

**Female breeding-site preferences and
larval feeding strategies of carrion-breeding
Calliphoridae and Sarcophagidae (Diptera):
a quantitative analysis**

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Abstract

Protection from the elements, predators and parasitoids, and access to food is critical for insect larvae. Therefore, adult female insects are strongly selected to deposit offspring in safe, nutritious locations. Additionally, larvae may move to new feeding sites as food becomes depleted at the natal site. Maggots of carrion-breeding flies exploit patchy resources and are at risk from predators, desiccation and competition. Natural orifices, body folds, fur and feathers are protective locations that provide ready access to food, but their suitability as ovi- or larviposition sites may vary according to the degree of decomposition and presence of other larvae. Accordingly, female preference for ovi- or larviposition sites, and maggot distribution at feeding sites may depend upon carcass condition. We conducted a field experiment to investigate the preferences of female carrion flies for ovi- or larviposition sites on piglet carcasses. We also recorded movement of maggots on carcasses over the first 48 hours after carcass exposure. Females initially preferred to deposit offspring in the mouth; however, this preference changed to the body folds by 24 hours after the carcass exposure. Maggot distribution also changed over time, and the pattern suggested that individuals moved from food-depleted sites to more favourable locations.

Introduction

Adult female insects that breed in patchily distributed resources are under strong selection to deposit offspring in locations that maximise larval survival and growth rates. This is especially true of holometabolous insects because their larvae often possess limited dispersal powers, and may also be defenceless. Numerous studies of many insect taxa provide convincing evidence of host-animal or host-plant selection, and reveal a variety of mechanisms by which ovipositing females make these choices (e.g. Bernays and Weislo 1994; Renwick and Chew 1994; Strand and Peck 1995; Heimpel and Collier 1996; Mayhew 1997; Hopper 1999; Papaj 2000).

Carrion-breeding dipterans (flies) deposit their vulnerable offspring onto patchily distributed carcasses. Although flesh is nutritious, carcasses are risky environments for larvae. Maggots are prone to desiccation, especially during the egg and first larval instars (Erzinçlioglu 1996), and must therefore remain in moist regions of carcasses. Also, carcasses attract many predators, parasitoids and competitors. Beetles, such as silphids and histerids, prey on maggots (Fuller 1934), and many species of ants take large numbers of fly eggs and larvae (Payne 1965; Archer 2002). Additionally, parasitoid wasps, such as chalcids, attack both the egg and larval stages of carrion-breeding flies (Johnston and Tiegs 1921). The effects of competition with other flies may also be detrimental or fatal when high maggot densities remove food quickly and prevent individuals from reaching maximum prepupal size. Competition may therefore cause reduced adult body size, reduced female fecundity, and higher rates of juvenile mortality (Ulyett 1950; Webber 1955).

Selection should therefore favour carrion flies that select larvi- or oviposition sites that provide protection from desiccation and natural enemies, while allowing access to food. Surprisingly few studies have examined this in detail, perhaps because carcasses have been regarded as generally homogenous food resources for developing larvae. Field studies on blow flies (Calliphoridae) and flesh flies (Sarcophagidae) have indicated that most eggs and maggots are deposited in the natural orifices, body folds and fur or feathers of carcasses (Fabre 1919; Putman 1977). It is also known, largely through forensic entomology, that wounds on bodies are favoured sites for larvi- or oviposition (Smith 1986). Additionally, laboratory experiments show that female *Lucilia cuprina* Weidemann (Calliphoridae) preferentially oviposit in crevices or areas where there are large numbers of other eggs (Barton-Browne 1958; Barton-Browne *et al.* 1969), and do not oviposit unless their tarsi are in contact with moisture (Barton-Browne 1962). However, the value of different locations on carcasses may change rapidly as a result of decomposition and larval feeding. Therefore, females may select different oviposition sites according to their suitability for offspring development, rather than having a fixed preference for a particular site.

While females may deposit offspring at sites that are initially favourable, the quality of these sites should diminish as the carcass decays. Therefore, larvae may migrate to more favorable sites when resources become depleted. Typically, maggots feed in dense aggregations in moist, secure locations on carcasses (Deonier 1940; Norris 1964). However, there are no data describing maggot distributions within carcasses, nor is it known whether maggots move to another feeding site if the original site becomes unfavourable.

Calliphorids and sarcophagids are usually the first insects to colonise carcasses, and they rapidly deposit large numbers of offspring (Smith 1986). Ovipositing calliphorids can produce ~200 eggs per cycle (Mackerras 1933), while larvipositing sarcophagids and calliphorids usually produce ~30–50 live larvae per cycle (Mackerras 1933; Knipling 1936). Therefore, large maggot populations may rapidly become established on carcasses. We conducted a field experiment to examine the patterns of larviposition and oviposition preferences of carrion-feeding flies. In particular, we censused the number and location of feeding maggots 24 and 48 h after carcass exposure.

Methods

Carcass placement and study site

The study took place in the Coranderrk Bushland (37°40'59"S, 145°31'07"E), a damp sclerophyll forest dominated by the Myrtaceae species *Eucalyptus cephalocarpa* (silverleaf stringybark), *E. aromaphloia* (scent-bark), *E. obliqua* (messmate stringybark), and the Rubiaceae species *Coprosma quadrifida* (prickly currant bush).

Ten fresh, stillborn piglets with no external injuries were placed at least 50 m apart at 0900 hours on 21 February 2000. Differences between microclimates were minimised by placing carcasses on the west sides of mature trees. Carcasses were enclosed in scavenger-proof Weldmesh™ carcass cages (25-mm mesh), which prevented disturbance by scavengers. Daily temperature and rainfall data were recorded with a Davis Weather Wizard II weather station located approximately 1 km from Picaninny Swamp.

Carcass dissection and maggot collection

Five carcasses were randomly selected for dissection and maggot removal 24 h after placement, and the remaining carcasses were dissected on the following day, 48 h after placement. All carcasses were examined externally 24 and 48 h after they were placed in the field. The appearance and odour of each carcass were described, and any invertebrates visibly associated with each carcass were censused. Then, the five carcasses pre-selected for dissection were treated in turn.

Each dissected carcass was thoroughly examined both externally and internally for maggots and their feeding sites. All of the maggots located from each of the following body points were collected separately:

'eyes', 'ears', 'mouth', 'nostrils/nasal passages', 'anus', and 'body folds' (the areas in the creases of the body and between the legs). Maggots were prepared in the larval fixative KAA, which prevents discolouration after death and thus allows assessment of instar. The maggots were transferred to 80% ethanol, after preparation in KAA for 2 h, and later allocated into instars. Eggs were also collected from each site and placed in 80% ethanol. The remaining five carcasses were treated in the same way the following day, 48 h after placement.

Piglets were dissected in the following manner. The carcass was placed on a plastic sheet and beheaded. The ears were examined first, and maggots were collected from the pinna. The ear canal was then opened and any maggots were removed. Collections were then made from the eyes, and the eyelids were pulled back to allow examination of the eyeball. The eyeballs were then cut out to expose the flesh of the eye socket. The heads were handled very carefully during this procedure to ensure that no maggots were displaced from the mouth before they were collected.

Maggots were removed next from the mouth, and the cheeks were cut diagonally, and the jaws of the piglet were pulled apart. This facilitated collection of most remaining maggots and closer examination of feeding damage. The extent of infestation of maggots in the mouth made it impossible to collect all individuals, and therefore about 95% of the maggots were removed from the mouths of piglets.

The nasal sinuses and brain case were dissected next. The snout was split longitudinally to allow examination of the nasal passages, and the brain case was opened and the brain inspected. Finally, the body was examined, and maggots infesting the body folds were collected. Maggots were also collected from the anus, and a scalpel was used to open the rectum to remove maggots from inside.

Data analysis

The eggs and maggots collected were assigned to one of two categories: 'young', which included eggs, first-instar maggots, and larvae transitional between the first and second larval instars; and, 'old', which included second and third larval instar maggots, and larvae transitional between the second and third instars. It was assumed that the collection site of 'young' offspring reflects their mother's larval- or oviposition preference because eggs are immobile, and newly-hatched larvae tend to remain close to their hatching site for about 8–10 h (Kamal 1958). We have seen young larvae migrating over carcasses during rainfall; however, there was no rain during this experiment. We have only once observed first instars attempt to move across dry skin; all desiccated and died within minutes, and no maggot travelled further than 3 cm.

In contrast, the site of collection of 'old' larvae is assumed to reflect larval preferences because it is quite common to see second and third instars moving between different areas of a carcass (personal observation).

Larvae were identified only as calliphorid or sarcophagid, and eggs were identified only as calliphorid. However, we did not record relative numbers of maggots from these families at different piglets and body points since analysis of individual family's (and indeed species') reproductive strategies is beyond the scope of this study. Data were visually inspected for normality, log-transformed where appropriate, and analysed using Systat 7.

Results

Weather

The mean temperature on the day piglets were placed in the field was 25.1°C (range 17.8–34.8°C). On 22 February, when 24-h piglets were dissected, the mean temperature was 20.6°C (range 17.9–23.9°C), and on 23 February, when the 48-h piglets were dissected, the mean temperature was 21.8°C (range 18.6–26.8°C). There was no rainfall throughout the experiment.

Dissections

Dissections of all piglets took 6 h, commencing at 0900 hours on both days. Therefore, the carcasses dissected after 24 h were exposed for 27 ± 3 h, and those dissected after 48 h were exposed for 51 ± 3 h. For simplicity, these times are referred to as 24 and 48 h.

Invertebrates present and external appearance of carcasses

After 24 h the carcasses appeared mostly fresh, and were odourless. All piglets had large infestations of calliphorid maggots, and there were areas of swollen, discoloured flesh

Table 1. Insects other than maggots observed on carcasses at 24 and 48 hours, as well as the numbers of carcasses visited and the estimated numbers present on carcasses

Insect taxa (adults)	Role on carcass	Carcasses (<i>n</i> = 5)		Estimated population	
		24 h	48 h	24 h	48 h
Hymenoptera					
Formicidae					
<i>Crematogaster</i> sp.	Take flesh and maggots	3	3	10–100	2–20
<i>Anonychomyrma</i> sp.	Take flesh and maggots	0	1	0	<100
Vespidae					
<i>Vespula germanica</i>	Takes flesh and adult calliphorids	3	2	1–3	1–10
Coleoptera					
Silphidae					
<i>Ptomaphila lacrymosa</i>	Takes flesh and maggots	0	1	0	1
Diptera					
Calliphoridae					
<i>Calliphora augur</i>	Larviposits	5	5	10–20	10–20
<i>C. hilli</i> / <i>C. stygia</i> ^A	Larviposits / oviposits	5	5	10–50	10–20
<i>Chrysomya varipes</i>	Oviposits	0	3	0	2–20
<i>Ch. rufifacies</i>	Oviposits	0	1	0	20

^ASince *C. hilli* and *C. stygia* cannot reliably be distinguished in the field, these species are combined here.

around the mouth as a result of intense maggot feeding. Ants of the genus *Crematogaster* (Formicidae) and European wasps, *Vespula germanica* Fabricius (Vespidae) were seen on several carcasses (Table 1), and species of *Calliphora* (Calliphoridae) that breed in fresh carrion were present at all carcasses (Table 1).

After 48 h, the carcasses were entering putrefaction and had developed a decay odour; two were also bloating. Areas of the head and neck of three piglets, including the two that were bloating, displayed green skin discolouration. Ants of the genera *Anonychomyrma* and *Crematogaster*, as well as *V. germanica* were present at some piglets, and there was also a *Ptomaphila lacrymosa* Schreib (Silphidae) adult present at one carcass (Table 1). There were blow flies of the same species as those present on the piglets exposed for 24 h, together with two species of *Chrysomya* (Calliphoridae) that usually oviposit at the beginning of putrefaction (Table 1).

Feeding and infestation patterns

The carcasses were heavily infested with maggots after 24 h exposure, although the mouth and body folds were the only sites that were consistently colonised (Table 2). Maggots fed in dense masses and by 48 h exposure almost all had moved from the site of offspring deposition further into the carcass. Feeding *V. germanica* had made a shallow hole in the skin of one piglet after 24 h. This hole, approximately 30 mm long, 10 mm wide and 3 mm deep, was located on the dorsal surface behind the shoulder. Although it contained a small number of maggots, this feeding site was present on only one piglet, and was not considered in analyses.

The mean numbers of 'young' offspring (eggs, first-instar, transitional first to second instar maggots) collected from different body sites was influenced by an interaction between carcass exposure time and body site ($F_{5,48} = 3.0$, $P < 0.05$). Overall, the body folds contained the highest mean number of 'young' offspring after both 24 and 48 h exposure,

Table 2. Number of piglets with maggot infestations at each body point at both 24 and 48 hours after exposure
n = 5

Body point	No. of piglets with infestations	
	24 h	48 h
Mouth	5	5
Ear	4	4
Eye	1	5
Nostrils	4	0
Folds of body	5	5
Anus	4	5
Brain case	0	0

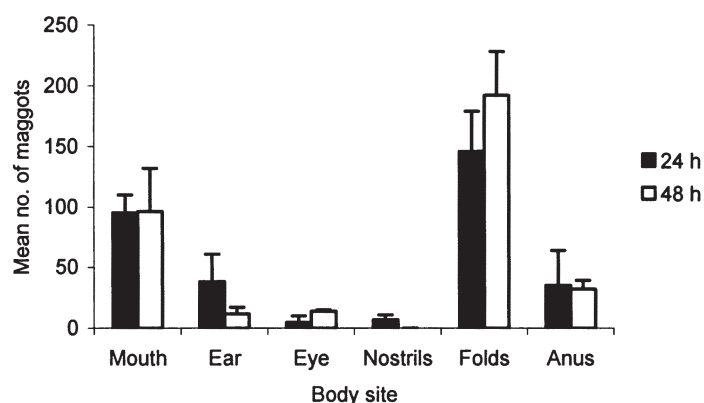


Fig. 1. Number of eggs and maggots in the first instar and transitional first to second instar at each body point of piglet carcasses (*n* = 5) exposed for 24 and 48 h. Values are means \pm s.e.

with the mouth containing the next highest mean number. However, the mouth was the initial preferred offspring deposition site because ~80–100% of ‘old’ maggots were collected from the mouths of piglets dissected after 24 h, and these represented the maggots that were deposited live in the earliest stages of carcass colonisation. After 24 h exposure, the third highest mean ‘young’ offspring population was collected from the ear, followed by the anus, nostrils and eyes (Fig. 1). After 48 h exposure, the anus contained the third highest number of ‘young’ offspring followed by the eye and ear. There were no ‘young’ offspring present in the nostrils after 48 h exposure (Fig. 1).

The mean numbers of ‘old’ maggots (second-instar, transitional second to third-instar and third-instar maggots) collected from each body site was also influenced by an interaction between carcass exposure time and body site ($F_{5,48} = 2.72$, $P < 0.05$). The greatest mean number of ‘old’ maggots at both exposure times was located in the mouth. The second highest mean number of ‘old’ maggots collected after 24 h exposure was located in the ear, followed by the body folds, anus, nostrils and eyes (Fig. 2). In contrast, after 48 h, the second highest mean number of ‘old’ maggots collected was from the body folds, followed by the eye, ear and anus. No ‘old’ maggots were located in the nostrils after 48 h exposure (Fig. 2).

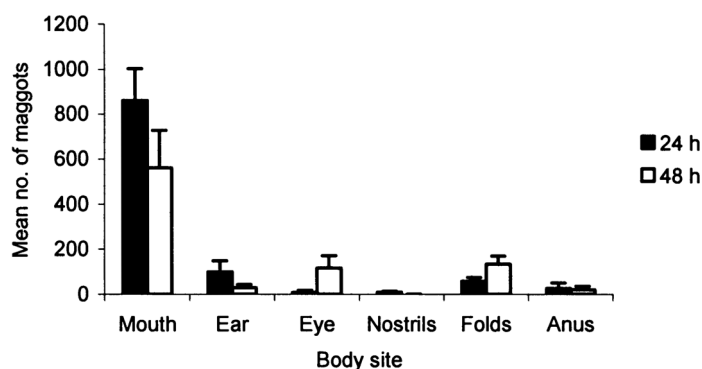


Fig. 2. Number of maggots in the second, third, and transitional second to third instars at each body point of piglet carcasses ($n = 5$) exposed for 24 and 48 h. Values are means \pm s.e.

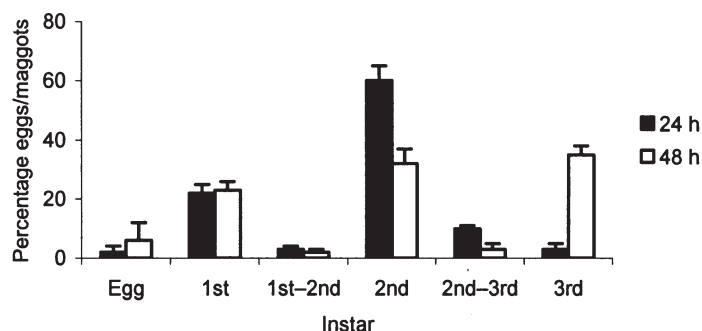


Fig. 3. Percentages of eggs and maggots in each instar present on piglet carcasses ($n = 5$) exposed for 24 and 48 h. Values are means \pm s.e.

Most of the flesh had been stripped from the mouth after 48 h exposure, and although many maggots were still feeding, others began to migrate through the flesh to other regions of the head. The increase in the numbers of 'old' maggots feeding in the eyes was largely due to this migration, and dissection revealed that feeding maggots had moved from the mouth through the cheek muscle, and under the bones of the eye socket. Some may also have moved along the undersurface of the carcass.

Infestations in the anus were always less than 20 mm deep, and this was probably due to the constricted nature of the orifice as well as blockage by faecal matter. Most maggots infesting the body folds were also unable to access the flesh for the first 24 h because they could not penetrate the skin. However, holes appeared in the moist chest and belly skin between the legs after 48 h and these provided some access points.

Age class structure over 24 and 48 hours

For each piglet, the number of offspring in each age class was converted to a percentage of the total offspring on the carcass. Mann-Whitney U tests revealed no significant difference between exposure times in the median percentages of eggs ($U = 12$, $P > 0.5$), first-instar larvae ($U = 8$, $P > 0.3$), and larvae transitional between the first and second instars ($U = 15$, $P > 0.5$) that were found on piglets (Fig. 3). However, there was a significantly lower

percentage of second-instar larvae ($U = 25$, $P < 0.05$) and larvae transitional between the second and third instars ($U = 22$, $P < 0.05$) present on piglets exposed for 48 h (Fig. 3). In contrast, there was a significantly higher percentage of third-instar maggots present on piglets after 48 h ($U = 0$, $P < 0.005$) (Fig. 3).

Discussion

The results suggest that female carrion flies select particular sites on the carcass where they will deposit offspring. Furthermore, their site preferences change with the length of time the carcass is exposed to the elements. This change in site preference probably reflects changes in the carcass resulting from decomposition and maggot feeding. Thus, gravid blow flies and flesh flies apparently assess carcasses in order to locate the most suitable feeding site for their offspring.

Alternatively, differential predation at body points may have been responsible for differences in mean numbers of maggots present at body points. However, this is unlikely because ants, the main predators in this study, usually concentrate their numbers at sites where the largest numbers of maggots are present (personal observation), and would therefore have taken fewer maggots from body points with small masses. More ants are attracted to heavily populated areas, especially the mouth (personal observation), because high prey density presumably increases their foraging efficiency. Indeed, for many ant species, the numbers of workers recruited to food sources are proportional to the amount of food present (Hölldobler and Wilson 1990).

It is likely that site selection by female blow flies and flesh flies is most important in the spring and summer when decomposition progresses rapidly and there are many predators, parasites and competitors present. Most larvi- and oviposition also seems to occur in the orifices and body folds in the winter and autumn (personal observation), but site preferences may differ in these seasons.

Females may prefer body points that maximise the chance of larval survival by providing the greatest amount of food, protection and space. The ears, eyes, nostrils and anus, in which few maggots and eggs were deposited, are small and constricted. Their entrances, which maggots must occupy in order to receive oxygen, are easily overcrowded and offer little food. Larger orifices, such as the mouth, offer much food and protection, as well as sufficient area to permit the formation of large maggot masses. Larger masses produce more heat, and thus speed growth (personal observation). Maggot masses examined here filled orifices to capacity, and therefore orifice size is possibly a critical factor in female ovi- and larviposition choice.

However, female preference for particular orifices may be transferred as the value of favourable sites reduces over time. The mouth was the initial preferred site since the most old larvae were found here after 24 h. It is the largest and most protective body orifice, and gives immediate access to flesh. However, after 24 h exposure, breeding-site preference was transferred to the moist, secure body folds since larger numbers of young larvae were found there. There is no immediate access to flesh in the body folds, and maggots did not begin penetrating the skin until 48 h after exposure. Thus, first- and early second-instar maggots are probably able to gain adequate nutrition from the skin surface by softening it with digestive enzymes and causing body fluids to leak. However, it is possible that they suffer a slightly reduced growth rate in comparison to maggots with direct access to flesh.

Although the mechanisms that allow site selection by the flies censused in this study are not known they are likely to be chemical and mechanical in nature. Females can frequently be observed walking over carcasses, probing with their labellae and ovipositors (personal

observation), and it is probable that they are examining the carcass for a suitable breeding site. The presence of water, egg masses of other females, and albuminous protein are known to stimulate oviposition in blow flies (Barton-Browne 1958, 1962; Erzinçlioglu 1996), and microbial products associated with feeding maggots also exert an attractive effect on gravid *L. cuprina* (Eisemann and Rice 1987).

Additionally, the presence of crevices in the oviposition medium, which are detected with the ovipositor, stimulate oviposition by blow flies (Barton Browne 1958). An ovipositing female may also gain information about the quality of an oviposition site, such as its surface area. For example, spatial information is collected by female gall midges, *Giraudiella inclusa* (Diptera: Cecidomyiidae), which lay more eggs on thicker grass shoots. Before laying, females probe the circumference of the shoot with their ovipositor, and it is thought that this enables them to gauge shoot diameter (Tscharncke 1988).

Other cues in site selection for larvi- or oviposition may be used by females, and these may mediate the apparently changing site preferences of the female flies in this study. Probing potential larvi- or oviposition sites may reveal to female blow flies the extent of maggot feeding that has already occurred there, and therefore whether food at the site is likely to be exhausted. Contact with maggots, or detection of heat produced by them, may also allow the female to assess larval density, and therefore crowding. Female treehole mosquitoes, *Aedes triseriatus* (Diptera: Culicidae) adjust their oviposition behaviour in accordance with the density of larvae already present in flooded tree holes. Early in the season, when eggs are likely to hatch, fewer females breed in artificial hollows with higher larval densities. Later in the season, however, when eggs are likely to enter diapause, more females oviposit in experimental hollows with higher numbers of larvae present, possibly because higher larval densities indicate to them that the water source is more permanent (Edgerly *et al.* 1998).

It would also benefit female carrion flies to assess predation pressure at a particular site, for example the presence of ants or parasitoids. The mosquito *Culiseta longiareolata* (Diptera: Culicidae) makes this type of assessment; it is less likely to oviposit in pools where predatory dragonfly nymphs, *Anax imperator* (Odonata) are present (Stav *et al.* 1999). When female carrion flies land at a potential larvi- or oviposition site that is ant infested, they are often driven away by attacking ants; however, it is not known whether they are less likely to deposit offspring at a particular site due to the presence of maggot predators and parasites.

The distribution of 'old' maggots on the carcass changed with time after exposure, and this change appears to reflect maggot migration to new areas as food at their natal site became depleted. 'Young' maggots were recruited onto the carcass at similar rates both 24 and 48 h after exposure; therefore the continuous appearance of competitors and the presence of established larvae would cause sites initially favoured by gravid females to become overcrowded and/or food depleted. After 48 h, changes in the mean populations of maggots at the body points indicated net emigration of maggots from the mouth, which was the most crowded body point, and from the ears and nostrils, which probably contained little food. There was net immigration into the body folds, which offered access to body cavities by the end of 48 h, and into the eyes, which had previously contained low mean maggot populations.

Our findings are of some additional interest forensically. It is essential that forensic entomologists possess a general understanding of the mechanisms by which calliphorids and sarcophagids colonise bodies, since it is maggots from these families that are most frequently used to make estimates of the time of death. If a discrete maggot mass is present

on a body in an unexpected area, such as the forearms, this may indicate that flesh trauma occurred before death at this location. It is then assumed that larvi- or oviposition occurred at this site because it was attractive to females. Significantly, we found that maggot feeding sites were not initiated in undamaged skin in exposed areas, although maggots eventually produced holes in skin at body folds. We also found that females deposited offspring only at sites where there is food and protection for them, and injuries such as lacerations or incised wounds fulfil these criteria. However, little is known about how the presence of flesh trauma affects patterns of female larvi- or oviposition choice.

The piglets used here represent only one example of the range of carrion encountered by calliphorids and sarcophagids. Some factors, apart from flesh trauma, that influence carcass colonisation and decomposition rates are habitat (Hanski 1976, Smith 1986), carcass size, and carcass taxon (Coe 1978; Kneidel 1984; Wells and Greenberg 1994). Additionally, body covering, such as fur, as well as body orientation potentially affect oviposition and maggot migration. However, these results indicate that choice of breeding and feeding sites are flexible, and that females can assess the most favourable site available, while maggots will migrate to more favourable feeding sites if food at the natal site becomes depleted.

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