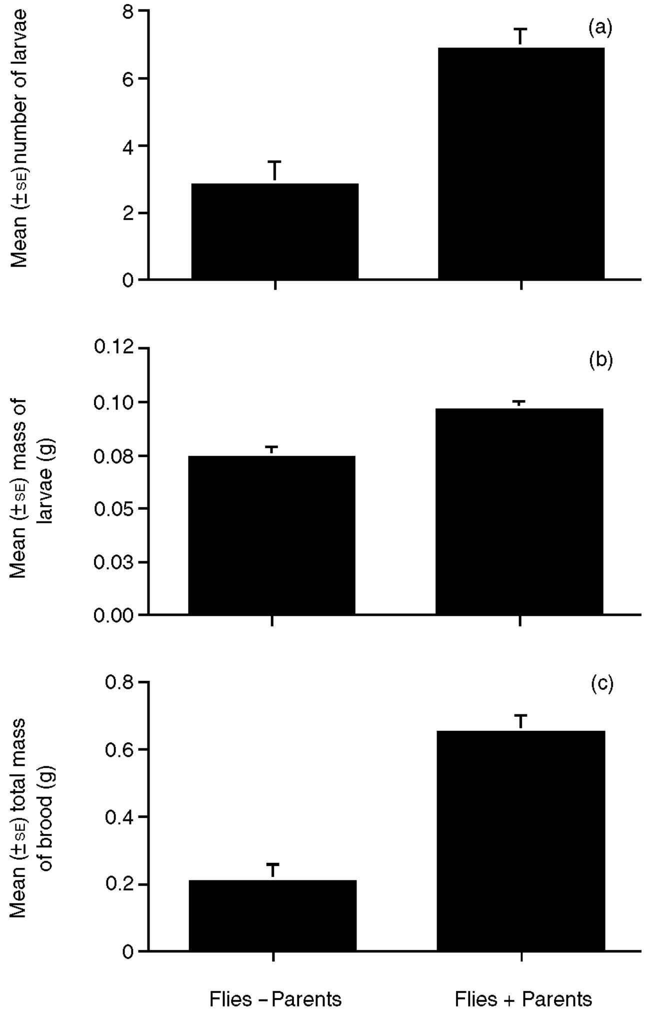

Fig. 9. Reproductive output (mean ± SE). (a) Number of larvae, (b) mean mass of larvae, and (c) total mass of brood of *Ptomascopus morio* on carcasses exposed to carrion fly oviposition (with or without preparation by parents) and then presented to larvae.

differ between treatments (Fig. 10; $F_{1,36}$= 0.47, $P > 0.20$, ANOVA). In no trial did the intruders kill all the young as commonly occurs during takeovers by *Nicrophorus* (Bartlett, 1987*b*; Trumbo, 1990*c*).

The male–female parents that were removed in the 'unprotected' treatment were placed together and briefly observed (10 min). In no case did fighting occur nor were any beetles heard to produce stridulations. Similarly, when a non-breeding male was introduced using forceps to a male–female pair on a carcass with third instar larvae, no biting, chasing or stridulations were recorded.

Ovarian mass and juvenile hormone titer in adult females

The changes in ovarian mass during the pre-reproductive (< 7 days post-emergence) and reproductive periods of *P. morio* are much less striking than in *Nicrophorus*.

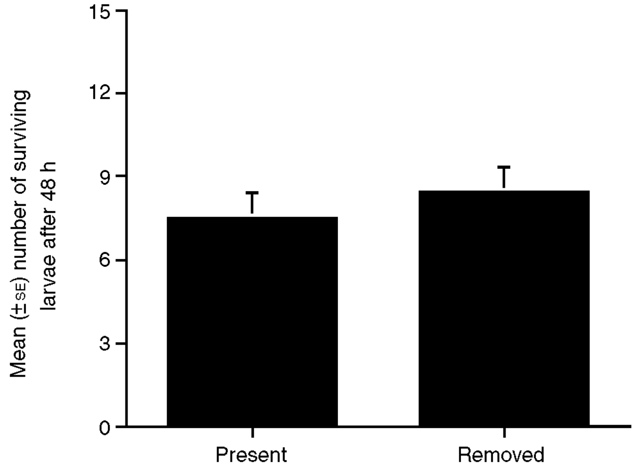

Fig. 10. The mean (± SE) number of surviving *Ptomascopus morio* young (in original broods of 15) when parents were present or absent during 48 h that a male and female *P. morio* intruder were in the breeding container.

Since ovarian mass was highly correlated with female pronotal width (PW), this variable was incorporated into analyses of covariance. There was a significant increase in ovarian mass during the pre-reproductive period (day 5 *vs.* day 15: $F_{1,29(\mathrm{day})} = 13.44$, $P = 0.011$, $F_{1,29(\mathrm{PW})} = 6.33$, $P = 0.01$, ANCOVA, Fig. 11a). There was no significant increase in ovarian mass 6 or 12 h after presentation of the carcass (6 h: $F_{1,29(\mathrm{day})} = 1.84$, $P > 0.20$, $F_{1,29(\mathrm{PW})} = 16.01$, $P < 0.001$; 12 h: $F_{1,29(\mathrm{day})} = 1.15$, $P > 0.20$, $F_{1,29(\mathrm{PW})} = 14.87$, $P = 0.001$). The oviposition response was quite fast. Fifteen of 16 females had oviposited by 12 h. Ovarian mass while larvae were on the carcass was significantly less than ovarian mass in females presented a carcass ($F_{1,45(\mathrm{day})} = 10.58$, $P = 0.001$, $F_{1,45(\mathrm{PW})} = 19.36$, $P < 0.001$).

Nicrophorus orbicollis experiences a rapid increase in titer of juvenile hormone, which is maintained until near the onset of oviposition. We found no evidence of such an increase in *P. morio* (Fig. 11b). In *P. morio* 6 h after presentation of a carcass, titres of juvenile hormone had fallen. Interestingly, titres of juvenile hormone appear to be higher on the first day that larvae arrive on the carcass than on the second day. This change is coincident with the cessation of mating behaviour and oviposition by the second day.

Field and laboratory studies in Kyoto

Four nicrophorines, *Nicrophorus quadripunctatus* Kraatz, *N. concolor* Kraatz, *N. maculifrons* Kraatz and *P. morio* were trapped in baited pitfall traps in Kyoto. The proportions for each species are shown in Fig. 12. During each of the four sampling periods *N. quadripunctatus* was the most commonly trapped beetle, followed in order by *N. concolor*, *P. morio* and *N. maculifrons*.

Since aged carrion in pitfall traps attracts a mixture of breeding and non-breeding individuals (Wilson &

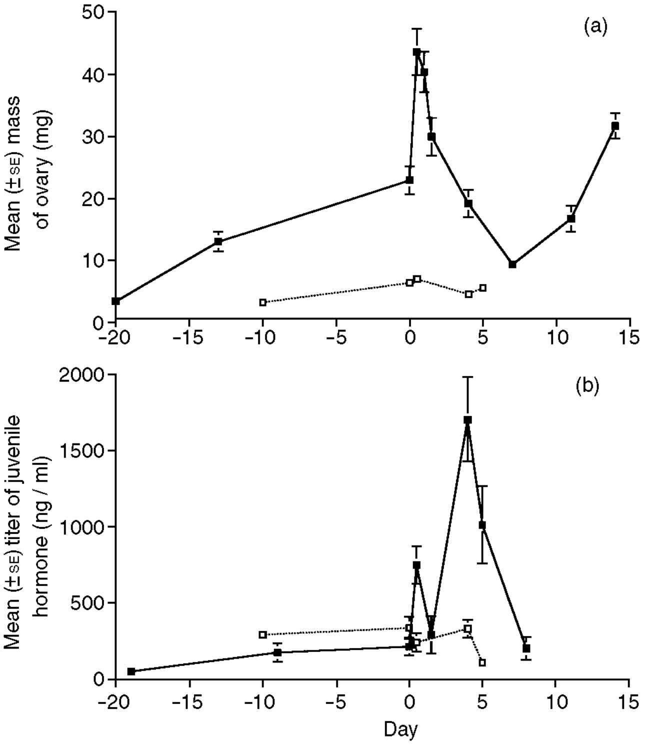

Fig. 11. (a) Mean (± SE) mass of ovaries and (b) mean (± SE) titer of juvenile hormone during the pre-reproductive and reproductive phases for adult *Ptomascopus morio* (open squares) and *Nicrophorus orbicollis* (solid squares). Day 0 is the day a carcass was presented to an adult pair. Negative values for days represent the pre-reproductive period. Larvae arrived on the carcass on day 4 for *Ptomascopus* morio and day 5 for *Nicrophorus orbicollis*. Data for *P. morio* are from three samples pooled from five to eight individuals each. Data for *N. orbicollis* are from individual samples (adapted from Trumbo *et al*., 1995). Error bars for *P. morio* may be obscured by the size of the points.

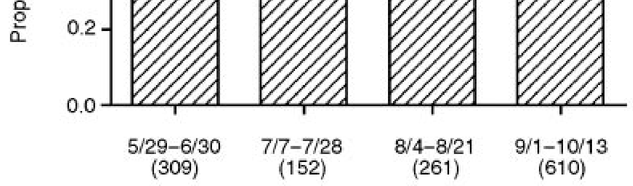

Fig. 12. The proportion of nicrophorines trapped in baited pitfall traps from 29 May until 13 October, 1988 that were *Nicrophorus quadripunctatus* (hatched bars), *N. concolor* (open bars), *Ptomascopus morio* (grey bars) and *N. maculifrons* (black bars). The sample sizes are shown in parentheses.

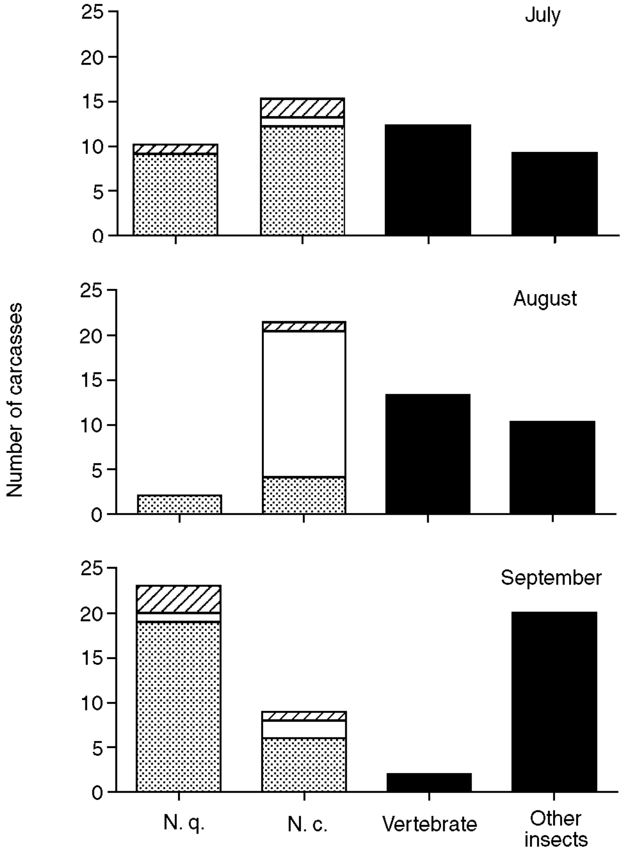

Fig. 13. The fate of 147 pieces of chicken carrion (30–40 g) left in the field for 10 days in a Kyoto forest during July, August and September, 1988. N. q. = possessed by *Nicrophorus quadripunctatus*. The lower bar (stippled) represents carrion with adult and larvae only. The middle bar (open) represents carrion with adults and larvae and larvae of *Ptomascopus morio*. The upper bar (hatched) represents carrion with adults only. N. c. = possessed by *N. concolor*. Bars as for *N. quadripunctatus*. Vertebrate = carcass removed from site. Other insects = no *Nicrophorus* or *Ptomascopus* adults or larvae and remains of carcass on site. Note there were two cases of *P. morio* larvae but no adult on buried carrion (not shown), one case of *N. quadripunctatus* larvae but no adult, one case of *N. quadripunctatus* larvae and *P. morio* larvae but no adult, and one case of *N. concolor* larvae and *P. morio* larvae but no adult.

Knollenberg, 1984; Ratcliffe, 1996), the only way to monitor breeding activity is to place fresh carrion in the field. The only nicrophorine adults to possess carrion placed on the substrate in a Kyoto forest were *N. quadripunctatus* and *N. concolor*. *Nicrophorus quadripunctatus* was more successful in July and September than in August while *N. concolor* was more successful in August and September (Fig. 13). Parasitism by *P. morio* (as indicated by *P. morio* larvae in broods of *Nicrophorus* tended by *Nicrophorus* adults) was rare for *N. quadripunctatus* (two of 35 broods) and for *N. concolor* during July and September (three of 24 broods). Brood parasitism, however, was very common in

N. concolor broods during August (17 of 21 broods). In the 21 broods of *N. concolor* parasitized by *P*. morio, there was a mean of 4.9 (± 0.6) *P. morio* young in the brood. The presence of *P. morio* larvae was not related to fewer larvae of *N. concolor* in the field (6.8 ± 0.7 without parasitism *vs*. 6.2 ± 0.7 with parasitism) ($F_{1,42}$= 0.36, $P > 0.20$, ANOVA).

There were no clear cases of *P. morio* breeding on its own in the field. There were two broods of *P. morio* larvae without *Nicrophorus* young or adults but these two broods were not tended by *Ptomascopus* adults. Since the carrion had been concealed under the soil, it is likely that *Nicrophorus* adults buried the carrion and then abandoned the nest.

In the laboratory, *P. morio* successfully parasitized *N. concolor* in 19 of 20 opportunities. Number of brood ($P < 0.001$, Mann–Whitney *U* test) and total mass ($F_{1,33}$= 13.83, $P < 0.001$, ANOVA) of *N. concolor* broods were significantly less in trials in which *P. morio* brood parasites were present than in trials in which *N. concolor* bred alone (Fig. 14). The mean mass of larvae was significantly greater in parasitized broods ($F_{1,33}$= 7.55, $P = 0.01$). Thus the reduction in total brood mass in broods of *N. concolor* was due solely to fewer larvae in parasitized broods and not to smaller larvae.

In separate trials, the number of eggs produced in the 3 days after *P. morio* was provided a carcass was not affected by the presence or absence of *N. concolor* (28.6 ± 2.4 *vs*. 28.9 ± 2.4, $F_{1,30}$= 0.01, $P > 0.20$, ANOVA).

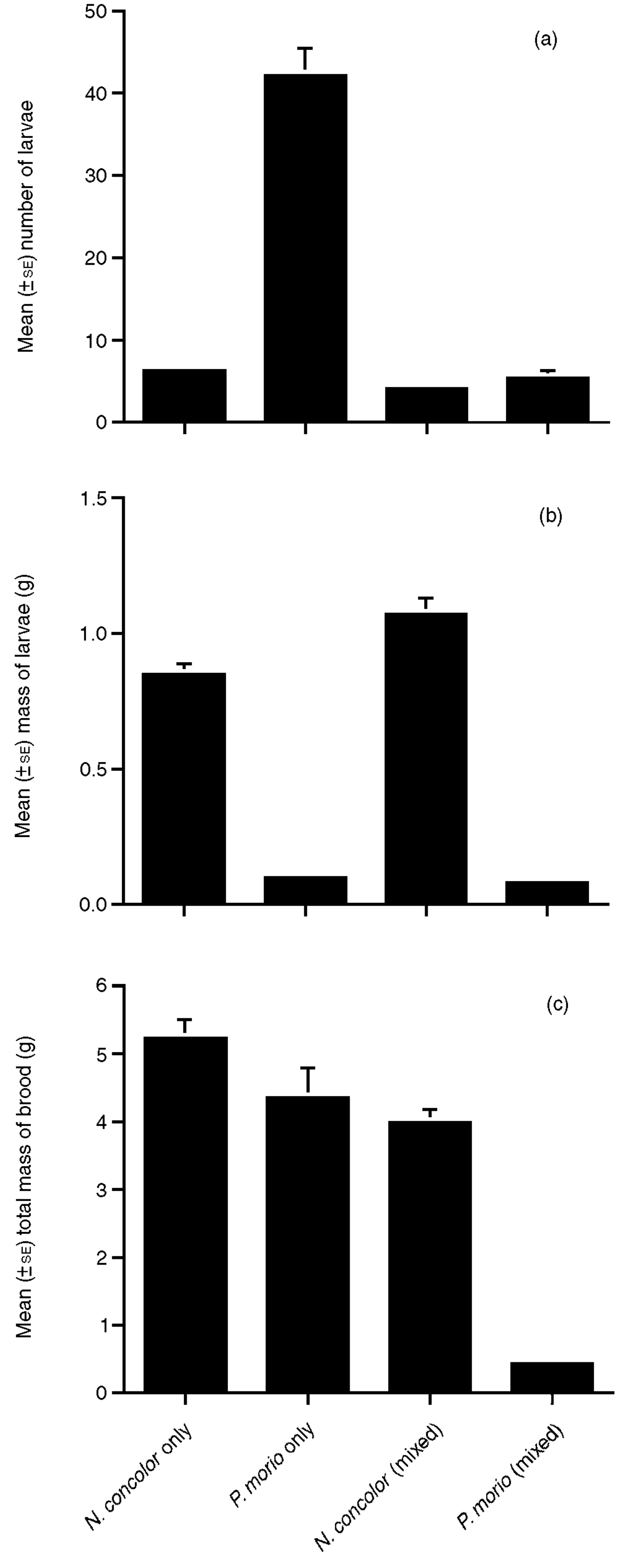

Fig. 14. Reproductive output (mean ± SE) (a) number of larvae, (b) mean mass of larvae, and (c) total mass of brood on 20 g of chicken for *Nicrophorus concolor* breeding alone, *Ptomascopus morio* breeding alone, and for *N. concolor* and *P. morio* producing mixed broods.

DISCUSSION

The case for *P. morio* as a brood parasite

The results of our field and laboratory studies support the hypothesis that *P. morio* is a brood parasite of *Nicrophorus* spp. *Ptomascopus morio* in Kyoto, Japan was found to parasitize two species in the field, *N. quadripunctatus*, and more commonly, *N. concolor*. While there were more than 20 confirmed cases of mixed broods of *Nicrophorus* and *Ptomascopus* larvae in the field, there was not a single unequivocal case of independent reproduction by *P. morio*. The two broods that contained only larvae of *P. morio* had no adults present and were taken beneath the leaf litter. Such burying behaviour was not seen in the laboratory study of *P. morio* (also see Peck, 1982) but is characteristic of all *Nicrophorus* species studied (Pukowski, 1933; Eggert & Müller, 1997; Scott, 1998). Laboratory study of *P. morio* from this same Kyoto population shows that *P. morio* can be a highly successful parasite of *N. concolor*. *Ptomascopus morio* from two laboratory colonies derived from wild populations from Otaru, Hokkaido and Kyoto, Honshu successfully parasitized the North American species *N. tomentosus* in our laboratory (S. Trumbo, per. obs.). It is not clear why *P. morio* had more difficulty parasitizing *N. quadripunctatus* than *N. concolor*. It is interesting that the breeding activity of *N. quadripunctatus* was least at the time when *P. morio* was most active (August). Whether this is an anti-parasitic strategy and whether other possible mechanisms for reducing parasitism exist, need investigation.

In the laboratory but not in the field, *P. morio* parasitism resulted in decreased brood production by *N. concolor*. The field result may have occurred for a number of reasons. It is possible that the negative effects of parasitism were partially offset by the clearing of carcasses of carrion fly eggs. This scenario would possibly require *P. morio* arriving first at the carcass. The order of arrival at carcasses is not known. Observations of interactions between *P. morio* and possible hosts would be of interest. It is also possible that greater variation in reproductive output in the field and greater variation in resource size obscured real differences between parasitized and unparasitized broods of *N. concolor* (despite the larger sample in the field the standard errors for reproductive output of *N. concolor* were twice as large as in the laboratory). We believe that parasitism by *P. morio* is likely to have negative effects on reproduction of *Nicrophorus* hosts.

Observations made in the laboratory support the hypothesis that *P. morio* is a brood parasite. *Ptomascopus morio* demonstrates little attention or manipulation of a fresh mammal carcass. Most noteworthy is that the carcass is not buried, covered, rounded or preserved. It is difficult to imagine how the smaller-sized *P. morio*, breeding independently in the field, could prevent loss of an unprotected, small carcass for the 10–15 days required to complete larval development. The carrion-feeding community is highly competitive and consists of vertebrate scavengers, ants, carrion flies and other nicrophorines (Fuller, 1934; Payne, 1965; Putnam, 1978; Scott, Traniello & Fetherston, 1987; Scott, 1994*b*; Ohkawara, Suzuki & Katakura, 1998). In the forests of Kyoto, carcasses that are not buried typically are consumed by carrion fly larvae within 5 days (M. Kon, pers. obs.). We feel, therefore, that the long association between *P. morio* and their offspring in the laboratory is artificial in that it is unlikely that an unprotected, small carcass would remain undiscovered for a suitable duration in the field.

In the laboratory, mouse carcasses used by *P. morio* had small patches of hair removed, primarily around points where adults fed. Hair was not removed from the carcass in any systematic fashion, however, and in no case was the hair removed from even one-half the carcass. Using small carcasses, *Nicrophorus* completely removes hair or feathers within 2–3 days, usually beginning on the underside (Pukowski, 1933). We suspect the loss of hair noted in our experiments occurred as a by-product of feeding and because of normal loosening of hair on a decomposing corpse.

As occurs in *Nicrophorus*, *P. morio* opened feeding holes on the carcass and larvae tended to congregate at these points of entry. *Nicrophorus* larvae are highly dependent on their parents for gaining access to the interior of the carcass. If *Nicrophorus* larvae are provided a carcass without openings, growth and survival are poor (Eggert *et al.*, 1998). In contrast, *P. morio* young do not appear to benefit from openings into the carcass. In our experiments, young of *P. morio* fared better with a fresh, unopened carcass than with a carcass opened by their parents, presumably because they obtained access to a resource that had not deteriorated over 4 days. We hypothesize, therefore, that the opening of holes in the carcass evolved from typical adult feeding behaviour, but only became necessary parental behaviour once nicrophorine larvae became more dependent on care. Some *Nicrophorus* species will not survive to the second instar without continued parental care (Trumbo, 1992).

Adult *P. morio* were not observed to regurgitate to larvae, and larvae were not seen to beg for feedings as occurs in *Nicrophorus* (Rauter & Moore, 1999). It is unlikely that feeding behaviour was missed in both Peck's (1982) and our study. During the first 24-h larvae are on the carcass, *N. orbicollis* Say parents feed larvae, on average, once every 4 min (Fetherston, Scott & Traniello, 1990). It would be of interest to determine whether larvae of *P. morio* beg from *Nicrophorus* foster parents. In avian brood parasites, the young of the parasite are often larger than host young, facilitating competition for parental feedings (Payne, 1998). Perhaps in parasitic species that feed from gathered resources rather than directly from foster parents, such as occurs in parasitic dung beetles (Cambefort, 1991) and *P. morio*, parasitic young can be much smaller than host young.

There also was no evidence that adult *P. morio* control the decomposition of the resource. *Ptomascopus morio* was not observed to manipulate the carcass and the young grew and survived just as well on carcasses not prepared by parents as on carcasses prepared by parents. This suggests that *P. morio*, utilizing a carcass without the care of foster parents, receive a deteriorated resource compared to *Nicrophorus* young. One measure of resource quality is the conversion efficiency (total mass of the brood at dispersal/ mass of the resource). In 10 laboratory experiments from the present study in which no manipulation of the resource took place, the conversion efficiency ranged from 11.2–21.8% (mean ± SE: 14.9 ± 0.7). Only in one experiment did the conversion efficiency exceed 16.5%. From the literature, the conversion efficiency of *Nicrophorus* ranges from 16.7–28.5% (Table 1; mean ± SE: 22.3 ± 1.0), a significantly greater conversion rate than *P. morio* ($P < 0.001$, Mann–Whitney *U* test). Although the total mass of the brood can vary with the timing of the measurement (larval mass peaks and then declines before dispersal) the near lack of overlap between these values suggests that parental care in *Nicrophorus* increases utilization efficiency of carrion resources. Manipulation experiments with *Nicrophorus* have clearly demonstrated the beneficial effects of care on growth (Scott & Gladstein, 1993; Eggert *et al.*, 1998).

Ptomascopus morio parents did not protect their brood from predatory intruders as do *Nicrophorus* parents (Scott, 1990; Trumbo, 1990*a*,*c*; Robertson,

Table 1. Efficiency of conversion of carcass mass to mass of dispersing *Nicrophorus* third instars

Species	Carcass size (g)	Efficiency (%)	Reference
N. defodiens	5.5	19.8	(Trumbo, 1990*a*)
N. defodiens	8.0	22.6	(Trumbo, 1990)
N. orbicollis	17.5	23.5	(Wilson & Fudge, 1984)
N. orbicollis	32.5	20.3	(Wilson & Fudge, 1984
N. orbicollis	8.0	16.7	(Trumbo, 1990*a*)
N. orbicollis	26.0	18.0	(Robertson, 1993)
N. orbicollis	21.0	19.2	(Scott & Gladstein, 1993)
N. orbicollis	33.5	23.5	(Scott & Gladstein, 1993)
N. orbicollis	18.3	27.2	(Trumbo & Fernandez, 1995)
N. orbicollis	29.2	28.5	(Trumbo & Fernandez, 1995)
N. tomentosus	12.5	19.2	(Trumbo, 1990*b*)
N. tomentosus	30.0	28.3	(Trumbo, 1990*b*)
N. vespilloides	23.8	18.0	(Müller *et al*., 1990*a*)
N. vespilloides	15.0	19.7	(Eggert *et al*., 1998)
N. concolor	20.0	26.2	This study

1993; Scott, 1994*a*). In *Nicrophorus* a successful congeneric intruder will kill all the young (usually within 24 h) and exploit the resource for its own reproduction (Trumbo, 1990*c*; Robertson, 1993). *Ptomascopus morio* intruders never killed all young suggesting that usurpation of a carcass is not a strategy used by this species (some larval mortality occurs because of normal predatory behaviour of adults). The absence of overt aggression by parents towards intruders similarly suggests that defence of the brood is not a benefit of parental care. In a brood parasite, parental defence would not be selected.

Ptomascopus morio females adjust the size of their clutch to the size of the resource. This adjustment would prevent wasting eggs on a small resource, and would be important for either a parental species (Müller *et al*., 1990*b*) or a brood parasite (also it is possible that too many eggs on a small carcass would cause the host to desert). *Nicrophorus* makes a second adjustment of brood size by killing excess young during the period after larvae hatch and begin to arrive on the carcass (Bartlett, 1987*b*; Trumbo, 1990*b*; Trumbo & Fernandez, 1995). Such filial cannibalism, observed at a rate greater than one per h in *N. vespilloides* (Bartlett, 1987*b*) was not observed in *P. morio*. Filial infanticide would not be expected in a brood parasite. Since we did note larval mortality in *P. morio* broods without a host parent, there is a question of mechanism. We suspect that the lengthy period of oviposition by *P. morio* results in starvation as the latter-arriving larvae attempt to feed from an exhausted resource. This hypothesis was supported by the greater production of *P. morio* third instars when first instar larvae were placed on the carcass all on the same day, compared to introducing the same number of first instar larvae over a 4-day period.

One important difference between *P. morio* and *Nicrophorus* spp. is the long period of consistent oviposition in *P. morio*. We suggest that this oviposition pattern may be an adaptation to ensure host acceptance of *P. morio* young (and not as a mechanism to regulate brood size). *Nicrophorus* parents only accept young on the carcass when larvae arrive at a time 'expected' by the parents (eggs are oviposited in the soil and hatching young crawl to the carcass) (Müller & Eggert, 1990). This period of acceptance corresponds to the earlier period of oviposition. *Nicrophorus* parents do not have an absolute ability to recognize their own young and will accept even congeneric young that arrive on the carcass at the appropriate time (Müller & Eggert, 1990). The timing of egg-laying is similarly important in avian brood parasites (Payne, 1998; Slagsvold, 1998). In parasitic systems in which timing is important, spreading out oviposition, even ovipositing before a potential host arrives, might increase the chance that some young will be accepted by the host.

Several *P. morio* pairs mated frequently after first instar larvae were on the carcass. This is additional evidence that oviposition is occurring at this time. Matings by *Nicrophorus* pairs at this time are rare (Müller & Eggert, 1989; Fetherston *et al*., 1990), presumably because the female has terminated oviposition much earlier (Müller & Eggert, 1989). Copulation in *Nicrophorus* is generally not associated with mate-guarding because mating occurs during a period of active resource preparation. Mate-guarding is common in the non-caring silphines (pers. obs.). We suggest that the brood parasitic lifestyle of *Ptomascopus*, which does not require resource preparation, makes mate-guarding by males a fitness-enhancing behaviour.

There are several additional differences between *P. morio* and *Nicrophorus* that we believe are related to differences in oviposition behaviour. A *Nicrophorus* female, upon the discovery of a carcass suitable for reproduction, experiences a surge in juvenile hormone (the principal reproductive hormone of insects) and a threefold increase in ovarian mass within 18–24 h (Wilson & Knollenberg, 1984; Scott & Traniello, 1987; Trumbo *et al*., 1995). A large clutch of eggs is then oviposited over a 24-h period. *Ptomascopus morio* females have a less pronounced increase in both levels of juvenile hormone and in ovarian mass after discovery of a carcass. We suggest this is related to the production of fewer eggs per day over a greater number of days. Interestingly, *P. morio* can oviposit more quickly than *Nicrophorus* in response to a discovery (15 of 16 females oviposited within 12 h and some as quickly as 8 h). A fast response to a suitable resource might be especially beneficial when a potential host discovers the resource first and may have already begun to oviposit. The order of discovery of the carcass will depend, in part, on diurnal activity rhythms. *Ptomascopus morio* has two peaks of activity as indicated by pheromone-releasing behaviour of males. This is similar to *N. maculifrons* and *N. vespilloides* Herbst but different from *N. quadripunctatus* (Ohkawara *et al*., 1998), potential hosts with overlapping geographic ranges (information on the diurnality of *N. concolor* is not available). It is probable that *Ptomascopus* will sometimes discover carcasses before and sometimes after the host. A flexible oviposition response in the parasite would appear to be adaptive.

Pheromone emission by males occurs in both *Ptomascopus morio* and *Nicrophorus* spp., but has not been recorded for other silphids. We suggest that pheromone emission is an adaptation for exploiting small, fresh carcasses which females may not discover. Silphine males typically encounter a large number of ovipositing females on large fly-ridden carcasses.

In summary, we believe that the evidence that *P. morio* is a brood parasite of *Nicrophorus* in Kyoto is strong. Whether it is a brood parasite throughout its range is undetermined. This conclusion is suggested by: (1) the absence of resource preparation or pre-emption in the midst of a competitive carrion community; (2) the absence of behaviours that enhance the fitness of the brood (with the exception of killing fly larvae); (3) the finding of brood parasitism in the field and laboratory; (4) the pattern of reproductive physiology and behaviour that are consistent with a life history of brood parasitism.

Comparative study of *Ptomascopus* and *Nicrophorus* points to the need to understand better the range of behaviours and life history of the silphines. Only a few silphines have been studied. It would be instructive to know whether any silphines emit pheromone, whether the developmental period of larvae is always longer than nicrophorines (Ratcliffe, 1972 reports rather fast development of *Necrodes surinamensis* under optimal conditions), whether there is adjustment in clutch size, whether small fly-ridden carcasses are sometimes used for reproduction, and how the ovarian response to carcass discovery and oviposition patterns differ from nicrophorines.

Is brood parasitism in *P. morio* obligatory and how did parasitism evolve?

Some brood parasitic species exhibit parasitism facultatively. Among birds, most facultative brood parasites are generally independent breeders and only occasionally parasitic (Payne, 1998). The reverse (generally parasitic and occasionally breeding independently) is rare. In *Nicrophorus*, interspecific brood parasitism does occur although independent breeding seems to be the common reproductive mode for all species (Trumbo, 1992). Although *P. morio* appears to be a parasite at Kyoto, other populations require study.

Ptomascopus morio occurs with *N. concolor* (its most common host at Kyoto) over much of Honshu (Kamimura, Nakane & Koyama, 1964). *Nicrophorus concolor* is absent or very rare, however, at Hokkaido localities where *P. morio* is quite abundant (Katakura & Ueno, 1985; Katakura, Sonoda & Yoshida, 1986; Ohara, 1995). At each of these sites on Hokkaido, *N. quadripunctatus* is a common potential host; additional species of *Nicrophorus* are also present. In one study on Hokkaido, however, *P. morio* was commonly trapped in open areas but was rare in woodlands where its potential hosts were common (Katakura *et al.*, 1986). These distributions were determined by trapping feeding beetles (pitfalls with aged carrion), which do not always indicate breeding habitat. A second study (Ohara, 1995) also presents difficulty for the hypothesis that *P. morio* is parasitic throughout its range. At this Hokkaido site, *P. morio* were trapped more than twice as often as all other nicrophorines combined. Most models of brood parasitism predict that the numbers of brood parasites will be much smaller than the population of potential hosts. Further study would be of interest to understand the reproductive biology of these populations of *P. morio* and to ascertain whether *P. morio* breeds independently in some populations. Populations of *P. morio* on Honshu and Hokkaido are known to exhibit marked differences in seasonal activity (Ohara, 1995).

One hypothesis for the evolution of interspecific brood parasitism is that it developed from intraspecific parasitism (Hamilton & Orians, 1965). Since intraspecific brood parasitism appears to be fairly common in *Nicrophorus* (Müller, Eggert & Dressel, 1990*a*), this hypothesis is feasible for the nicrophorines. If this were the case then the ancestor of *P. morio* would have been an independent breeder. Species of dung beetles with derived pre-emptive and parental behaviours are thought to have replaced species with less developed competitive behaviours (Cambefort, 1991). Some less competitive groups of dung beetles have apparently survived this competition by giving rise to species that are brood parasites of more sophisticated nest builders (Hanski & Cambefort, 1991). A possible scenario is that the ancestor of *Ptomascopus* spp. was able to pre-empt small carcasses before the evolution of *Nicrophorus*. There is morphological and molecular evidence that *Ptomascopus* is intermediate between other silphids and *Nicrophorus. Ptomascopus* may have been a much more species-rich group in the past than it is today. Supporting this is the existence of an extinct species *P. aveyronensis* Flach, known from a fossil, thought to be from the lower Oligocene (Mroczkowski, 1959). This fossil is older than any recovered fossil of *Nicrophorus*. The hypothesis that *P. morio* was an independent breeder on small carcasses before the evolution of *Nicrophorus* would be supported if populations of *Ptomascopus* (*P. morio* or one of the other two extant species) were found to breed on small carcasses in the field.

A second and not mutually exclusive hypothesis for brood parasitism is that it evolved from nest usurpation where dominant individuals first displaced and later tolerated a 'host' that will care for its eggs (Payne, 1998). Similar scenarios have been proposed for social insects (where it is termed 'social parasitism') in which a usurper intrudes into a nest and appropriates resources and workers, usually after killing the host queen (Wilson, 1971). This evolutionary pathway seems unlikely for *P. morio* because it is smaller in size than all recorded species of *Nicrophorus* (*P. morio* is about onetenth the mass of *N. concolor* and one-half the mass of *N. quadripunctatus*). Brood parasites that are much smaller than their host also occur in dung beetles (Cambefort & Hanski, 1991), which like *P. morio*, may not have to compete for feedings from the foster parent. A third hypothesis for the evolution of brood parasitism is that the ancestor of *P. morio*, like silphines, exploited larger carcasses and underwent the shift to parasitism only after the evolution of *Nicrophorus* made this lifestyle possible. Strong support for this hypothesis would be the use of large carcasses for reproduction by at least one of the three extant species of *Ptomascopus*.

One behaviour of adult *P. morio* which benefits its young is clearing the carcass of some carrion fly eggs and/or larvae. This behaviour would prevent the resource from being consumed until a potential *Nicrophorus* host arrived. *Nicrophorus* has several behaviours which are useful in minimizing competition from carrion fly larvae. The removal of hair and pressing the hair against the side walls of the crypt is thought to destroy many eggs (Pukowski, 1933). *Nicrophorus* adults, like *Ptomascopus* and most silphids, will also eat carrion fly larvae. The ability to clear a carcass of carrion fly eggs raises the possibility that *P. morio* benefits its host in some circumstances. In a similar fashion it has been argued that *N. defodiens* Mannerheim sometimes keeps carcasses 'clean' until a larger congener arrives and displaces it (Trumbo, 1990*a*). Brood parasites that sometimes have beneficial effects on their host are known (Rothstein, 1990). Because of the extensive parasitism of *N. concolor* by *P. morio*, it seems doubtful that the net effect of *P. morio* is positive. Most importantly, in cases in which a brood parasite is known to benefit its host, the benefits are conferred by the young and are ongoing. Presumably, any benefit from *P. morio* occurs from adult behaviour before the host arrives. Selection, therefore, would favour a host that accepted the benefit of the parasite and then destroyed the eggs of the parasite. Acceptance of the young of *P. morio* by *Nicrophorus* will possibly be seen as a failure to evolve a mechanism for discriminating against heterospecific young.

Among eusocial insects, social parasites (nest usurpers) are close phylogenetic relatives of their hosts. This is not necessarily true, however, for brood parasitic social insects (Michener, 1944; Wilson, 1971), birds (Payne, 1998) or dung beetles (Cambefort, 1991; Hanski & Cambefort, 1991). A close phylogenetic relationship might facilitate acceptance of parasitic young in host nests (Danforth & Eickwort, 1997), but acceptance occurs among groups not closely related as well.

We hypothesize that *Ptomascopus* spp. may provide clues to the evolution of advanced parental care in *Nicrophorus*. Since parasitic species often lose habits which existed in ancestors (Pamilio & Varvio-Aho, 1981; Carpenter *et al.*, 1993), *P. morio* may be of only limited usefulness in this regard. Since feeding on fly eggs and larvae are common silphid behaviours, a more systematic clearing of fly eggs may have been one of the first behaviours selected after the nicrophorine switch to small resources. It can also be speculated that the release of sex pheromone from a small carcass would evolve early because a small, fresh resource will not always attract potential mates. Study of the two other extant species of *Ptomascopus*, and of similarly basal lineages to or within *Nicrophorus* (e.g. *Eonecrophorus tenuicornis* Kurosawa), is a high priority. Many lineages of bees, wasps and dung beetles have species that appear to represent early stages in the evolution of complex nesting and social behaviour (Michener, 1944; Evans, 1958; Halffter & Edmonds, 1982; Cowan, 1991; Starr, 1991). Comparable species of nicrophorines have yet to be found to enlighten the study of *Nicrophorus*.

Summary

Several lines of evidence support the hypothesis that *P. morio* is a brood parasite of *Nicrophorus* species: (1) the absence of resource preparation or pre-emption in the midst of a competitive carrion community; (2) the absence of behaviours that enhance the fitness of the brood; (3) the clear indication that brood parasitism occurs in the field and laboratory; (4) the pattern of reproductive physiology and behaviour which are consistent with a life history of brood parasitism. Additional study of possible use of large carcasses and of different populations throughout the geographic range is necessary before it can be concluded that *P. morio* is an obligate parasite. We speculate that *Ptomascopus* species were largely replaced ecologically by the more derived *Nicrophorus* group. *Ptomascopus morio* may persist because of its parasitic strategy.

Ptomascopus morio and its hosts are a potential model system for the study of brood parasitism, and its *Nicrophorus* hosts may well be the most adaptable brood parasitic system for study in the laboratory. These easily reared species are highly manipulable as evidenced by the large body of behavioural studies of *Nicrophorus* (Eggert & Müller, 1997; Scott, 1998). Questions that might be addressed include local adaptation to different hosts, regulation of brood size in the presence and absence of a brood parasite, possible benefits that parasites confer upon hosts, the suitability of hosts and parasites for maintaining a phoretic community, and the evolution of signals that parasites use to gain acceptance by their host.

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