Blowfly succession from possum (*Trichosurus vulpecula*) carrion in a sheep-farming zone

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Abstract. The significance of brushtail possum, *Trichosurus vulpecula* Kerr (Diprotodontia: Phalangeridae) carcasses to the succession and production of Diptera species and its relevance to fly strike management in Tasmania, Australia was examined. *Calliphora stygia* (Fabricius), *Lucilia sericata* (Meigen) and *Calliphora vicina* Robineau–Desvoidy (Diptera: Calliphoridae) were found to be the most abundant and *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) always the least abundant (< 1%) of the putative primary fly invading species to emerge. Carcasses that were left for up to 15 days in the field before being exposed to flies for 2 days also acted as breeding sites for large numbers of all primary fly species, with the exception of *L. cuprina*. Ordination analysis revealed no relationship between possum carcasses according to their length of exposure but did show significant negative associations between the number of putative secondary invaders (*Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae), *Chrysomya varipes* (Macquart) (Diptera: Calliphoridae) and putative tertiary flies (*Hydrotaea rostrata* Robineau–Desvoidy (Diptera: Muscidae)) to the number of *C. vicina* or *C. stygia* to emerge. There was enormous variability in the numbers of secondary/tertiary fly species to emerge from carcasses (0–11 450) that negatively correlated with the proportion of all flies to emerge that were primary, and with the mean size of adult *L. sericata*. Although carcass temperatures, especially those with a large larval population, were elevated, this did not appear to result in significant pre-adult fly mortality. The most important primary fly strike species *L. cuprina* was only found in insignificant numbers, whereas three other members of the fly strike fauna *C. stygia*, *L. sericata* and *Ch. rufifacies* did use possum carrion as an important breeding resource, but left implications for fly strike management inconclusive.

Key words. *Lucilia cuprina*, *Lucilia sericata*, *Chrysomya rufifacies*, *Calliphora vicina*, *Calliphora stygia* Calliphoridae, competition, fly strike, possum carrion, sheep, Tasmania.

Introduction

Vertebrate carcasses are a common breeding site for blowflies (Calliphoridae) and are a focus of strong competition among the fly larvae within them for the available resources (Norris, 1965; Denno & Cothran, 1975). Larval densities may be high enough to result in the consumption of entire carcasses (Hanski & Kausela, 1977; Hanski, 1987). Despite competition, up to 10 carrion fly species have been found to coexist in a carcass (Kneidel, 1984; Tantawi et al., 1996). Subtle niche differences may allow this coexistence. One such difference may involve temporal separation, described as fly succession within a carcass (Denno & Cothran, 1975; O’Flynn, 1983; Wells & Greenberg, 1994). In relation to this succession, carrion flies are often defined as
primary, secondary or tertiary depending on their sequence of arrival. Pioneer or primary colonizers of carrion may experience less intense interspecific competition than species that arrive later and, to compensate, secondary and tertiary species require an advantage over those already in residence (Lane, 1975).

Lucilia cuprina (Wiedemann) is considered the most economically important species in the fly strike of sheep in Australia and in several other countries, including New Zealand and South Africa (Anderson & Simpson, 1991). Few, if any, L. cuprina have been found to develop into adults from vertebrate carcasses in the semi-arid and arid regions of mainland Australia (O’Sullivan et al., 1983; Anderson et al., 1988; Cook et al., 1995). Factors that severely limit the production of L. cuprina in carrion may include the presence of the predatory larvae of Chrysomya rufifacies (Macquart), considered a secondary fly (Waterhouse, 1947), and the greater competitiveness of other species of calliphorid larvae (Mackerras, 1936). However, C. rufifacies has not been recorded in the south of Tasmania (McQuillan et al., 1983), and laboratory studies suggest that in Tasmania L. cuprina larvae should be successful competitors in carcasses that have temperatures elevated > 30 °C (Williams & Richardson, 1984). Furthermore, in south-eastern mainland Australia, a greater emergence of L. cuprina from sheep carcasses exposed during late autumn was observed, compared with carcasses exposed during the summer months (Barton, 1982). These studies suggest that carrion may provide a significant resource for the maintenance of L. cuprina populations in Tasmania.

As a result of the predominance of L. cuprina in fly strike of sheep in Australia, management strategies have focused on control of this species. This approach is justified in the semi-arid and arid areas of mainland Australia (McQuillan et al., 1983) and Watts et al. (1976) confirmed the predominance of L. cuprina in Tasmania, with its involvement in 50–79% of single species strikes. However, Watts et al. (1976) also noted that Lucilia sericata and Calliphora stygia were found in 32% and 18% of all mixed species strikes, respectively, whereas McQuillan et al. (1983) also found C. stygia to initiate up to 14% of all single species strikes. Thus, some management strategies may be better directed at reducing field populations of all strike-initiating calliphorid species.

The aim of the present study therefore was to examine the composition of flies breeding in brushtail possum (Trichosurus vulpecula) carcasses in Tasmania. Brushtail possum populations are culled for crop protection in Tasmania; an estimated 190,000 possums were killed during 1998/1999 (Hocking, 1999). This abundance of possum carrion represents a major resource for potential exploitation by fly strike species. To further understand the succession of flies exploiting this resource, the time after death when possum carcasses were available for oviposition was manipulated. By doing this we aimed to exclude putative secondary and tertiary fly species, and to enhance the probability of successful emergence of L. cuprina from the carrion resource.

Materials and methods

A sheep property 10 km north-east of Hobart in the south of Tasmania (42°48′S, 147°25′E, 10–20 m a.s.l.), of 340 ha carrying approximately 300 Merino ewes, was selected. Twelve possums with a mean weight (± standard error [SE]) of 3.5 ± 0.1 kg were killed by a single gunshot wound to the head, and were immediately stored in airtight plastic bags. They were allocated randomly to one of four areas (blocks) within the property, and then assigned to one of three independent sites within that block. Sites within a block were approximately 200 m apart. To maintain uniformity, sites were chosen from the most homogeneous sheep grazing land available. Selected carcasses were positioned at each site within 12 h of death. The experiment was conducted from 9 April 2000 (mid-autumn) and dismantled on 20 November 2000 (late spring) after over-wintering flies had emerged.

Each possum carcass was placed on 10 cm of sieved coarse sand in a 55 × 36.5 × 21-cm polystyrene packaging box. To allow rainwater drainage, four 1-cm diameter holes covered with aluminium insect exclusion mesh were positioned in the base of each. To prevent the loss of wandering-stage larvae, a 3-cm inward facing rim was located at the top and perpendicular to the box sides. To prevent predation and interference from vertebrates, protective cages were placed over the boxes.

In blocks 1–3, nine carcasses were available for immediate oviposition from the initial placement of the carcass in the field. However, in each block oviposition was precluded after 2, 5 and 15 days, respectively, by enclosing the possum cage within an insect emergence net. Thus, in each of the three blocks, one possum carcass was available for oviposition at day 0 and unavailable after day 2, one was available for oviposition at day 0 and unavailable after day 5, and one was available for oviposition at day 0 and unavailable after day 15.

Oviposition was possible in possum carcasses in block 4 for 2 days only following staggered time intervals. Oviposition was precluded for a 2-, 5- or 15-day interval, and then allowed for 2 days, before the box was again covered with netting. By doing this one possum carcass each was available for oviposition at day 2, and unavailable after day 4, one was available for oviposition at day 5 and unavailable after day 7, and one was available for oviposition at day 15 and unavailable after day 17.

At all sites, insect emergence nets were used that sealed at the bottom around the box base and at the top to a circular 3.2-L clear plastic fly trap container positioned 1 m above ground level. Fly trap containers were emptied weekly, with flies stored at –20 °C until identification.

Possum core temperatures were monitored using probes positioned 5 cm into the chest cavity of all carcasses in blocks 3 and 4. The carcass in block 4 not exposed to flies for 15 days acted as a control for that time interval. An ambient temperature data logger was positioned 1 m above ground level in an upturned 5-L white plastic container to shelter the logger from direct sunlight and wind, within 1 m of one carcass site at block 4. Both ambient and possum core temperatures were recorded at 1-h intervals.

The species composition of adult flies at the property was assessed using a total of three wind-orientated fly traps (Vogt et al., 1985) opened at blocks 1, 2 and 3 within 24 h of setting out carcasses. Fly traps were located approximately 100 m from the central possum carcass within a block. Trap heights were standardized to 1 m above ground level. Fly trap baits comprised
25 g of minced sheep liver, 50 mL of cattle dung (frozen for 2 weeks prior to bait preparation) and 1.5% w/v sodium sulphide solution. Fly traps remained open for the first 12-h period after carcass exposure from 07.00 hours.

All flies that emerged from possum carcasses were identified to species, and, with the exception of Chrysomya varipes and Hydrotaea rostrata, sexed. An index of the size of emerging L. sericata was established by measuring the posterior cross-vein between the fourth and fifth longitudinal veins of the left wing of a random sample of 15 males and 15 females to the nearest 0.01 mm (Smith & Wall, 1997a). The sex ratio of fly species to emerge from carcasses was considered only for carcasses where at least 30 flies of that species emerged.

Two split-plot ANOVA analyses were performed on the possums in blocks 1–3, with whole plots being defined as carcasses and subplots being defined as species within carcasses in the first ANOVA, and sex of the fly in the second ANOVA. The first ANOVA investigated how the number of flies (log$_{10}$ transformed) varied according to exposure time and species of fly. Initially, both a block term and a covariate for weight of carcass were included in the model. However, both the covariate and block term were then removed from the model as the former was not significant at the $P = 0.1$ level and the latter did not explain any more variation of the random noise. The second split-plot analysis investigated how the average size of L. sericata varied according to exposure time and sex of the fly. Initially, both a block term and a covariate for the number of secondary/tertiary (log$_{10}$ transformed) were included in the model. The covariate was transformed, as a plot of the average size vs. the untransformed number of secondary/tertiary flies did not appear anywhere near as linear as the plot of average size vs. the transformed number. Once again the block term was removed from the model as it did not explain much variation in the outcome. In both cases residual plots were inspected for departures from the assumptions of the ANOVA method.

Finally, to better understand the interactions between the fly species, the abundance of each fly species was ordinated using semistrong hybrid multidimensional scaling with the computer program PATN (Belbin, 1993). The fly species that were significant describers of the variation in fly emergence from carcasses ($P < 0.05$) were fitted to the ordination plot as vectors.

### Results

Lucilia cuprina and L. sericata were the only species of fly caught in the wind-orientated traps during the first day of carcass exposure. Both species were present in low numbers, L. sericata averaging (SE) 4.7 ± 0.7 and L. cuprina 2.3 ± 1.9 flies per trap with no significant difference between the number of either species caught ($t$-test: $t = 1.07, P = 0.40$). Eight species of fly emerged from carcasses; the putative primary species Calliphora hilli Patton, C. stygia, Calliphora vicina, L. cuprina, L. sericata, the putative secondary species Ch. ruffiacies, Ch. varipes and the putative tertiary species H. rostrata (Table 1). Lucilia sericata was the only species to emerge from all 12 carcasses, with C. stygia and H. rostrata each emerging from 11 of the 12 carcasses. Prevention of access to carcasses for more than the first 2 days excluded the secondary flies Ch. ruffiacies and Ch. varipes, with the exception of one carcass where 10 Ch. ruffiacies emerged. The putative tertiary species H. rostrata was found to oviposit on fresh carcasses within the first 2 days of exposure.

The total number of flies to emerge from a carcass varied from 102 to 11 472 flies per carcass and did not vary according to exposure time ($F_{2,6} = 0.83, P = 0.43$) (Table 1). Furthermore, although the number of species did not change with exposure time ($F_{3,142} = 1.27, P = 0.27$) there were significant differences between species ($F_{7,142} = 4.96, P < 0.001$). Despite the presence of L. cuprina in the fly traps, it emerged infrequently from carcasses of any age. Furthermore, on the six occasions when L. cuprina was present in carcasses, it was the least abundant species to emerge. Among the five primary fly species, the most abundant to emerge were L. sericata (six carcasses), C. stygia (four carcasses) and C. vicina (two carcasses). Only the secondary species exceeded 1000 flies emerging.

The three carcasses that were left for 2, 5 or 15 days in the field before exposure to flies for 2 days attracted and reared significant numbers of all primary species, with the exception of L. cuprina. In the 2- and 5-day-old carcasses collectively, more secondary and tertiary flies emerged than primary flies. The carcass left for 15 days in the field prior to exposure attracted no secondary flies.

The proportion of primary flies to emerge from a carcass varied between 0.2% and 100% of the total fauna and was

### Table 1. The species total of carrion flies emerging from possum carcasses available for oviposition for the first 2 (0–2), 5 (0–5) and 15 (0–15) days, and for 2 days from days 2–4, 5–7 and 15–17.

<table>
<thead>
<tr>
<th>Exposure day</th>
<th>0–2</th>
<th>0–5</th>
<th>0–15</th>
<th>2–4</th>
<th>5–7</th>
<th>15–17</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Lucilia cuprina</td>
<td>6</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Lucilia sericata</td>
<td>287</td>
<td>307</td>
<td>74</td>
<td>287</td>
<td>22</td>
<td>136</td>
</tr>
<tr>
<td>Calliphora hilli</td>
<td>30</td>
<td>37</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>Calliphora stygia</td>
<td>452</td>
<td>48</td>
<td>19</td>
<td>200</td>
<td>–</td>
<td>48</td>
</tr>
<tr>
<td>Calliphora vicina</td>
<td>376</td>
<td>242</td>
<td>8</td>
<td>296</td>
<td>–</td>
<td>21</td>
</tr>
<tr>
<td>Chrysomya ruffiacies</td>
<td>10</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>6501</td>
<td>339</td>
</tr>
<tr>
<td>Chrysomya varipes</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2963</td>
<td>6</td>
</tr>
<tr>
<td>Hydrotaea rostrata</td>
<td>487</td>
<td>13</td>
<td>5</td>
<td>1986</td>
<td>289</td>
<td>162</td>
</tr>
<tr>
<td>Total</td>
<td>1648</td>
<td>647</td>
<td>102</td>
<td>790</td>
<td>11 472</td>
<td>840</td>
</tr>
</tbody>
</table>

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independent of the length of exposure of the carcass to flies ($F_{2,6} = 1.96, P = 0.22$). There was, however, a significant negative relationship between the proportion of primary flies to emerge from a carcass and the log$_{10} + 1$ number of secondary/tertiary species (Pearson’s $r^2 = 0.85, n = 12, P < 0.001$) (Fig. 1).

Ordination of the fly species that were significant describers of the variation in fly emergence from carcasses revealed no major separation of the possum carcasses according to their age or length of exposure (Fig. 2). The most distant carcass from the others within its treatment was the 0–5-day carcass in block 1, in which < 1% of the fly population consisted of secondary/tertiary species. However, the ordination did show significant associations between several of the species. The putative secondaries, Chrysomya rufifacies, Ch. varipes, and putative tertiary, H. rostrata, were all associated with vectors pointing to the north of the plot. The vectors for C. vicina and to a lesser extent C. stygia were strongly opposed to those for the non-primary species. The vector associated with L. sericata was distinct from all others, and was not opposed to that described by the non-primary flies.

The mean size of L. sericata to emerge from a carcass varied according to sex, with males being significantly smaller than females ($F_{1,6} = 22.75, P = 0.003$). Length of exposure of fresh carcasses to flies had no significant effect on the mean size of L. sericata ($F_{2,5} = 3.40, P = 0.12$), nor was there any significant interaction between size and exposure time ($F_{2,6} = 1.85, P = 0.24$). However, the log$_{10} + 1$ number of secondary/tertiary flies did have a significant effect on the mean size of L. sericata ($F_{1,5} = 11.74, P = 0.02$). Indeed the log$_{10} + 1$ number of secondary/tertiary flies was a significant determinant of the mean size of L. sericata to emerge across all 12 carcasses (males: $F_{1,10} = 18.80, P = 0.002$; females: $F_{1,10} = 15.45, P = 0.003$) (Fig. 3). The mean size of males decreased 1.4-fold and that of females 1.5-fold as the number of secondary/tertiary flies increased from zero to over 11 000. The sex ratio of emerging L. sericata was female-biased (mean 0.56 ± 0.02 [SE]) in 80% of the carcasses and hence was significantly different from unity (paired t-test: $t = 2.79, d.f. = 9, P = 0.02$). In instances where C. vicina, C. stygia and Ch. rufifacies each had sufficiently large emergent populations per carcass to test, none had sex ratios significantly different from unity. However, Ch. rufifacies had very skewed sex ratios at emergence (range 0–64% female [n = 7]) and consequently had a coefficient of variation (0.64), over four-fold that of the other three species of fly.

Over the 15-day interval after possums were first exposed to flies their core temperature was often elevated above that of the control possum carcass. Maximum elevations above the control carcass temperature occurred during continuous time-spans and varied between 41 h (0–2 days) and 278 h (0–15 days). There was a significant positive relationship between the maximum elevation above the control carcass (range 5.5–24.8 °C) and the number of flies to emerge from each of the other five temperature-recorded carcasses ($F_{1,5} = 149.8, P = 0.001$) (Fig. 4). The maximum temperature reached by a carcass was 38.0 °C. For the carcasses exposed to flies when fresh, the timing of the
maximum elevation in carcass temperature increased with increasing length of exposure to flies, being 230 h, 279 h and 355 h post-exposure for the 0–2-, 0–5- and 0–15-day carcasses, respectively.

**Discussion**

Altering the exposure time of possum carcasses to flies in the field did not significantly affect the success of the primary species, nor did it affect the total number of all flies to emerge from a carcass. This can be attributed largely to the fact that fresh carcasses exposed for at least 5 days to fly oviposition showed enormous variability in the numbers of secondary/tertiary fly species to eventually emerge. With such variability in fly numbers between carcasses, the small sample sizes in this study somewhat reduced the power to detect differences. Nevertheless, the most significant determinant of the proportion of primary flies to emerge was the number of secondary/tertiary maggots present in a carcass. Exposure of fresh carcasses to flies for the first 2 days only excluded the secondary fly species *Ch. variipes* and most *Ch. rufifacies*. In Australia, *Ch. rufifacies* has been recorded as a primary carrion fly in southern Queensland (O’Flynn & Moorhouse, 1979) and may possibly act as a primary fly in the arid zone of New South Wales (Anderson et al., 1988). There is also strong circumstantial evidence that *Ch. rufifacies* acts as a primary strike fly in New Zealand (Tengquist & Charleston, 2001). However, as was found in this study, *Ch. rufifacies* is generally considered to be a secondary carrion species in the temperate regions of Australia (Fuller, 1934; Mackerras & Fuller, 1937; Palmer, 1980). Similarly, in climatic conditions comparable with those of Tasmania, such as in North Island, New Zealand, *Ch. rufifacies* was identified as a secondary invader of carcasses (Heath & Appleton, 2000). In the present study, the putative tertiary species *H. rostrata* was capable of colonizing fresh carcasses within 2 days of exposure. This is in contrast with the findings of Froggatt (1918) where *H. rostrata* was a latecomer to carcasses in comparison with calliphorid species. Furthermore, the carcasses aged in the field for up to 15 days prior to fly exposure were not only still attractive to primary fly species, but within the 2-day exposure time were frequently colonized by secondary species and in all cases by *H. rostrata*.

This study also reports new information for both of the putative secondary species. Firstly, *Ch. variipes* was found to be a carrion breeder, whereas previous studies in Tasmania had never found it so (McQuillan et al., 1983; Williams, 1987). Secondly, both *Ch. variipes* and *Ch. rufifacies* were found in southern Tasmania for the first time (McQuillan et al., 1983; Williams, 1987). *Chrysomya rufifacies* is generally regarded as a tropical species (Baumgartner, 1993) and is of significant veterinary importance as it is frequently reported to be involved in fly strike of live sheep (Waterhouse, 1947; Watts et al., 1976; Barton, 1982; McQuillan et al., 1983; Anderson et al., 1988) and may increase the incidence of sheep mortality (Hughes & Shanahan, 1979). *Chrysomya rufifacies* is thought to be restricted to the warmer months in Tasmania (McQuillan et al., 1983) and its distribution hypothesized to parallel that of the Australian bushfly *Musca vetustissima* Walker; that of a southwards migration from the Australian mainland under the influence of an anticyclonic weather pattern (Hughes, 1970; Hughes & Nicholos, 1974). As the seasonal distribution of *Ch. variipes* corresponds to that of *Ch. rufifacies* in the Canberra area of mainland Australia (Norris, 1959), we propose that the
distribution of Ch. varipes within Tasmania may also parallel that of Ch. rufifacies.

Of the five species of primary fly in this study, L. cuprina is considered the most important with respect to the management of fly strike in sheep. Despite our attempts to provide a carrion environment favourable to L. cuprina, with cooler autumn temperature conditions, exclusion of secondary/tertiary species and carcasses placed outside the previously known geographical range of the predatory species Ch. rufifacies, L. cuprina emergence from all carcasses was minimal (maximum of six flies). Even in those carcasses where Ch. rufifacies was absent, L. cuprina did poorly. Fly traps placed near fresh carcasses over the first 24 h of carcass exposure demonstrated that the small numbers of L. cuprina in carcasses were not due to their relative paucity at the site as they were collected in similar numbers to L. sericata. Rather, the low numbers of L. cuprina found emerging from carcasses may be attributed to either low attraction to carcasses and/or to poor larval competition. Whatever the reason, it would seem that possum carcasses are not important in maintaining large population sizes of L. cuprina in southern Tasmania in autumn. However, in the absence of live sheep, it is possible that possum carcasses may provide a sufficient resource for sustaining small local populations of L. cuprina.

Among the four remaining primary species, C. hilli emerged in very low numbers, whereas the two fly strike species L. sericata and C. stygia, as well as C. vicina, were, in most carcasses, the dominant primary species. The prevalence of L. sericata in carrion is variable in other ecosystems. Studies on North Island, New Zealand record L. sericata commonly breeding in freshly exposed and frozen/thawed possum carcasses and other carrion (Dymock & Forgie, 1993; Heath & Appleton, 2000). By contrast, studies on mainland Australia on large (i.e. adult sheep, goat), small (i.e. lamb, hare) and very small (i.e. mouse, bird, lizard) carcasses found that L. sericata was a relatively rare or non-existent colonizer of vertebrate carcasses (Waterhouse, 1947; Barton, 1982; O'Sullivan et al., 1983; Anderson et al., 1988; Cook et al., 1995). This significant disparity between the prevalence of L. sericata in Tasmania compared with mainland Australia has also been observed in fly trap catches (McQuillan et al., 1983). This difference is proposed to be due to Tasmania having large fluctuations in day length, cool, temperate climatic and rainfall regimes and intensive farming operations (McQuillan et al., 1983). In northern Europe, L. sericata is also frequently found in carcasses, although it is an uncommon colonizer of very small carcasses (Kuusela & Hanski, 1982; Blackith & Blackth, 1990; Smith & Wall, 1997b).

Other studies have shown carrion location to be a significant determinant of the dominant fly species, although this was controlled for in this study. Smith & Wall (1997a) suggested that the distribution of adult L. sericata and C. vicina in different habitats is a major function in shaping the carrion community. They found C. vicina to be more prevalent in wooded sites than pasture sites, whereas L. sericata was found to be more abundant in pasture sites. Similarly, Heath & Appleton (2000) found greater emergence of L. sericata from carcasses in pasture sites compared with shelter-belt sites, although they did not record the distribution of C. vicina in their study. The carrion in the present study was exposed on pasture sites, with L. sericata being the most abundant primary species in six of the 12 carcasses and just one carcass with C. vicina representing more than 40% of the emergent primary fly species. In our study, ordination vectors for C. vicina and, to a lesser extent, C. stygia showed that the major determinant of their numbers was the number of secondary/tertiary species in the carcass. The number of L. sericata was less affected by the number of secondary/tertiary species in the carcass than either C. vicina or C. stygia. By contrast, Smith & Wall (1997a) found that the addition of C. vicina into laboratory cultures of L. sericata resulted in a higher proportion of L. sericata mortality in comparison with those cultures where only L. sericata was present. They interpreted this as L. sericata suffering more from interspecific than intraspecific competition. However, the survival to adult emergence of L. sericata was still significantly greater than that of C. vicina in mixed and pure cultures at the highest initial larval numbers tested (i.e. 300 larvae per 15 g liver) (Smith & Wall, 1997a). This suggests that the competitive ability of a species is not the only factor in explaining relative abundance from carcasses.

Temperature elevation has also been hypothesized to be a major determinant of fly breeding success in carrion. Waterhouse (1947) suggested that high temperatures resulting from insolation and larval activity reduce C. stygia emergence from carcasses. The lethal temperature upper limit for C. stygia approaches 35 °C; O’Flynn (1983) found no adult emergence in the laboratory for larvae held at a constant 34 °C. Similarly, the lethal temperature upper limit of C. vicina is 30–35 °C (Williams & Richardson, 1984). In our study, maximum temperature elevations in the carcass were significantly correlated to the total number of fly larvae, with carcass temperatures elevated above ambient for up to 11.6 days, with a maximum difference of 24.8 °C. These temperatures are in accord with those found by Appleton (1993) in possums on pasture sites in North Island, New Zealand, where temperatures up to 18.5 °C above ambient were recorded over a period of 13.5 days. Deonier (1940) suggested that in carcasses with very high temperatures, calliphorid larvae move to areas of lower temperature, although Turner & Howard (1992) found that major movement of dipteran larval aggregations in rabbit carcasses only occurred when the food source was exhausted. Appleton (1993) recorded a maximum carcass temperature of 42 °C, yet failed to find evidence of immature larvae leaving possum carcasses because of this extreme. Similarly, in our study the maximum temperature reached by a carcass was 38.0 °C and we found no evidence of early larval egress.

The intensity of density-dependent competition on larvae in the carrion environment has been shown to relate to adult size in many insect species, and Smith & Wall (1997a) found intraspecific and interspecific competition mediated the size of emergent L. sericata. In the present study, the effect of competition was also shown to mediate L. sericata size, with the emergence of smaller adults, along with increasing emergence of Ch. rufifacies, Ch. varipes and H. rostrata. As with Smith & Wall (1997a), L. sericata females were larger than males and also had greater size plasticity than males. Furthermore, the emergent sex ratio was female-biased, suggesting males may also suffer greater pre-adult mortality in L. sericata. However, there are strong species-specific responses to competition. For instance, although competition in carcasses can affect the pupal size of L.
cuprina (Levot et al., 1979), the relative weight of the egg clutch increases with decreasing adult size (Williams & Richardson, 1983). This Williams & Richardson (1983) interpret as a response to the sedentary nature of L. cuprina’s primary host (i.e., sheep), and suggest that the energy allocated to reproduction is justified even at the expense of the lowered mobility of adult flies.

In conclusion, the most important fly strike species L. cuprina was found in insignificant numbers, even in carcasses where Ch. rafflesi fies was absent and where other criteria encouraging oviposition appeared to have been met. However, all other fly strike species C. stygia, L. sericata and Ch. rafflesi did use possum carrion as an important breeding resource. It was the number of secondary/tertiary fly species, rather than exposure time per se that had the most significant impact on the proportion of all primary flies to emerge, upon the numbers of C. vicina and C. stygia, and on the size of adult L. sericata. Although carcass temperatures were elevated, especially in those with a large fly population, the effect appeared insufficient to result in significant pre-adult fly mortality. In terms of fly strike management the prevalence of live strike by C. stygia, L. sericata and Ch. rafflesi in sheep needs to be evaluated further before the importance of possum carrion as a resource for fly strike can be fully assessed.

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