Leaping behaviour and responses to moisture and sound in larvae of piophilid carrion flies

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Abstract—Observations suggesting that mature larvae of some carrion flies (Piophilidae) tend to leap off carcasses during rain motivated an investigation of the ontogeny and possible functions of larval leaping behaviour and larval responses to two stimuli associated with rain: moisture and sound. These behaviours were investigated in larvae of *Prochyliza xanthostoma* Walker (Diptera: Piophilidae) by means of laboratory and field observations and experiments. Mature larvae left their feeding substrates (rotting meat) in response to either moisture or rattling sound. The response to moisture was exhibited also by immature larvae. Once on the carcass surface, however, only mature larvae leaped off and pupated in the surrounding soil. The response to sound and the ability to leap only appeared late in larval development and were lost in the prepupal stage. Because rain may facilitate larval locomotion on carcass surfaces, and leaping appears to represent a more rapid and efficient means of leaving a carcass than creeping, these responses may reduce the metabolic costs and predation risks experienced by mature larvae moving to pupation sites in the soil. Thus, the ability to leap and the responses to moisture and sound may represent "ontogenetic adaptations" associated with a brief stage of larval development.

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Résumé—L'observation des larves de certaines mouches de la viande (Piophilidae) a révélé que les larves à maturité ont tendance à sauter en bas des carcasses lorsqu'il pleut, un comportement qui nous a motivés à examiner l'ontogenèse et les avantages possibles du saut ainsi que les réactions des larves à deux stimulus reliés à la pluie, l'humidité et le son. Ces comportements ont été étudiés chez *Prochyliza xanthostoma* Walker (Diptera : Piophilidae) par simple observation et par des expériences en nature et en laboratoire. Les larves à maturité quittent leur substrat alimentaire (viande en décomposition) en réaction à l'humidité ou à des crépitements. Les larves immatures aussi réagissent à l'humidité. Cependant, une fois à la surface de la carcasse, seules les larves à maturité sautent en bas de la carcasse et font leur pupaison dans le sol environnant. La réaction au son et la capacité de sauter n'apparaissent que vers la fin du développement larvaire et disparaissent durant le stade de pré-pupe. Comme la pluie peut faciliter les déplacements des larves à la surface des carcasses et que le saut semble représenter un moyen plus rapide et plus efficace de quitter la carcasse que la reptation, ces réactions peuvent réduire les coûts métaboliques et les risques de prédation reliés aux déplacements des larves à maturité vers le site de leur pupaison dans le sol. Conséquemment, la capacité de sauter et les réactions à l'humidité et au son sont peut-être, en fin de compte, des « adaptations ontogéniques » associées à un développement larvaire de courte durée.

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Introduction

The larvae of some carrion flies (Piophilidae) exhibit several complex behaviours of unknown function. These behaviours appear to be confined to a brief phase of larval life, thus potentially representing "ontogenetic adaptations" (Oppenheim 1980, 1981). Few examples of such transient adaptations are known within the larval or imaginal ontogenies of insects (but see Manning 1967; Sakai *et al.* 1990).

As first described more than three centuries ago (see below) in the synanthropic "cheese skipper" fly *Piophila casei* Linné (Diptera: Piophilidae), piophilid larvae possess the ability to leap (McAlpine 1977). It has been suggested that larval leaping serves to reduce parasitism or predation (Oldroyd 1964: 176), especially during movement from feeding substrates to pupation sites (Maitland 1992). This view is consistent with new observations suggesting that mature piophilid larvae leave feeding substrates during rain and move to pupation sites by creeping and leaping. On carcass surfaces, larvae face the high metabolic costs of creeping locomotion (Berrigan and Lighton 1993) and the risk of predation. Thus, both leaping ability and responses to stimuli associated with rain (*i.e.*, moisture and sound) may represent ontogenetic adaptations associated with larval movement to pupation sites. This hypothesis predicts that these behaviours are lacking in immature larvae, being developed and expressed only in mature larvae (*i.e.*, those ready to pupate), near the time of pupation.

The leaping behaviour of piophilid larvae was apparently first described by Jan Swammerdam (1669), based on his observations of the "cheese skipper" *P. casei* (to which he referred as the "Mite"). Because this excellent work has not been cited since Dufour (1844), part of Swammerdam's description is given below (1669, part II, p 65):

> When this creature intends to take a leap, it first erects itself upon its anus... Immediately after this, the creature bends itself into a circle, and having brought its head...towards its tail, it presently stretches out its two black crooked claws, and directs them to the cavities formed between the two last or hindmost tubercles of the body, where it fixes them in the skin... The Mite having thus made itself ready, contracts its body with such force, that from a circular, it becomes of an oblong form...the contraction extending in a manner to every part of its body. This done, it again reduces itself with so prodigious a force to a straight line, that its claws, which are seated in the mouth, make a very perceivable noise on parting from the skin of the last ring of the body: and thus the Mite, by first violently bending, and afterwards stretching out its body, leaps to a most extraordinary height, if compared with the smallness of the creature... I have indeed seen a Mite, whose length did not exceed the fourth part of an inch, leap out of a box six inches deep, that is, to a height twenty-four times greater than the length of its own body; others leap a great deal higher.

Brief redescriptions of the leaping behaviour of *P. casei* were subsequently published by several other authors (*e.g.*, Redi 1688; Williston 1908: 270; Oldroyd 1964: 176; Chapman 1998: 173). In addition, a similar mode of leaping was recently described and illustrated in the larvae of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) (Maitland 1992); however, the authors of recent works on locomotion in dipteran larvae seem to have been unaware of the older work.

The ontogeny, expression, and possible functions of leaping behaviour and responses to sound and water were investigated in larvae of *Prochyliza xanthostoma* Walker (Diptera: Piophilidae) by means of laboratory and field observations and experiments. The results provide the first evidence of a complex response to sound in dipteran larvae and contribute to the small set of apparent ontogenetic adaptations known within the major life-cycle stages of an insect.

Materials and methods

This work was carried out at the Wildlife Research Station (45°30′N, 78°40′W) in Algonquin Park, Ontario, Canada, from May to August of 1999 and 2000. Adult females (n = 37) of *P. xanthostoma* were captured on a moose carcass and transferred to a 1.5-L population cage containing soil, a sugar cube, and a petri dish (5.3 cm in diameter, 1.2 cm deep) filled with extra-lean ground beef for oviposition. Water was provided through a filter-paper wick immersed through a slit in a closed plastic container filled with water. A second population cage was set up 2 weeks later with additional wild-caught females (n = 17) and a petri dish filled with ground beef. About 6 weeks after the first population cage was set up, the petri dishes from both cages were transferred to plastic cups containing a layer of soil and used in the experiments outlined below. Because females oviposited in each petri dish over a span of several weeks, both petri dishes contained larvae at various stages of development.

To determine whether the ability to leap was present in *P. xanthostoma* larvae throughout their development or only appeared near the time of pupation, larvae of various sizes (about 2–7 mm long) were placed into clean petri dishes and touched repeatedly with fine forceps for up to 2 min. As an index of larval development, larval body width was measured at the widest point using a dissecting microscope fitted with an ocular micrometer. Larval leaping behaviour was observed and photographed under a dissecting microscope using larvae submerged in a shallow layer of water, as recommended by Swammerdam (1669). To determine whether leaping ability is retained in prepupae (larvae in quiescent state), 15 mature larvae were allowed to burrow into soil in each of 3 cups, extracted after 3, 20, and 48 h from cups 1, 2, and 3, respectively, and placed into clean petri dishes. The larvae were then touched with fine forceps for several minutes and their behaviour (leap *versus* no leap) was recorded.

In the laboratory, larval responses to moisture and rattling sound were tested by subjecting *P. xanthostoma* larvae of various degrees of development (all feeding on ground beef in a petri dish) to three combinations of moisture and sound treatments, and counting the number of larvae leaving the petri dish (by leaping or creeping over the edge) in response to each 30-min treatment (see Fig. 2). In the moisture treatment, about 3 mL of water (equal to about 10% of petri-dish volume and enough to saturate its contents) was slowly transferred onto the surface of the ground beef using a pipette. In the sound treatment, a rattle was shaken about 15 cm above the ground beef, taking care not to contact the petri dish or the surface on which it rested. The rattle was designed to approximate the sound of rain and consisted of a petri dish (5.3 cm in diameter, 1.2 cm deep) containing eight stones (about 0.6 cm in diameter). The two halves of the petri dish were attached using a glue gun. When shaken rapidly (about 5 times/s), the rattle produced a sound closely resembling (to the human ear) the sound of heavy rain striking a hard surface. Larvae leaving the meat were collected using moistened forceps and placed into a water-filled petri dish for examination. To determine whether the responses to water and sound persist in prepupae, two treatments were applied to a cup of dry soil into which 88 larvae had burrowed 2 h previously, and 16 additional larvae had burrowed 5 min previously. First, water (20 mL) was added to the cup using a pipette. Second, rattling sound was produced over the soil for 10 min.

In the field, larval behaviour was investigated on two 5-kg pieces of a moose carcass (2–3 months old, consisting of dried skin and flesh on bones) placed about 5 m apart in the forest. Piophilid larvae represent the dominant dipteran fauna inside carcasses at this stage of decomposition (R Bonduriansky, unpublished observation). A test for response to water was conducted by comparing the number of larvae that came to the surface of one carcass piece during 30 min without manipulation with the number that came to the surface during 30 min of slowly pouring water (about 25 L) over the carcass surface. A test for response to sound was conducted by comparing the number of larvae that appeared on the surface of the other (dry) carcass piece during 30 min without manipulation with the number that came to the surface during 30 min of rattling over the carcass without touching its surface. Because this treatment produced no response (see Results), a stronger stimulus was subsequently applied by rubbing a stick over a rough section of the carcass for 30 min.

Larval behaviour was observed with the unaided eye on carcass surfaces. Adult flies reared from larvae collected on carcasses were identified using keys in McAlpine (1977). Voucher specimens of all piophilid species used in this study have been deposited in the University of Guelph Insect Collection. Binomial tests (Zar 1996) for larval response to moisture and sound stimuli compare the number of larvae leaving their feeding substrate during a 30-min treatment with the number of larvae leaving during the preceding 30 min. Because the number of mature larvae in the feeding substrate decreased over the course of each experiment, these tests are conservative.

Results

Leaping behaviour

In the field, during dry conditions, small numbers of larvae (all typically >4 mm long) were usually visible on or near carcass surfaces. Typically, larval creeping movement was slow and leaps resulted in horizontal displacement of <5 cm. Spider webs on or near carcasses usually contained several trapped larvae, and larvae were often observed being devoured by beetles (Staphylinidae) or mites. In contrast, during rain, several hundred larvae (range in length about 2–7 mm) were typically present on the surface of each carcass piece. Small individuals (<4 mm long) tended to wander over the carcass surface without leaving it, but larger larvae (>4 mm long) usually left the carcass by creeping or leaping off. On moist carrion surfaces, creeping locomotion appeared to be faster and leaping larvae often achieved horizontal displacements >20 cm. Leaping behaviour was exhibited by larvae 4–7 mm long. Excavating around carcasses revealed large numbers of prepupae and pupae at a radius of 20–50 cm and a depth of 5–10 cm. Samples of larvae collected while leaping or attempting to leap off carcass pieces during rain (n = 447 larvae) developed into adults of six species of Piophilidae (Diptera): *P. xanthostoma*, *Stearibia nigriceps* (Meigen), *Liopiophila varipes* (Meigen), *Protopiophila latipes* (Meigen), and two undescribed species of *Parapiophila* McAlpine.

Leaping behaviour was investigated further in laboratory-reared larvae of *P. xanthostoma*. Typically, the larva raised the anterior part of its body off the substrate and curved the raised portion downwards while bringing its posterior end forward until the two ends of its body came into contact (Fig. 1*a*). The larva implanted its mouth hooks into the integument of the posterior tip of its body and pulled with its anterior while resisting with its posterior (Fig. 1*b*). After 2–3 s, the resulting tension broke the hold of the mouth hooks on the integument, causing the larva's posterior end to strike the substrate and propelling the larva off the substrate by the force of the recoil (Fig. 1*c*). Leaping resulted in horizontal displacement of up to 0.5 m. If placed on soil immediately after leaving their feeding substrate, some mature larvae burrowed immediately, whereas others performed several leaps before burrowing. If denied access to soil, all mature larvae began to leap within about 5 min of leaving the feeding substrate.

The ability to leap appears to develop relatively late in larval development. In laboratory trials, no larva less than about 4 mm long performed a leap. Of 89 larvae in the mature body length range for *P. xanthostoma* (about 4–7 mm), those that leaped (body

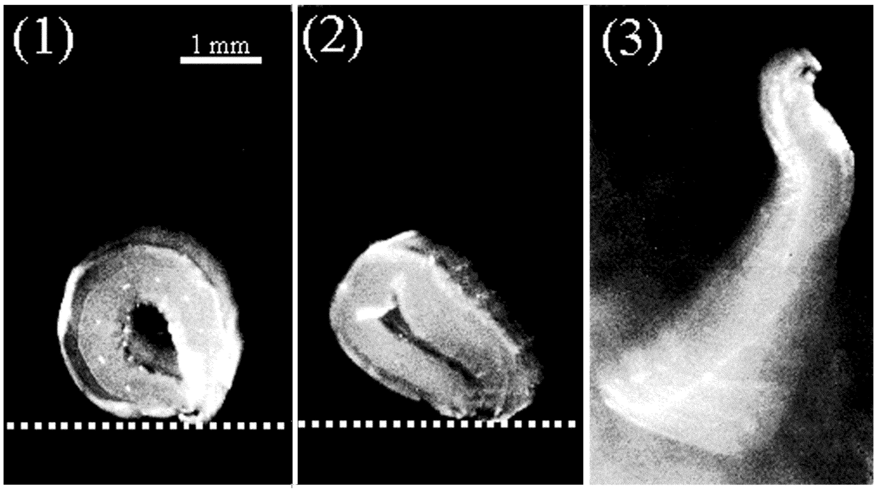

FIGURE 1. Leaping behaviour of the larva of *Prochyliza xanthostoma* photographed through a thin layer of water. Larva is shown grasping its posterior end with its mouth hooks (*a*), pulling with its mouth hooks and tensing its musculature (*b*), and abruptly releasing its grip (*c*) (see text). The arrow indicates the larva's mouth hooks and the broken line represents the typical position of the substrate in relation to the larva as it prepares to leap (*i.e.*, the larva stands on its joined anterior and posterior ends).

width: mean ± SD = 0.82 ± 0.07 mm, $n = 72$) were larger (two-sample t test: $t_{87} = -7.9$, $P < 0.0001$) than those that did not (body width: mean ± SD = 0.66 ± 0.10 mm, $n = 17$). This ability or propensity to leap disappears gradually during the prepupal stage. Of larvae that had been in soil for 3 h, all 15 (100%) performed successful leaps within 2 min. Of larvae that had been in the soil for 20 h, 11/15 (73%) performed successful leaps within 5 min. All 15 of the larvae that had been in soil for 48 h had contracted their bodies into a pupa-like shape and did not leap.

Response to moisture and sound

In laboratory trials, mature larvae left their food medium in response to both moisture and rattling sound (Fig. 2), although sound appeared to elicit a stronger response (Figs. 2*a*, 2*b*). Some immature larvae (*i.e.*, individuals <4 mm long that never attempted to leave the petri dish and eventually burrowed back into the ground beef) came to the surface in response to moisture (with or without rattling), but no immature larvae appeared in response to rattling only. Larvae ceased to respond to water and rattling sound soon after burrowing into the soil; no larvae returned to the surface in response to either stimulus.

In the field, more larvae came to the carcass surface during 30 min of water addition ($n = 100$ larvae, ranging from about 2–7 mm in length) than came to the surface during 30 min without manipulation ($n = 11$ larvae, all >4 mm long) (χ^2 test: $\chi^2_1 = 720$, $P < 0.0001$). Thus, both mature and immature larvae responded to moisture. There was no difference between the number of larvae that came to the surface during 30 min of rattling over the carcass without contacting it ($n = 5$ larvae) and the number that appeared during 30 min without manipulation ($n = 6$ larvae) (χ^2 test: $\chi^2_1 = 0.17$, not significant). In contrast, at least 138 larvae (nearly all >4 mm in length) came to the surface during 30 min of rubbing a stick over the carcass surface (χ^2 test: $\chi^2_1 = 2904$, $P < 0.0001$). Thus, mature larvae did not respond to sounds produced at a distance but responded to

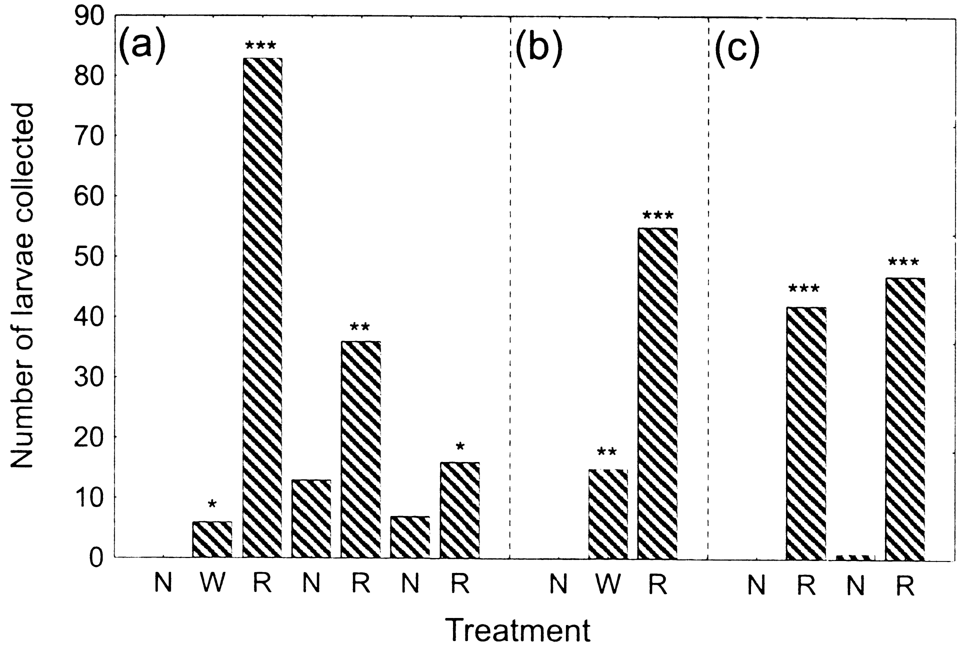

FIGURE 2. Response to water and sound of *Prochyliza xanthostoma* larvae. Bars indicate numbers of larvae that left their feeding substrate by creeping or leaping during 30-min treatments of water addition (W) or rattling sound (R), separated by 30-min intervals without manipulation (N). Treatments were applied in three combinations (Experiments *a*, *b*, and *c*) on different days (binomial tests: one-tailed Z test = 2.45–8.16, $^{*}P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$; see text for further details).

stronger vibrations transmitted to the carcass by direct contact. Immature larvae did not respond to a vibration stimulus.

Discussion

Leaping behaviour

Experiments and observations in the laboratory and field suggest that *P. xanthostoma* larvae acquire the ability to leap as they near maturity and utilize this behaviour during their movement from the feeding substrate (carcasses) to the pupation site (the surrounding soil). Whereas immature larvae lack the ability to leap, mature larvae typically leap off carcasses en route to their pupation sites and gradually become unable to leap after burrowing into the soil.

The ability to leap may serve as a means of escaping rapidly from the carrion surface, where larvae are vulnerable to a variety of predators. This is consistent with Oldroyd's (1964: 176) suggestion that larval leaping represents "a way of getting quickly out of an unfavourable situation, and avoiding a tedious crawl over an exposed surface". Oldroyd (1964: 176) was puzzled, however, by the evolution of this behaviour in piophilids that develop inside solid larval substrates, such as the food pest *P. casei*: "what use is the power to leap inside a ham?". The present study resolves Oldroyd's paradox by showing that larvae acquire the ability to leap shortly before leaving their solid feeding substrate to migrate to pupation sites, as suggested by Maitland (1992) for larvae of *C. capitata*. Although observations suggest that leaping reduces predation risk for larvae, a definitive test of this hypothesis awaits experimental verification.

Aside from speed, a second possible advantage of leaping relative to creeping may be a reduction of the metabolic cost of moving to the site of pupation. Creeping is slow and extremely inefficient compared with walking on legs (Berrigan and Lighton 1993; Berrigan and Pepin 1995). Leaping enables maggots to move much more rapidly (Oldroyd 1964: 176; Maitland 1992), and perhaps at reduced metabolic cost. Maggots lack fine control over the direction or distance of their leaps (R Bonduriansky, personal observation), probably making this mode of locomotion unsuitable for immature larvae, which would risk falling off the carcass and failing to relocate it (see below). It is also likely that very young larvae are physically unable to leap: first-instar larvae of *P. xanthostoma* lack mouth hooks (R Bonduriansky, personal observation), which appear to be essential for leaping (see above). For mature larvae, however, leaping offers a rapid and apparently efficient means of moving radially from the carcass to the surrounding soil.

In this study, leaping behaviour was observed in the larvae of six species of piophilid carrion flies (see Results). This behaviour has also been reported in three other piophilids: the "bone skipper" *Centrophlebomyia furcata* (Fabricius) (Freidberg 1981), the "antler fly" *Protopiophila litigata* Bonduriansky (Bonduriansky 1995), and the "cheese skipper" *P. casei* (see above). The ontogeny and mechanics of this behavioural synapomorphy appear to be highly conserved in piophilid flies (Freidberg 1981; R Bonduriansky, personal observations). In addition to the Piophilidae, larval leaping has been reported in some Clusiidae, Tephritidae, Agromyzidae, and Cecidomyiidae (Oldroyd 1964: 176; Maitland 1992; Chapman 1998: 173). In *C. capitata*, the mechanics of larval leaping (Maitland 1992) appear to be similar to those of the piophilids. Because both Tephritidae and Piophilidae belong to the superfamily Tephritoidea (McAlpine 1989: 1437), larval leaping may represent a synapomorphy of these two families. Whether this trait also occurs in the other (less well-known) families of Tephritoidea remains to be determined. Because these two families are rather distantly related to the Clusiidae and Agromyzidae (superfamily Opomyzoidea) (McAlpine 1989), and all four of these muscomorph families are distantly related to the nematoceran family Cecidomyiidae (McAlpine 1989), larval leaping appears to have evolved independently in at least three lineages of Diptera.

Responses to water and sound

Laboratory and field experiments indicated that both mature and immature larvae come to the surface of their feeding substrate in response to water, and the mature larvae subsequently leap or creep away from the feeding substrate. Mature larvae feeding on ground beef in a petri dish also come to the surface in response to rattling sound produced at a distance, but larvae inside a carcass respond only to vibrations produced by direct contact. This difference probably reflects the difference in density between the soft ground beef used in laboratory trials and the hard carcasses used in field trials. Immature larvae do not respond to sound or vibrations. Both responses disappear once mature larvae burrow into the soil (*i.e.*, become prepupae).

Larval responses to water and rattling sound are consistent with the interpretation that many mature larvae wait for rain inside their feeding substrates before moving to pupation sites. Because larvae appear to creep and leap more rapidly over wet carcass surfaces, rain may reduce the risk of predation (although this hypothesis requires experimental verification). Thus, mature larvae may use moisture and rattling sound (or the vibrations transmitted to carcasses by the impact of rain drops) to detect appropriate weather conditions for the journey to pupation sites. The observation that larvae inside a moose carcass did not respond to rattling at a distance but only to the much stronger vibrations produced by direct contact suggests a relatively high response threshold to this stimulus (corresponding to heavy rain?). This may be adaptive if risk of predation is reduced during heavy rain as a result of faster larval locomotion or decreased predator activity. This explanation is consistent with the relatively weaker response of mature larvae to moisture alone (corresponding to light rain or dew?).

If the above explanation for the response to water is correct, however, it is not clear why the response is present in immature larvae, given that it clearly exposes them to predation risk on the carcass surface. Perhaps immature larvae wander over the carcass surface during rain in search of better feeding patches. Alternatively, the response to water may represent an adaptation to avoid drowning when carcasses are inundated by rain.

A possible alternative explanation for the response to rattling sound is predator avoidance; for example, larvae may benefit by leaving a carcass that is in the process of being devoured by a vertebrate scavenger. This explanation is not consistent, however, with the observed lack of response in immature larvae. It also seems unlikely that larvae would often benefit by leaving a carcass under these circumstances. Carcass disturbance by vertebrate scavengers is probably frequent and unlikely to affect most larvae inside bones, yet mature larvae readily abandoned bones scraped with a stick (see Results).

This study may provide the first evidence of a complex response to sound in dipteran larvae, a discovery that suggests a number of avenues for further investigation into the physiology and functions of larval hearing. Given that the larvae were inside meat or bones, they probably perceived the sound as vibrations transmitted through a solid substrate. The ability to hear and respond to sound conveyed through solid or liquid media may be widespread in insects and other animals (Schmidt-Nielsen 1993: 527–9; also see Hölldobler and Wilson 1995: 51–4). It is not clear whether or not larvae are capable of hearing sounds transmitted through air. Although the hearing mechanism of *P. xanthostoma* larvae is not known, dipteran larvae possess a number of candidate sense organs that may be capable of detecting such vibrations. These include chordotonal organs in the body wall and in the antennal pedicel (Johnston's organ) that may be sensitive to sound (Chapman 1998: 617–21), multipolar neurons in the epidermis that detect physical distortion of the body (Chapman 1998: 631), sense organs associated with the cephalic lobes, and a variety of statocysts (Bullock and Horridge 1965: 1239). It is not known whether piophilid larvae possess a true "ear". The functions served by many larval sense organs are poorly known, perhaps because maggots have been seen as lacking complex behavioural responses amenable to experimental manipulation. The response to sound may offer a useful tool for this type of research.

Finally, if the response to sound represents a piophilid synapomorphy, it may offer an additional tool for biocontrol of the "cheese skipper" *P. casei*. Maggots of this fly infest cheeses and cured meats, and sometimes cause intestinal lesions when ingested (Mote 1914; Wille 1922; Hegazi *et al.* 1978; Costa *et al.* 1986; Rossi and Presciuttini 1996). Because *P. casei* breeds in carcasses in the wild (Rossi and Presciuttini 1996), it is not unreasonable to expect this species to exhibit a similar response to sound. If so, this response could perhaps be used to induce synchronized departure of mature larvae from infested cheese or meat, facilitating their removal.

Ontogenetic adaptations and insect behaviour

Because they represent complex and apparently adaptive behaviours that are expressed only during a brief stage of larval life, both the ability to leap and the response to sound exhibited by mature *P. xanthostoma* larvae fit Oppenheim's (1980, 1981) definition of "ontogenetic adaptations". Although it has long been recognized that selection acts semi-independently on each stage in a complex ontogeny (*e.g.*, Darwin 1868: 75), the ontogenetic adaptation hypothesis extends this idea by proposing that development need not merely represent a linear acquisition of "mature" characteristics, but may also involve the acquisition and loss of transient characteristics representing adaptations confined to particular ontogenetic stages. This seems obvious when considering the striking morphological, behavioural, and ecological transformations involved in the metamorphosis of some insects and amphibians. However, the ontogenetic adaptation hypothesis, which was developed with explicit reference to the more gradual ontogenies of mammals and birds, is equally applicable to the gradual ontogenies within the major life-cycle stages of organisms that undergo complete metamorphosis.

Few examples of ontogenetic adaptations have been identified thus far in larval or imaginal insects, perhaps because their ontogenies have seldom been investigated in sufficient detail. As in vertebrates (*e.g.*, Hoffman *et al.* 1999), the ontogenetic adaptations of insects may be quite subtle. Potential examples include courtship "practicing" by late-instar cricket nymphs (Sakai *et al.* 1990) and age-related changes in female mate-acceptance threshold in adult flies (Manning 1967; Cook 1973; Trabalon and Campan 1984). Larval leaping and response to sound provide particularly clear examples. However, many other age-related changes are known to occur in the physiology and behaviour of insect adults (*e.g.*, Ford *et al.* 1989; Chapman 1998: 239–42, 389) and larvae (*e.g.*, Schwalm 1988: 64–5; Chapman 1998: 365–78), and some of these processes may represent ontogenetic adaptations.

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