

Biology and population dynamics

The biology and ecology of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) – an update

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Summary

This paper presents a review of research conducted during the past two decades on the biology and ecology of L. cuprina. It highlights several areas where further research is merited. The more important of these include: information on the factors that regulate the time of onset of pre-pupal overwintering; data on the factors that regulate juvenile survival both on the sheep and in the soil; information on the relative importance of carrion and sheep faeces as sources of adult protein, particularly in the more arid parts of the species range; and the elucidation of the relative importance of carrion and live sheep as Lucilia oviposition sites. It concludes that sufficient is now known about the life-cycle of L. cuprina to enable the completion of a weather-driven simulation model developed by the Late WG Vogt. By modelling existing field data, we may be able to anticipate many of the existing gaps in our knowledge of the species biology. The model may also indicate knowledge gaps of which we are currently unaware.

Keywords

Lucilia cuprina, developmental biology, ecology, myiasis

Introduction

The Australian sheep blowfly, *Lucilia cuprina*, is the primary myiasis fly of sheep in Australia (e.g. Mackerras and Fuller, 1937; Watts *et al.*, 1976; Murray, 1978; Barton, 1982; McQuillan *et al.*, 1984). *L. cuprina* is thought to have arrived from South Africa, perhaps as early as the mid- to late- 19th century (Norris, 1990). There were reports of fly blown sheep as early as 1870 (Tillyard and Seddon, 1933), but evidence of a pending national problem did not emerge until 1897, when major outbreaks of flystrike occurred simultaneously in Victoria (Cameron, 1908) and in the Riverina district of New South Wales (Froggatt, 1915). Over the next decade, flystrike became an endemic problem in most of the sheep grazing areas of mainland Australia. This progressive escalation of fly activity was almost certainly related to the successful establishment of *L. cuprina*, but because of the species' close resemblance to *L. sericata*, its importance as the main initiator of strike defied detection for a further twenty years (Mackerras, 1930). By the mid-1900s, *L. cuprina* had been recorded from most parts of Australia (Waterhouse and Paramonov, 1950), with Tasmania being the last major sheep grazing region to be colonised (Ryan, 1954).

Broadmeadow *et al.* (1984) claim that flystrike may cause the death of some 3 million sheep annually. As such, it imposes a substantial annual cost to the Australian sheep industry. Dependence on, and resistance to, broad-spectrum insecticides has become widespread, as has community concern over pesticide residues in sheep products and in the 'on-farm' environment. The need to minimise insecticide usage, either through the more timely application of chemicals (e.g., Monzu and Mangano, 1984; Mackenzie and Anderson, 1990), or through the development of alternative, non-chemical methods of control (e.g. genetic control, Whitten *et al.*, 1977) has stimulated much new research on the population dynamics of *L. cuprina*. However, it is now more than two decades since the last major reviews of biology and ecology of *L. cuprina* were conducted (see Vogt and Woodburn, 1979; Barton Browne, 1979). This update will use both published and unpublished data and will examine the question of whether or not sufficient information currently exists to finalise the development and validation of an incomplete *Lucilia* population model developed by the late Dr W.G. Vogt (see Appendix 1). It will focus on the factors that regulate seasonal abundance and survival,

and will highlight areas in which either new research or the further analysis of existing data is desirable.

Developmental biology

The distribution of *L. cuprina* is closely associated with sheep grazing and, in some areas, its status is effectively that of an obligate parasite of sheep (Anderson *et al.*, 1984a; Anderson *et al.*, 1988). However, the presence of persistent populations of *L. cuprina* around Darwin and elsewhere in northern Australia (Norris, 1990), indicates that the species can subsist in the absence of sheep over a very wide range of environmental conditions. Throughout most of its distribution area, *L. cuprina* is active only during the warmer parts of the year. In Queensland (O'Sullivan *et al.*, 1984) and in the northern parts of Western Australia (Monzu, 1979), adults are present throughout the year, but elsewhere the species passes the winter in the prepupal stage (Foster *et al.*, 1975). Numbers tend to be highest in wet years, yet populations can endure in areas or seasons that are habitually dry. Tolerance of such a wide range of habitats and seasonal conditions reflects the multiplicity of adaptive traits that regulate the species life-cycle. These are examined in more detail below.

Egg and larval stages

Eggs of *L. cuprina* are acutely sensitive to desiccation (Foster *et al.*, 1975). Survival is uniformly high if eggs are held in a saturated atmosphere at 15-40°C, but falls off sharply with a decrease in ambient humidity, or at temperatures higher than 40°C (Vogt and Woodburn, 1980). Females oviposit preferentially on sheep affected by some pre-disposing cause of strike, such as fleece-rot or urine stain (e.g. Mackerras and Mackerras, 1944; Seddon, 1967). They usually lay their eggs in clusters close to the skin (Rogoff and Barton Browne, 1958) and often behave gregariously so that several egg masses may be laid together (Barton Browne, 1958; Barton Browne *et al.*, 1969; Wardhaugh *et al.*, 1988). Such behaviour probably affords the innermost eggs some protection against desiccation and high fleece temperatures which commonly reach 40°C (Froggatt, 1915). Vogt and Woodburn (1980) have determined that the maximum development rate of *Lucilia* eggs and their greatest tolerance of desiccation occurs at, or about, 35°C. Accordingly, when the fleece is moist (i.e. after rain or in an existing strike), eggs near the sheep's skin are likely to experience conditions close to their optimum for development and survival.

Newly-hatched larvae are also very susceptible to desiccation and require a moist environment in which to develop successfully (Foster *et al.*, 1975). Such conditions are a prerequisite for oviposition (for a more detailed exposition of oviposition requirements, see Wardhaugh *et al.* 2001, these proceedings), but first instar larvae enhance their chances of survival by releasing enzymes that digest ovine epidermal cells and induce a discharge of a protein-rich, serous exudate, which is then ingested. Later instars use a combination of enzymes and large mouthhooks to penetrate deep into the dermis thereby sustaining exudate production (Sandeman *et al.*, 1987).

Although many of the mechanisms by which myiases develop are now well understood, almost no quantitative data are available about egg or larval survival within a strike, or how this may change with the type of lesion (breach, body, hoof etc.) or as the strike develops. From an investigation related to density dependence, Dallwitz (1987) obtained data on larval survival from artificially induced shoulder strikes in some 29 sheep. Larval establishment was assisted by wetting the implant site and placing eggs over a small wound. Strikes developed in most instances, but survival at larval drop-off was rather poor (about 30% on average) and varied without respect to the size of the initial egg or larval infestation, which involved up to 18,000 individuals (80-90 egg-masses) per strike. More realistic studies, in which sheep were induced to scour and then exposed to natural oviposition in the field (Dallwitz *et al.*, 1984), also indicated low percentage survival (17% (range 0-48%)). However, in this instance, most of the exposed animals received only a single egg mass (about 200 eggs), which may have been insufficient for initiating myiasis development (Wardhaugh and Morton, 1990). Moreover, scouring had been in progress for less than 24 h, which probably meant that the

affected skin was still intact. High levels of larval survival were observed only in the case of two sheep with pre-existing strikes. Both animals attracted multiple ovipositions and, in one, survival between the egg and post-feeding larval stage was estimated at 70%. Although it is probably unwise to generalise on the basis of such limited information, these data are consistent with the notion that larval survival may be poor in the initial stages of a myiasis, but increases as surviving larvae generate a more favourable environment for development (Fenton *et al.*, 1999). However, it is difficult to reconcile such a simple survival concept with the occurrence of persistent covert strike, which is a common phenomenon in Australian sheep (Wardhaugh and Dallwitz, 1984; Dobbie and Kennedy, 1984; O'Sullivan *et al.*, 1984). Given the tendency for *L. cuprina* to aggregate in the presence of a struck animal (Mackerras and Mackerras, 1944; Woodburn and Vogt, 1982; Dallwitz *et al.*, 1984), it would be reasonable to expect strike development to be rapid. The occurrence of persistent, sub-clinical myiasis is therefore problematic. Clearly, the factors regulating larval survival on the living sheep is an area requiring much further study.

Post-feeding larvae and overwintering

Fully-fed larvae may leave the sheep at any time between nights 3 and 7 after eggs are laid. Maximum drop-off usually occurs on the fourth or fifth night of the myiasis, irrespective of time of year (daylength), or the prevailing weather conditions. Larval exodus is confined to the hours of darkness and is regulated by an endogenous rhythm (Smith *et al.*, 1981). This suggests that, except under hot conditions when sheep may graze at night, post-feeding larvae will be concentrated in sheep campsites, where the soil is usually loose and friable. Laboratory data indicate that soil compaction, ambient temperature and the presence of sub-surface moisture exert a strong influence on the depth to which larvae penetrate (Wardhaugh and Reid, unpublished). Similar conclusions may be drawn from 3 years of field-pot data (Wardhaugh and Dallwitz, unpublished), in which the depth to which larvae penetrated varied from 1.0 - 7.5 cm at air temperatures ranging from 7–35°C respectively. Over summer, larvae were commonly found at depths of about 6 cm, whereas those that overwintered were mostly confined to the top 1-2 cm; this latter finding is similar to the data given by Foster *et al.* (1975). At Fowlers Gap, which experiences higher autumn temperatures than those common in the Canberra region, McLeod (1997) found that larvae placed in outdoor pots during late autumn, mostly pupariated in the top 3-6 cm, a difference which appears to be consistent with the fact that depth of pupariation varies with temperature.

Information collected under semi-natural conditions (Dallwitz and Wardhaugh, 1984) indicate that the period from drop-off to pupariation varies seasonally, taking 1-4 days (median 2 days) in summer, but increasing to 15 days as temperatures decrease during autumn. The nature of this relationship has not been quantified, but the data to do this are still available (Dallwitz, *pers. comm.*). This same data-set could also be used to provide an estimate of the effects of temperature and rainfall on the survival of post-feeding larvae across all seasons. A preliminary appraisal of the 1979 data of Dallwitz and Wardhaugh (1984) indicated that survival was higher among non-overwintering larvae (61%) than on those that overwintered (36%) (Dallwitz, *pers. comm.*).

Dallwitz and Wardhaugh (1984) found that between mid-March and mid-April the propensity of post-feeding larvae to pupariate decreased sharply in a way which was only partly dependent on temperature. Such individuals remained as larvae until spring, yet emerged synchronously with cohorts that entered the ground at any time between June and September. Dallwitz and Wardhaugh (1984) interpreted these findings as indicating the existence of an explicit developmental arrest, probably mediated in part via daylength (as experienced by the parent insects and/or the feeding larvae) and in part by the temperatures experienced after the larvae entered the ground. In other words, larvae developing from eggs laid by field-conditioned females from mid-March onwards were predisposed to 'diapause' but induction was temperature dependent. This implies that the date of onset of overwintering is likely to vary regionally in accordance with differences in seasonal temperatures. Trap data for Inverell (Wardhaugh, unpublished data), Fowlers Gap (McLeod, 1997), and central Queensland (O'Sullivan *et al.*, 1984) support this suggestion. However, it should be noted that in a

separate study of post-feeding larvae at Fowlers Gap, McLeod (1997) found no consistent evidence for the interruption of development over winter, except in the first season of her study. This may be related to the fact that most of the larvae used in these experiments were produced by laboratory-bred females held at constant temperature and daylength.

Foster (unpublished) used the data of Dallwitz and Wardhaugh (1984) to develop a computer model (FlyAlert) for estimating the time of spring emergence. Anecdotal feed-back from groups that have used this model has indicated that it provided useful results. However, there has been no formal attempt at validation. Vogt (*pers. comm.*) applied the Foster model to field data from Murrumbateman, but found the results less than satisfactory and incorporated changes to improve its predictive capacity (see Appendix 1). One of these involved upgrading the soil-air temperature relationship and another allowed for the occurrence of rain sufficient to cause pupariation delays.

A similar model has been developed by McLeod (1997 and these proceedings) on the basis of her Fowlers Gap data and it would be interesting to compare the performance of the two models on the same data sets.

Pupal stage

Dallwitz (1984) has compared the development of pupae of *L. cuprina* under a range of constant and fluctuating temperatures. Survival and development rates were similar under constant and fluctuating temperature regimes between 15-30°C. Under constant conditions, pupal survival was limited to temperatures within the range 15-35°C, whereas with fluctuating temperatures, pupae were able to tolerate brief exposures to temperatures as low as -10°C or as high as 46°C. Under continuously fluctuating temperature regimes, pupal development was confined to temperatures of 6-42°C.

Dallwitz (1984) did not examine the effect of substrate moisture on pupal survival, or its interaction with temperature. Rumbo (1979) has shown that *L. cuprina* pupae are highly susceptible to waterlogging, particularly at the time of pupariation and again at emergence. In the intervening stages of growth, they are able to cope with a wide range of humidity and oxygen conditions (Gilby and Rumbo, 1980). Since post-feeding larvae are unlikely to pupariate when the soil is wet (Foster *et al.*, 1975), waterlogging is likely to be important only in the later stages of pupal development. Information pertinent to understanding pupal survival in the field are not available.

Adult stage

The development, survival and activity of the adult *L. cuprina* has been the subject of an enormous research effort and, in reality, ought to have been the subject of a separate presentation, as it was at the First National Blowfly Symposium (see Barton Browne, 1979). Since Barton Browne (2001) has just completed a comprehensive essay on the regulation of ovarian development in Diptera, which makes extensive reference to the reproductive biology of *L. cuprina*, treatment of the topic has been very much compressed. Readers requiring information more detailed than is given here are referred to the Barton Browne review.

Nutritional requirements for growth and sexual maturation

L. cuprina needs water and carbohydrate to sustain life and a source of protein to support egg maturation (Webber, 1957; Webber, 1958). Although flies may ingest water in the field (Barton Browne, 1979), their moisture requirements are probably satisfied, at least in part, during the acquisition of carbohydrate and protein. Webber (1957) has shown that nectar from at least three species of *Eucalyptus*, and honeydew associated with coccid or psyllid infestations, were important sources of carbohydrate. By examining the crops of field-caught females, he also showed that *L. cuprina* fed extensively on carrion and animal excreta, in particular, the faeces of sheep. In the Southern Tablelands of New South Wales, sheep faeces were found to support ovarian development in both autumn and spring, but not in summer. In a more recent study, Wardhaugh, Mahon and Whitby (unpublished), have determined that rates of ovarian development on sheep dung are positively correlated with faeces protein

content and, in non-parous flies (i.e. those in their first ovarian cycle), vary linearly from about 4% per day with a protein content of 8% (dry, native summer pasture) to 18% per day as protein content rises to 25% (lush, improved spring pasture). Except during drought conditions, sheep dung was found to be adequate for ovarian development, the only proviso being that access was unlimited and prolonged. At protein contents of less than about 10%, the number and size of mature eggs decreased markedly.

The faeces of several other animals (horses, rabbits, possums and dogs (Webber, 1958; Clift and McDonald, 1976) are also known to support ovarian development in *L. cuprina* and it is possible that avian faeces, in particular those of ducks and geese, may also be an effective source of protein. On Flinders Island, the faeces of Cape Baron geese, were especially attractive and, when fresh, were frequently smothered with *L. cuprina* (Wardhaugh, pers. observation). Serous exudate derived from strike lesions is also a commonly cited source of protein. However, non-gravid flies are infrequent visitors to struck sheep (Mackerras and Mackerras, 1944; Woodburn and Vogt, 1982; Dallwitz *et al.*, 1984). Moreover, Wardhaugh and Woodburn (unpublished) found that ovarian development in females allowed access to strike exudate was delayed in comparison with liver-fed flies and was accompanied by substantial amounts of resorption. Thus, while it is possible that parous flies may feed on serous exudate at the time of oviposition, it seems unlikely that strike exudate plays a major role in adult diet.

Barton Browne (1979) and Vogt and Woodburn (1979) have summarised the large number of early studies that underpin our current understanding of the process of ovarian development in *L. cuprina*. Without access to protein, oocyte development ceases before the onset of vitellogenesis, which is also the stage at which females become highly protein motivated (Roberts and Kitching, 1974; Kitching and Roberts, 1975). The number of oocytes that a female can mature depends on her size, as well as the amount and quality of protein-rich material ingested (Vogt *et al.*, 1985a). In fully-fed females, oocyte development is synchronous and strongly temperature dependent. To mature their first complement of eggs, females require a minimum of 57 day degrees (dds) above 8°C. In the Southern Tablelands, females usually obtain enough protein to reach maturity, but rarely mature their full egg complement, i.e. most females resorb some of their developing oocytes (Vogt *et al.*, 1985c). This process has been estimated to prolong ovarian development by 0.3 dds/oocyte resorbed and, in field populations, has the effect of reducing potential fecundity by an average of about 53 eggs per female; this is equivalent to a lifetime loss of almost 25% of a female's egg-laying capacity.

According to Vogt *et al.* (1985a), females must imbibe protein of sufficient quality and quantity to mature a minimum of 110 eggs, otherwise the development of all oocytes is arrested. In the sheep dung experiments of Wardhaugh, Mahon and Whitby (unpublished), flies fed on faeces with the lower protein contents (8-10%) developed an average of 170 eggs (range 86-248), indicating the resorption of some 67 oocytes. This value is not markedly different from the average figure given by Vogt *et al.* (1985c) for field-fed flies and, *prima facie*, would seem to offer some support to Webber's contention (Webber, 1958) that sheep dung is an important constituent in the diet of *L. cuprina*. However, on sheep dung, the production of mature eggs required 10-17 days at 28°C (Wardhaugh, Mahon and Whitby, unpublished), which is the equivalent to a delay of some 143-283 dds (or about 2-4 dds per oocyte). This range is approximately an order of magnitude greater than the estimate of delay derived for field-caught females (Vogt *et al.*, 1985c) and suggests that when markedly sub-optimal diets are involved, the processes of development and resorption may not be regulated solely by temperature.

In most seasons in the Southern Tablelands, female *L. cuprina* can develop a batch of eggs every 4-8 days (Foster *et al.*, 1975). But, with a life-expectancy of less than 3 weeks (Vogt and Woodburn, 1979), few females survive long enough to produce a third batch of eggs. Even so, Vogt *et al.* (1985b) have shown that under favourable seasonal conditions, *L. cuprina* were able to sustain a 9-fold increase in population over the course of a single generation. Under hot dry conditions, rates of increase were generally well below replacement (0.1-0.6). These

calculations were facilitated by the development and application of a method of standardising fly catches for effects due to the prevailing weather (Vogt *et al.*, 1983). This latter development (see also Vogt and Morton, 1991; and Vogt *et al.*, these proceedings) is an important innovation that allows the transformation of raw trap catches into estimates of relative or absolute density.

Almost all of the information currently available about ovarian development in *L. cuprina* has been derived from studies in the Southern Tablelands. Detailed information is available for northern New South Wales (Wardhaugh unpublished) and Flinders Island (Mahon, unpublished), but has not yet been analysed. As far as can be determined, there are no data on the longevity, ovarian development or survival rates of adult *L. cuprina* in arid, or tropical parts of Australia, where protein and carbohydrate resources are likely to be limiting during large parts of the year. This is clearly a topic worthy of further study.

Mating

Mating is normally associated with the ingestion of protein rich material and the onset of vitellogenesis (Barton Browne *et al.*, 1976; Barton Browne *et al.*, 1987). In the field mating has been observed only rarely and, on each occasion, it occurred in the vicinity of carrion or dead sheep (Mahon, *pers. comm.*). However, gravid females collected in the field are almost invariably inseminated (Kitching and Smith, 1986). Hence, as a factor affecting the population dynamics of *L. cuprina*, failure to find a mate is unlikely to be an important issue except in relation to SIRM or genetic control programs (see Mahon, these proceedings).

Oviposition and attraction to sheep

The widely held notion that carrion was an important breeding ground for *L. cuprina* was first contested by Waterhouse (1947). Numerous studies since then (for example, O'Flynn, 1982; Barton, 1982; Anderson *et al.*, 1988; Monzu *et al.*, 1984; McLeod, 1997) have confirmed that competition from other species renders carrion a poor substrate for the development and survival of *L. cuprina* larvae. Thus, while carrion is now regarded as contributing little to the maintenance of *Lucilia* populations by way of breeding, the fact that carcasses act as oviposition 'sinks' implies that the carrion factor is likely to play a key role in the species' population dynamics. However, the magnitude of this effect, and how it varies in space or time has never been quantified. From an experimental viewpoint, the problem of estimating how *L. cuprina* partitions its egg laying between live sheep and carrion appears intractable, but a study of the availability of carrion and its attractiveness to flies (along the lines of Dallwitz *et al.*, 1984) might be an appropriate way to begin.

L. cuprina has been observed to visit clean dry sheep; most are female and almost all are gravid (Mackerras and Mackerras, 1944; Woodburn and Vogt, 1982). Oviposition is dependent on the presence of moisture, which is usually associated with the occurrence of some predisposing factor, such as fleece rot, faecal or urine stain, or a pre-existing strike (Tillyard and Seddon, 1933). However, the sequence of behaviours leading to oviposition remains uncertain. A number of studies has shown that odours associated with sheep faeces and many common fleece bacteria are important in attracting *L. cuprina* to sheep (e.g. Emmens, 1981; Emmens and Murray, 1982; Emmens and Murray, 1983; Eisemann, 1995; Morris *et al.*, 1997; Morris *et al.*, 1998), but there are no data to indicate the distance over which these chemicals may be detected. Eisemann (1988) compared the relative attractiveness of wet and dry sheep and sheep affected by a cutaneous myiasis and found that all test animals elicited significant upwind movement by *L. cuprina*. This increased from 10 m for sound dry sheep to 20 m for struck sheep. Oviposition pheromones may also be important to the detection process, although these are thought to be involved mainly in the aggregation of egg laying (Barton Browne *et al.*, 1969; Emmens, 1981).

Hobson (1936) and Mackerras and Mackerras (1944) envisaged that oviposition on sheep depended on the presence of a putrefaction factor 'P' and a sheep factor 'S' possessed only by live sheep. Later insectary experiments (Rogoff and Barton Browne, 1958; Barton Browne and Rogoff, 1958), in which flies were offered a choice between live sheep and the pelts of freshly

killed animals, cast doubts on the veracity of an 'S' factor and suggested that 'livingness' was unimportant in attracting oviposition. More recently, however, Wardhaugh *et al.* (1988) monitored oviposition on *L. cuprina* in the field by attaching squares of soiled fleece to newly-shorn sheep. Although oviposition on fleece squares varied in accordance with variations in both air temperature and the density of gravid females, squares attached to free-ranging sheep attracted up to 10x more oviposition than those placed at ground level on the edge of a sheep campsite. Since gravid females are known to congregate preferentially in sheep camps (Wardhaugh *et al.*, 1984), the reverse result might have been expected, i.e. that a group of static sources of odour would have attracted more oviposition than dispersed, mobile targets. The fact that this did not arise would seem to provide renewed support for the existence of an 'S' factor.

Spatial distribution and movement

Factors regulating the movement and spatial distribution of *L. cuprina* are not well understood and seem likely to vary according to weather and pasture conditions. In the arid, western districts of New South Wales, Anderson *et al.* (1984b) found that *L. cuprina* was uncommon in open pasture and concluded that its preferred habitats were sheep camps, patches of *Acacia* scrub and shady creek beds, with or without water. In western Queensland, O'Sullivan *et al.* (1984) also identified proximity to water as being an important influence on fly distribution.

In contrast, in temperate areas of south-eastern Australia, *L. cuprina* is predominantly a species of open pasture, being rare or absent in bushland habitats (Vogt and Woodburn, 1979). Dry sclerophyll forest is an effective barrier to fly movement (Wardhaugh *et al.*, 1983), and flies released in such habitats disperse rapidly.

In open pasture, fly distribution is usually highly clumped (Gilmour *et al.*, 1946). Such patchiness often persists over an entire fly season (see, for example, Vogt and Woodburn, 1979; Anderson *et al.*, 1984b) and even between seasons (Wardhaugh *et al.*, 1983). Even dense wind-breaks have the potential to affect fly movement, flies tending to disperse along a tree line rather than through it (Mahon and Wardhaugh, unpublished, Flinders Island). Using a grid of baited sticky traps, Wardhaugh *et al.* (1984 and unpublished) found *L. cuprina* to be more abundant in the vicinity of sheep than cattle. Highest catches occurred in traps sited in green patches grazed by sheep, or in sheep campsites, which yielded up to 40x as many gravid flies as was encountered in the adjoining cattle paddock. Moreover, the movement of sheep to fresh grazing was accompanied by a corresponding redistribution of flies, but with a lag-time of 1-2 days. Nevertheless, although sheep appear to act as a highly effective attractant for itinerant flies, a study of the physical characteristics (aspect, exposure, shade, vegetation, nearness to livestock, water, sheep camps etc.) of some 49 trapping sites over a full fly season, did not reveal any obvious factor(s) that could be used to interpret variations in observed ranking of fly catches in either time or space (Reid and Wardhaugh, unpublished).

Mark-recapture experiments have yielded much information about fly mobility. In temperate sheep pasture, displacements of 4-7 km for individual flies during the first 1-2 days after their release have been recorded by several authors (Gilmour *et al.*, 1946; Norris, 1959; Foster *et al.*, 1975). However, in all of these studies, most insects remained within 1-2 km of the emergence site, suggesting that under favourable conditions, *L. cuprina* is rather sedentary. Kitching (1981) drew a similar conclusion on the basis of the distinctly discontinuous nature of insecticide resistance detected in parts of eastern Australia. In New Zealand, where *L. cuprina* is a relatively recent colonist, Gleeson and Heath (1997) have suggested, on the basis of gene flow measurements, that the species has a slow rate of spread and would be an ideal target for genetic control. However, in more hostile environments (e.g. forested areas, or areas without sheep) mark and recapture experiments indicate the occurrence of higher rates of dispersal and suggest that movement of *L. cuprina* may be facultative and dependent upon the availability of adequate sustenance or oviposition sites. For example, in the Gudgenby valley (near Canberra, ACT), where delayed ovarian development and massive oocyte resorption indicated an acute shortage of protein (Vogt *et al.*, 1985c), marked flies were recovered on 19

occasions at distances of 6-17 km from the initial release site (Wardhaugh *et al.*, 1983). Likewise, in two mark-recapture experiments in the Tallaganda State Forest (near Braidwood, NSW), released flies were caught in sheep pastures on the outer perimeter of the trapping grid (10-11 km distant) within 24 h of being liberated (Woodburn and Wardhaugh, unpublished). The first of these trials was conducted under hot, dry conditions and, by day 3, flies had almost entirely vacated the central 5 km annulus of the trapping grid. In the second trial, which coincided with two days of cool, showery weather, the pattern of spread was similar, but the rapid evacuation of the release site was less conspicuous. These findings suggest that fly dispersal is likely to be more rapid and far-reaching when food and/or oviposition sites are inherently scarce (e.g. in the arid, low-density sheep grazing areas of western New South Wales). They clearly have important implications for control strategies that depend on the reduction or eradication of *Lucilia* populations. However, there is no evidence of an obligatory dispersive phase in *L. cuprina*, or of large-scale displacements comparable to those characteristic of the bush fly (*Musca vetustissima*) (Hughes, 1970).

Density dependence

Nicholson's classic carrion experiments (Nicholson, 1957) demonstrated the potential importance of density dependent regulation of *L. cuprina* populations. Using artificially induced strikes containing 100-18,000 larvae, Dallwitz (1987) attempted to confirm the existence of this process on living sheep. However, evidence of a correlation between larval density and survival was lacking. Both development rate and offspring size (which determines fecundity in the next generation) were negatively associated with increasing larval numbers but, in comparison with the effects observed by Nicholson (1957), their overall effect was negligible. Dallwitz (1987) considered that density dependent effects were more likely to occur when strikes became large enough to cause the death of the struck animal, or frequent enough to provoke insecticidal intervention.

Using spectral and time-series analysis, Cruikshank and Wall (2001) have detected strong evidence of compensatory, density dependent regulation in two populations of *L. sericata* in south-western England. Although in both populations, the clearest signal detected by spectral analysis was related to season, signals with frequencies of 0.0038 and 0.0037 day degree⁻¹ were also present in each population. These were found to be equivalent to the day degree requirements for a complete generation. Quite independently, McLeod (1997) used a similar approach to examine the long-term fluctuation of *L. cuprina* populations in the western districts of New South Wales. Her spectral analysis results indicated a strong seasonal cycle with a period of 12 months (frequency 0.080-0.085), together with several unexplained minor peaks with periodicities of 6 months or less. The smallest of these (frequency 0.44) was equivalent to about 80 days. Although flies may experience protein deprivation, oviposition delays and a paucity of oviposition sites in an arid environment such as Fowlers Gap, NSW, 80 days appears excessive for an average generation, in which case McLeod's (*loc. cit.*) findings appear to differ from those of Cruikshank and Wall (2001). On the other hand, since McLeod (1997) did not convert her data to day-degrees, or test her results for density dependence, it may be worthwhile to subject these records to further investigation.

Cruikshank and Wall (2001) did not elucidate a mechanism underlying the occurrence of density dependence in *L. sericata*, but Wall (*pers. comm.*) considers that a shortage of oviposition sites and/or flock management might be involved. With respect to flock management, Wardhaugh and Morton (1990) have shown that under Australian conditions, the proportion of graziers reporting strike rarely exceeds 80-90%, even when strike rates are high. This probably arises from the fact that when strike incidence is low, graziers treat only those animals found to be struck. Since, in their early stages, most strikes will be covert (Wardhaugh and Dallwitz, 1984), it is probable that numbers of larvae will reach the 'drop-off' stage before control measures are implemented. But as the size and incidence of strikes increase, so too will the probability that the entire flock will be treated with insecticide, thereby depriving females access to a suitable breeding substrate. How females respond to the presence of insecticide will determine whether or not they are induced to seek oviposition sites elsewhere, but with

insecticides that do not have a deterrent effect yet render the animal non-susceptible, the living sheep may be transformed into an oviposition sink.

Conclusions

L. cuprina is a facultative ectoparasite of sheep. It also breeds on carrion, but because of competition with a range of other species, survival is invariably poor. The species has become established in most parts of Australia, but is most abundant in high rainfall areas associated with sheep grazing. In the latter habitats, it is predominantly a species of open pasture and is rare or absent in forested areas. In pastureland, its distribution is highly clumped especially in the presence of sheep. However, the suite of factors that regulate its distribution are, as yet, poorly understood. Although there is no evidence that *L. cuprina* has an obligatory dispersal phase, the species displays a facility for rapid displacement when the habitat becomes unfavourable.

Most aspects of the developmental biology of *L. cuprina* have been thoroughly researched and have already been encapsulated in a preliminary simulation model by the late W.G. Vogt. Little further work will be required to update and transform this model into a form that could be used and tested by graziers and researchers. Key areas that merit further research are concerned mainly with immature survival and resource partitioning. They are summarised as follows:

- defining what *L. cuprina* feeds on in the field, particularly in respect of protein acquisition; this determines the number of eggs that are matured and the interval between emergence and oviposition;
- determining the relative importance of sheep and carrion as oviposition sites; this is vital for estimating potential rates of increase;
- factors that regulate the survival of eggs and larvae on sheep. We need to know if survival can be predicted on the basis of weather, fleece length etc., and whether or not it varies with the type of lesion and/or as the strike develops;
- factors that control the time of induction of pre-pupal overwintering; this determines the length of the fly season and hence the period over which sheep are at risk.

It is possible that some of the above gaps in our understanding of the biology and ecology of *L. cuprina* can be allowed for during model evaluation, providing there are an adequate number of data sets encompassing a wide enough range of environmental conditions. It is also conceivable that attempts to model the population dynamics of *L. cuprina* will reveal knowledge gaps of which we are currently unaware. Since model validation is likely to need access to strike and fly data from widely different habitats, it is suggested that consideration be given to the establishment of a National Database.

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Appendix 1

A preliminary weather - driven model for estimating the seasonal phenology and abundance of *Lucilia cuprina*

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Computation of air and soil temperatures

The model requires estimates of hourly air and soil temperatures to accumulate development and estimate survival. Since hourly data are available for relatively few locations, a method of estimation, based on daily maximum and minimum air temperature, has been developed.

Hourly temperature records for the Canberra region places the respective daily minima and maxima of air and soil (depth = 2 cm) temperature at 05.00 15.00, and 07.00 14.00. Hourly temperatures are estimated from successive minima and maxima using sine curves and the model is updated every 6 h. Daily maximum and minimum soil temperatures (S_{max} and S_{min} , °C) are estimated from daily maximum and minimum air temperatures (A_{max} and A_{min} , °C), daily solar radiation totals (R , mWh/cm²), daily precipitation totals to 0900h (P , mm), and soil depth (D , cm) using the relationships:

$$S_{max} = 0.99 + 0.787A_{max} + 0.0157R + 0.074P - 0.298D,$$

$$S_{min} = 6.79 + 0.924A_{min} + 0.173D.$$

The above relationships, which were fitted as multiple linear regressions to 303 d of weather data recorded from October, 1991 to July, 1992, explained 88% and 78% respectively of the total error variances.

Development rates of immature stages

A nonlinear rate function, $R = \exp(-6.18 + 0.30T - 0.0043T^2)$, applies to all immature stages and uses the average hourly temperature (T) to accumulate development in arbitrary development units (adu). A total of 100 adu is required from oviposition to female eclosion.

Duration of egg and larval stages

At constant temperature and 100% RH, the duration of the egg stage corresponds to 3.1 adu. At approximately constant temperatures ranging from 16°C to 38°C ($\pm 3^\circ\text{C}$) the duration of the larval stage on rearing medium corresponds to 28.4 adu. On sheep, larval development time is essentially constant irrespective of weather conditions or fleece length. Based on data from artificially induced strikes, a mean duration of 4.5 d has been assumed for the period between oviposition and larval exodus, with 50% of larvae leaving the sheep at midnight on each of days 4 and 5. At this point in time, accumulated development is equivalent to 31.5 adu.

Duration of prepupal stage

At temperatures ranging from 16°C to 38°C ($\pm 3^\circ\text{C}$), the duration of the prepupal stage corresponds to 16 adu. At temperatures below 16°C, pupariation is inhibited. The pre-pupal stage is the stage at which overwintering occurs. However, the induction of overwintering involves additional seasonal cues that are as yet unknown. In the Canberra region, prepupae from natural strikes become 'preconditioned' for overwintering during mid-March, whereafter increasing proportions fail to pupate despite favourable soil temperatures. The proportion

¹ This document was prepared in 1993 and may not be the latest version of Bill Vogt's model. Both Richard Dallwitz and myself recall later discussions over ways in which field estimates of overwintering and pupal development might be improved. Accordingly, the search for later versions of the model is continuing (Keith Wardhaugh).

overwintering is assumed to increase linearly from 0 to 1 during the period between 14/3 and the date when pupation is precluded by low soil temperatures.

Delays in pupation

The major requirement for the pupation of 'overwintered' prepupae is that soil temperatures remain above the pupation threshold (16°C) until the prepupae have accumulated their necessary 16 adu for pupation. Developmental sequences that fail to achieve this condition are discounted (accrued development set to zero). A second criterion is that all accrued development is discounted if rainfall in the preceding 24 h exceeds 12 mm. This is to accommodate the observation that prepupae will evacuate water-logged soil to seek drier ground. A third criterion is that no development accrues above 37°C, the upper thermal limit for pupariation.

Duration of pupal stage

Under constant and fluctuating temperatures ranging from -1.5° to 42.5°C, the duration of the pupal stage was 52.5 adu for females and 47.5 adu for males. Adult eclosion is centred at dawn (06.00h). Pupae that complete development after 06.00 emerge as adults at 06.00 on the following day.

Development rates of adult females

At constant and fluctuating temperatures ranging from 10°C to 40°C, ovarian development rates are linearly related to temperature with an estimated developmental threshold of 8°C. Females require access to a food source rich in protein to develop their full complement of eggs.

Duration of ovarian cycles

The first ovarian cycle has a duration of 57 day degrees and subsequent cycles have durations of 33 day degrees if dietary protein is not limiting. In the field however, females invariably experience protein shortage, which causes them to resorb some of their developing oocytes and mature less than full complements of eggs. On average, resorption delays completion of each ovarian cycle by a constant 16 day degrees throughout the fly season.

Durations of ovarian stages

Ovarian development can be divided into 10 stages, the first 9 (pre-gravids) occupying 24, 8, 4, 5.5, 2.5, 3, 4.5, 2.5 and 3 day degrees respectively and the first stage being confined to the first ovarian cycle. Oocyte resorption prolongs the durations of stages 3, 4 and 5 which take the values of 9.0, 9.5 and 9.5 day degrees respectively. The gravid stage (10) is assumed to have a mean duration of 0.5 d unless a). more than 5 mm of rain were recorded in the previous 24 h, in which case oviposition is delayed by 24 h; or b). flies become ready to oviposit at night, in which case oviposition is delayed until 06.00h the following day; or c). when the ambient temperature is less than an assumed threshold of 12°C, in which case oviposition is delayed until all the above conditions are fulfilled.

Survival of immature and adult stages

Egg survival

Intrinsic egg mortality is 15% at constant temperatures between 15 and 40°C and there is an absolute hatching threshold of 75% RH below which eggs fail to hatch. Females oviposit readily on carrion, but survival to pupation is negligible due to larval competition from native calliphorids. The proportion of females that oviposit on carrion, rather than on sheep, is not known but initially can be treated as constant. Egg survival on sheep can be treated as a function of sheep susceptibility which is related to weather conditions.

This is one of the main parameters to be estimated by modelling the available field data.

Survival of larvae on sheep

Data from numerous artificially induced strikes indicate that survival to larval exodus is highly variable (0% to 95%) but is independent of larval density (100 to 18,000 larvae per strike). Estimated mean survival to larval maturity (larval exodus), assuming an 85% egg hatch, is 38%.

Survival of prepupae and pupae

Data from weekly releases of prepupae in the field over two years (November to March), and recovering them one month later as 'empty' or 'non-empty' pupal cases indicate that:

- 75% of prepupae pupate within 2.5 cm of the soil surface
- prepupae consistently experience high mortality rates
- prepupae that pupate have a constant 90% survival rate independent of depth of pupation.

Prepupal mortality is one of the main parameters to be estimated by modelling available field data on fly abundance.

Survival of adults

Data from mark recapture experiments indicate that mortality of field adults is age-dependent but is independent of fly size. Proportions of males (PMS) and females (PFS) surviving in relation to reproductive age (A) in day degrees are given by the lognormal relationships:

- $PMS = 1 - \text{normal}((\ln(A)-4.509)/0.459)$
- $PFS = 1 - \text{normal}((\ln(A)-4.619)/0.418)$,

where 'normal' refers to the normal probability integral and the figures in parentheses, when evaluated, correspond to normal deviates.

Female fecundity

Potential female fecundity is a linear function of female size, which is measured as headwidth in mm. Seasonal variation among field females, although significant, is only marginal (2.9 mm to 3.1 mm) and the mean headwidth corresponds to a potential fecundity of 232 eggs. Assuming a mean reduction of 52 eggs per cycle through oocyte resorption, the mean realised fecundity is 180 eggs per female per cycle of which 50% will give rise to females.

References

- Anderson J.M.E., Shipp E. and Anderson P.J. (1984a). Blowfly populations and strike incidence in the arid zone of NSW. *Wool Technology and Sheep Breeding* **32** 12-14.
- Anderson J.M.E., Shipp E. and Anderson P.J. (1984b). Distribution of Calliphoridae in an arid zone habitat using baited sticky traps. *General and Applied Entomology* **16**, 3-8.
- Anderson P.J., Shipp E., Anderson J.M.E. and Dobbie W. (1988). Population maintenance of *Lucilia cuprina* (Wied.) in the arid zone. *Australian Journal of Ecology* **36**, 241-249.
- Barton Browne L. (1958). The choice of communal oviposition sites by the Australian sheep blowfly, *Lucilia cuprina*. *Australian Journal of Zoology* **6**, 241-247.
- Barton Browne L. (1979). *National Symposium on the Sheep Blowfly and Flystrike in Sheep*. New South Wales Department of Agriculture Sydney, Australia, p33-43.
- Barton N.J. (1982). Studies of sheep blowflies in Victoria. *Research Project Series* **116**, Victorian Department of Agriculture, Australia.
- Barton Browne L. (2001). Quantitative aspects of the regulation of ovarian development in selected anautogenous Diptera: integration of endocrinology and nutrition. *Entomologia Experimentalis et Applicata* (in press).
- Barton Browne L. and Rogoff W.M. (1958). The 'sheep factor' and oviposition in *Lucilia cuprina*. *Australian Journal of Science* **21**, 189-190.
- Barton Browne L., Bartell R.J. and Shorey H.H. (1969). Pheromone mediated behaviour leading to group oviposition in the blowfly *Lucilia cuprina*. *Journal of Insect Physiology* **15**, 1003-1015.
- Barton Browne L., van Gerwen A.C.M. and Smith P.H. (1987). Relationship between mated status of females and their stage of ovarian development in field populations of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Bulletin of Entomological Research* **77**, 609-615.
- Barton Browne L., Bartell R.J., van Gerwen A.C.M. and Lawrence L.A. (1976). Relationships between protein ingestion and sexual receptivity in females of the Australian sheep blowfly *Lucilia cuprina*. *Physiological Entomology* **1**, 235-240.
- Broadmeadow M.E., Gibson, J.E. Dimmock, C.K., Thomas R.J. O'Sullivan, B.A. (1984). The pathogenesis of flystrike in sheep. *In Sheep Blowfly and Flystrike in Sheep*. Second National Symposium, NSW Department of Agriculture, Sydney, Australia, p 327-331.
- Cameron S.S. (1908). Diseases of the skin. II – Parasitic skin diseases. I – Animal Parasites. Fly-blow in sheep. *Journal of Department Agriculture, Victoria* **6**, 444-445.
- Clift A.D. and McDonald F.J.D. (1976). Some relationships between diet and ovarian development in *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae). *Australian Journal of Zoology* **24**, 87-93.
- Cruickshank I. and Wall R. (2001). Abundance and density-dependence in two blowfly field populations. *Journal of Animal Ecology* (in press).
- Dallwitz R. (1984). The influence of constant and fluctuating temperatures on development rate and survival of pupae of the Australian sheep blowfly *Lucilia cuprina*. *Entomologia Experimentalis et Applicata* **36**, 89-95.

Dallwitz R. (1987). Density independence of survival in myiasis breeding of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Bulletin of Entomological Research* **77**, 171-176.

Dallwitz R. and Wardhaugh K.G. (1984). Overwintering of pre-pupae of *Lucilia cuprina* (Diptera: Calliphoridae) in the Canberra region *Journal of the Australian Entomological Society* **23**, 307-312.

Dallwitz R., Roberts J.A. and Kitching R.L. (1984). Factors determining the predominance of *Lucilia cuprina* larvae in blowfly strikes of sheep in southern New South Wales. *Journal of the Australian Entomological Society* **23**, 175-177.

Dobbie, W. R. and Kennedy, J.P. (1984) Observations on covert flystrike in wethers in far western New South Wales *In: Sheep Blowfly and Flystrike in Strike*. Proceedings of the Second National Symposium, New South Wales Agriculture, Sydney, pp. 130-132.

Eisemann C.H. (1988). Upwind flight by gravid Australian sheep blowflies, *Lucilia cuprina* (Wiedemann)(Diptera: Calliphoridae), in response to stimuli from sheep. *Bulletin of Entomological Research*. **78**, 273-279.

Eisemann C.H. (1995). Orientation by gravid Australian sheep blowflies, *Lucilia cuprina* (Diptera: Calliphoridae), to fleece and synthetic chemical attractants in laboratory bioassays. *Bulletin of Entomological Research* **85**, 473-477.

Emmens R.L. (1981). Evidence for an attractant in cuticular lipids of female *Lucilia cuprina* (Wied.), Australian sheep blowfly. *Journal of Chemical Ecology*. **7**, 529-541.

Emmens R.L. and Murray M.D. (1982). The role of bacterial odours in oviposition by *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae), the Australian sheep blowfly. *Bulletin of Entomological Research* **72**, 367-375.

Emmens R.L. and Murray M.D. (1983). Bacterial odours as oviposition stimulants for *Lucilia cuprina* (Wiedemann)(Diptera: Calliphoridae), the Australian sheep blowfly. *Bulletin of Entomological Research* **73**, 411-415.

Foster G.G., Kitching R.L., Vogt W.G. and Whitten M.J. (1975). Sheep blowfly and its control in the pastoral ecosystem. *Proceedings of the Ecological Society of Australia* **9**, 213-229.

Fenton A., Wall R. and French N.P. (1999). Oviposition aggregation by the blowfly *Lucilia cuprina* *Medical and Veterinary Entomology* **13**, 453-456.

Froggatt W.W. (1915). Sheep-maggot flies. *Farmers Bulletin* **95**, 1-52.

Gilby A.R. and Rumbo E.R. (1980). Water loss and respiration of *Lucilia cuprina* during development within the puparium. *Journal of Insect Physiology* **26**, 153-161.

Gilmour D., Waterhouse D.F. and McIntyre G.A. (1946). An account of experiments undertaken to determine the natural population density of the sheep blowfly, *Lucilia cuprina* Wied. *Council for Scientific and Industrial Research Bulletin*, **195**, 1-39.

Gleeson D.M. and Heath A.C.G. (1997). The population biology of the Australian sheep blowfly, *Lucilia cuprina*, in New Zealand. *New Zealand Journal of Agricultural Research* **40**, 529-535.

Hobson R.P. (1936). Sheep blowfly investigations. III Observations on chemotropism of *Lucilia sericata* Mg. *Annals of Applied Biology* **23**, 843-851.

- Hughes R.D. (1970). The seasonal distribution of bushfly (*Musca vetustissima*) in south-east Australia. *Journal of Animal Ecology* **39**, 691-706.
- Kitching R.L. (1981). The sheep blowfly: a resource-limited specialist species. In *The ecology of pests.* (Eds.) RL Kitching and RE Jones. CSIRO, Australia, pp, 193-214.
- Kitching R.L. and Roberts J.A. (1975). Laboratory observation on the teneral period in sheep blowflies, *Lucilia cuprina* (Diptera: Calliphoridae). *Entomologia Experimentalis et Applicata* **18**, 220-225.
- Kitching R.L. and Smith P.H. (1986). Gravid sheep blowflies are rarely virgin. *General and Applied Entomology*. **18**, 10.
- Mackerras I.M. (1930). Recent developments in blowfly research. *Journal of Council Scientific and Industrial Research Australia* **3**, 212-19.
- Mackerras I.M. and Fuller M. (1937). A survey of Australian sheep blowflies. *Journal for Council of Scientific and Industrial Research, Australia* **10**, 261-270.
- Mackerras I.M. and Mackerras M.J. (1944). Sheep blowfly investigations. The attractiveness of sheep for *Lucilia cuprina*. *Bulletin for Council of Scientific and Industrial Research, Melbourne* **181**, 1-44.
- McLeod L.J. (1997). The Australian sheep blowfly, *Lucilia cuprina* (Wied.) and the hairy maggot blowfly, *Chrysomya rufifacies* (Macq.) in the arid zone of New South Wales. M. Sc. Thesis, CERIT, School of Biological Sciences, University of New South Wales, pp 1-166.
- McKenzie J.A. and Anderson N. (1990). Insecticidal control of *Lucilia cuprina*: strategic timing of treatment. *Australian Veterinary Journal* **67**, 385-386.
- McQuillan P.M., Jones A.L. and Williams H. (1984). Recent studies on sheep blowflies in Tasmania. In *Sheep Blowfly and Flystrike in Sheep*. Second National Symposium, NSW Department of Agriculture, Sydney, Australia, p 100-104.
- Monzu N. (1979). The importance of alternative primary blowfly species to the Australian sheep blowfly *Lucilia cuprina* (Wiedemann). *National Symposium on the Sheep Blowfly and Flystrike in Sheep*. New South Wales Department of Agriculture Sydney, Australia, p33-43.
- Monzu N, Gheradi S.G. and Zental, E. (1984) the importance of carrion breeding in the maintenance of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) in low rainfall areas of western Australia. In: *Sheep blowfly and Strike*. Proceedings of the Second National Symposium, New South Wales Agriculture, Sydney, pp141-144.
- Monzu N. and Mangano G.P. (1984). The development of an early warning system for the timing of insecticide application to prevent body strike on sheep in Western Australia. Western Australia Department of Agriculture, Agdex 612, 57pp.
- Morris M.C., Joyce M.A., Heath A.C.G., Rabel B. and Delisle G.W. (1997). The responses of *Lucilia cuprina* to odours from sheep, offal and bacterial cultures. *Medical and Veterinary Entomology* **11**, 58-64.
- Morris M.C., Woolhouse A.D., Rabel B. and Joyce M.A. (1998). Orientation stimulants from substances attractive to *Lucilia cuprina* (Diptera: Calliphoridae). *Australian Journal of Experimental Agriculture* **38**, 461-468.
- Murray M.D. (1978). The species of flies reared from struck sheep in Western Australia. *Australian Veterinary Journal* **54**, 262.

Nicholson A.J. (1957). Competition for food among *Lucilia cuprina* larvae. *Proceedings 8th International Congress of Entomology*, 277-281.

Norris K.R. (1959). The ecology of sheep blowflies in Australia *In Biogeography and Ecology in Australia* (Eds) Keast A, Crocker RL and Christian CS. Junk, The Hague, pp 514-544.

Norris K.R. (1990). Evidence for multiple exotic origin of Australian populations of the sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Australian Journal of Zoology* **38**, 635-48.

O'Flynn M.A. (1982). The blowfly problem in Queensland. *Queensland Agricultural Journal* **108**, 212-214.

O'Sullivan B.M., Perkins I., Vokes L., Suter G. and Hopkins P.S. (1984). The ecology of *Lucilia cuprina* in Western Queensland *In Sheep Blowfly and Flystrike in Sheep*. Second National Symposium, NSW Department of Agriculture, Sydney, Australia, p 96-100.

Rogoff W.M. and Barton Browne L. (1958). The oviposition behaviour of the Australian sheep blowfly, *L. cuprina* (Wied.). *Proceedings Xth International Congress of Entomology* **2**, 589-593.

Roberts J.A. and Kitching R.L. (1974). Ingestion of sugar, protein and water by adult *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae) *Bulletin of Entomological Research* **64**, 81-88.

Rumbo E.R. (1979). Oxygen requirements of *Lucilia cuprina* during development within the puparium. *Entomologia Experimentalis et Applicata* **26**, 67-73.

Ryan A.F. (1954). The sheep blowfly problem in Tasmania. *Australian Veterinary Journal*, April edition 109-113.

Seddon H.R. (1967). *Diseases of Domestic Animals in Australia. Part 2. Arthropod infestations (Flies, Lice and Fleas)*. Second Edition, revised by HE Albiston. Commonwealth Department of Health, Australia 152 pp.

Sandeman R.M., Collins B.J. and Carnegie P.R. (1987). A scanning electron microscope study of *L. cuprina* larvae and the development of blowfly strike in sheep. *International Journal for Parasitology* **17**, 759-765.

Smith P.H., Dallwitz R., Wardhaugh K.G., Vogt W.G. and Woodburn T.L. (1981). Timing larval exodus from sheep and carrion in the sheep blowfly, *Lucilia cuprina*. *Entomologia Experimentalis et Applicata* **30**, 157-162.

Tillyard R.J. and Seddon H.R. (1933). The sheep blowfly problem in Australia. Joint Blowfly Committee, Report No.1. Council for Scientific and Industrial Research Australia, Pamphlet No. 37.

Vogt W.G. and Woodburn T.L. (1979). Ecology, distribution and importance of sheep myiasis flies in Australia. *National Symposium on the Sheep Blowfly and Flystrike in Sheep*. New South Wales Department of Agriculture Sydney, Australia, p23-32.

Vogt W.G. and Woodburn T.L. (1980). The influence of temperature and moisture on the survival and duration of the egg stage of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann)(Diptera: Calliphoridae). *Bulletin of Entomological Research* **70**, 665-671.

Vogt W.G. and Morton R. (1991). Estimation of population size and survival of sheep blowfly, *Lucilia cuprina*, in the field from serial recoveries of marked flies affected by

weather, dispersal and age-dependent trappability. *Researches in Population Ecology* **33**, 141-163.

Vogt W.G., Woodburn T.L., Morton R. and Ellem B.A. (1983). The analysis and standardisation of trap catches of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Bulletin of Entomological Research* **73**, 609-617.

Vogt W.G., Woodburn T.L. and van Gerwen A.C.M. (1985a). The influence of oocyte resorption on ovarian development rates in the Australian sheep blowfly. *Entomologia Experimentalis et Applicata* **39**, 85-90.

Vogt W.G., Woodburn T.L. and Foster G.G. (1985b). Ecological analysis of field trials conducted to assess the potential of sex-linked translocation strains for genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann). *Australian Journal of Biological Sciences* **38**, 259-273

Vogt W.G., Woodburn T.L., Ellem B.A., van Gerwen A.C.M., Barton Browne L. and Wardhaugh K.G. (1985c). The relationship between fecundity and oocyte resorption in field populations of *Lucilia cuprina*. *Entomologia Experimentalis et Applicata* **39**, 91-95.

Vogt W.G., van Gerwen A.C.M. and Walker J. (2001). Estimating population densities of the Australian sheep blowfly *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) from catches in wind-oriented traps. FLICS Conference, Launceston, Tasmania, June 2001.

Wardhaugh K.G. and Dallwitz R. (1984). Covert flystrike. *Wool Technology and Sheep Breeding* **32**, 15-19.

Wardhaugh K.G. and Morton R. (1990). The incidence of flystrike in sheep in relation to weather conditions, sheep husbandry, and the abundance of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Australian Journal of Agricultural Research* **41**, 1155-1167.

Wardhaugh K.G., Smith P.H. and Crompton G.W. (1983). A comparison of ground and aerial release methods for the genetic control of *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae). *General and Applied Entomology* **15**, 37-46.

Wardhaugh K.G., Read P.A. and Neave M.J. (1984). A sticky-trap for studying the spatial distribution of the Australian sheep blowfly, *Lucilia cuprina*. *Australian Veterinary Journal* **61**, 132.

Wardhaugh K.G., Read P.A. and Neave M.J. (1988). A method of measuring the oviposition rate of the sheep blowfly, *Lucilia cuprina* under field conditions. *Australian Veterinary Journal* **65**, 75-77.

Waterhouse D.F. (1947). The relative importance of live sheep and carrion as breeding grounds for the Australian sheep blowfly, *Lucilia cuprina*. *Bulletin for Council of Scientific and Industrial Research*, No. 217.

Waterhouse D.F. and Paramanov S.J. (1950). The status of two species of *Lucilia* (Diptera: Calliphoridae) attacking sheep in Australia. *Australian Journal for Scientific Research (B)* **3**, 310-336.

Watts J.E., Muller M.J., Dyce A.L. and Norris K.R. (1976). The species of flies reared from struck sheep in south-eastern Australia. *Australian Veterinary Journal* **52**, 488-489.

Webber L.G. (1957). Utilisation and digestion of carbohydrates by the Australian sheep blowfly *Lucilia cuprina*. *Australian Journal of Zoology* **5**, 164-172

Webber L.G. (1958). Nutrition and reproduction by the Australian sheep blowfly *Lucilia cuprina*. *Australian Journal of Zoology* **6**, 139-144.

Woodburn T.L. and Vogt W.G. (1982). Attractiveness of Merino sheep before and after death to adults of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Journal of the Australian Entomological Society*. **21**, 131-134

Whitten M.J., Foster G.G., Vogt W.G., Kitching R.L., Woodburn T.L. and Kononov C. (1977). Current status of genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) *In* Proceedings of XV International Congress of Entomology. Washington, p129-139.