THE STATUS OF THE TWO SPECIES OF LUCILIA (DIPTERA, CALLIPHORIDAE) ATTACKING SHEEP IN AUSTRALIA

By D. F. Waterhouse* and S. J. Paramonov* 

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Summary
Evidence presented demonstrates that L. cuprina and L. sericata are distinct species. A number of characters previously unrecognized are described whereby larvae and both sexes of adults of the two species may be recognized without difficulty. The geographical distribution of the two species is different, as is also their habitat preference and their degree of attraction to living sheep. Furthermore, hybridization experiments indicate that there is great difficulty in obtaining successful matings. L. cuprina is the principal Australian sheep blowfly, whereas L. sericata is comparatively rare in sheep-raising country and does little damage. There are two subspecies of L. cuprina, one from the Oriental and American regions (L. cuprina cuprina) and one from the African and Australian regions (L. cuprina dorsalis).

I. INTRODUCTION
It was not clearly recognized until 1930 that a species of Lucilia was responsible for most of the blowfly strike of sheep in Australia (Mackerras 1930) and until about 1932 the English sheep blowfly L. sericata was thought to be the only Lucilia species causing strike (Fuller 1932; Mackerras and Fuller 1937), although L. cuprina had been recorded from Australia several years earlier (Malloch 1927). Since the early 'thirties a considerable amount of evidence has been accumulated, which demonstrates that the most important sheep blowfly in this country is L. cuprina and that this species is quite different in its distribution, habits, and morphology from the economically unimportant L. sericata. The distinctiveness of these two species has to a large extent been assumed in most Australian publications dealing with sheep blowfly and no adequate account is available of the differences observed.

For many years in South Africa the Australian practice was followed of regarding L. cuprina as the principal sheep blowfly and L. sericata as of minor importance. In 1945, however, Ullyett reported that these two species mated in the laboratory and, using colour of fore femora and of abdomen as specific characters, he found that the F1 hybrid had legs typical of L. cuprina and abdomen typical of L. sericata. In the F2 generation these two colour characters segregated in a 1:4:1 ratio. Furthermore, field material always contained individuals having the appearance of hybrids and it was pointed out that, if femur coloration alone was considered, this would lead to all hybrids being considered as L. cuprina, resulting in far greater numbers of Lucilia specimens

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being recorded as *L. cuprina* than as *L. sericata*. Although it was considered for a time that this conclusion might be valid for the two "species" in South Africa, Ullyett's extension of it to cover the position in Australia was immediately recognized by Australian workers to be unsound. However, since he has recently reaffirmed his belief that the two species are identical (Ullyett 1950) it is important to consider not only the status of these two species in Australia, but also, where possible, their affinities with species bearing the same names in other parts of the world.

II. The Systematics of *L. cuprina* and *L. sericata*

(a) Taxonomy

(i) The Significance of the Genera *Lucilia* R-D and *Phaenicia* R-D.

Many authors have followed Robineau-Desvoidy (1830) and divided the genus *Lucilia* into two genera or subgenera, *Lucilia* and *Phaenicia*, on the basis of two characters which are illustrated by the following key:

Subcostal sclerite (at extreme base of stem vein on under side of wing) with short setulose hairs apically. Ocellar triangle reaches half way from the vertex to the lunule in females . . . .  *Lucilia* Robineau-Desvoidy Subcostal sclerite without hairs, although soft pubescence may be present. Ocellar triangle reaches less than half way from the vertex to the lunule in females . . . . . . . . . . . . . . . .  *Phaenicia* Robineau-Desvoidy

Neither of these characters can be regarded, however, as providing adequate justification for any more than subgeneric status. Both *cuprina* and *sericata* lack hairs on the subcostal sclerite and hence belong to *Phaenicia*. In view of the recommendation of the 7th International Entomological Congress (Rosenbaum 1939) that the use of subgeneric names should be avoided, it is preferable not to use this name and to regard both species as belonging to the genus *Lucilia*.

(ii) General Remarks on Species

(1) *Lucilia cuprina* (Wiedemann) 1830.—Originally described as *Musca cuprina* in Aussereurop. Zweift. Insektten. 2: 654. Type locality: China. Type female in the University Zoological Museum, Copenhagen, and not, as sometimes recorded, in the Leyden Museum (Senior White et al. 1940).

**Synonyms**

*Lucilia dorsalis* R-D., 1830, Myodaires, p. 453. Type locality: Cape of Good Hope. Type male in Paris.

*Lucilia amica* R-D., 1830, loc. cit. Type locality: Timor. Type male in Paris.


*Lucilia argyrocephala* Macq., 1846, Mém. Soc. Roy Agric. Arts Lille, p. 326; 1846, Dipl. Exot. Suppl. 1, p. 198. Type locality: Cape of Good Hope. Type specimen probably in Spinola's collection in Castello di Tassarols (Novi Ligure) (Horn and Kahle 1936).

Musca temperata Walk., 1852, loc. cit.
Somomyia pallifrons Big., 1877, Ann. Soc. Ent. Fr. 7: 257.
Strongyloineura nigricornis Sen. White., 1924, Spolia Zeylan. 13: 115. Type locality:
Cherat, North West Frontier Post, India. Type is a male.
Lucilia pallescens Shannon, 1924, Insect. Insct. Mest. 12: 78. Type locality: Wilming-
ton, North Carolina. Type male in U.S. National Museum.

The only species which requires discussion in this list of synonymy is L. pallescens (Shannon 1924). Although the author of this species himself later regarded it as synonymous with L. cuprina (Shannon 1925, 1926), Hall (1948) lists it as a valid species and gives several characters to distinguish cuprina from pallescens. These all concern the proportions of various regions of the head, but no definite measurements are given and the differences used (stated in such terms as “not so wide in comparison with . . . .”, “proportionately higher in comparison with . . . .” etc.) do not appear to be valid. A comparison of a large series of L. pallescens from Texas, New Orleans, and Washington with Australian L. cuprina, using the distinguishing characters mentioned later (Section II (b)), failed to reveal any differences between the two forms.

The authors have come to the conclusion that, over its vast geographical range, L. cuprina is represented by two readily distinguishable subspecies. For these the names L. cuprina cuprina (Wied.) and L. cuprina dorsalis R.D. appear to be most appropriate. Wiedemann’s type female cuprina has been carefully examined. The general coloration of the fly is dull olive-green (K. R. Norris, unpublished data). The typical subspecies (L. cuprina cuprina) occupies a very large area including China* (type locality), Japan*, Formosa*, Assam*, Malaya*, Java*, Soembawa*, Timor, Fiji†, Hawaii, North America* (= synonym L. pallescens Shan.), and South America*. It is easily recognized by its dull olive-bronze body coloration. The brilliant metallic coppery green, green, or bluish green sheen of L. cuprina dorsalis is absent or poorly developed. The general coloration of L. cuprina cuprina is suggestive of a fly of the genus Musca rather than of the genus Lucilia. The type specimen of amica R.D. from Timor, which is housed in the Paris Museum, is dull (Séguy, personal communication) and belongs to the typical subspecies.

L. cuprina dorsalis R.D. occurs in Africa*, India, and Australia*. It is very widespread in the sheep-raising areas of Australia (see Section IV), and South Africa, it has been recorded from Kenya (Lewis 1933), and the authors have examined one specimen from Cairo. This subspecies is easily recognized by its brilliant metallic coppery green, green, or bluish green coloration, which is similar in general character to that of other well-known Lucilia species, such as L. sericata and L. caesar. No intermediates between this and the other subspecies of L. cuprina have been seen.

The name dorsalis R.D. has been selected for this subspecies, the type male bearing this name coming from within the geographical distribution of the

* Localities from which material was examined in this study.
† Five specimens, identified by Bezzi (1928) as L. cuprina, were available.
STATUS OF TWO SPECIES OF *LUCILIA*

313

bright *cuprina* subspecies (Cape of Good Hope, South Africa, Robineau-Desvoidy 1830). This specimen is housed in the Muséum Nationale d'Histoire Naturelle, Paris. *L. dorsalis* has page priority over *L. elegans* R-D. also from the South African region (Ile de France).

(2) *Lucilia sericata* (Meigen) 1826.—Originally described as *Musca sericata* in *Syst. Beschr.* 5: 53.

Type locality: Germany. Type apparently lost. It is not in Paris Museum (Séguy, personal communication), but may be in Halle or Vienna.

**Synonyms**


*Lucilia barberi* Towns., 1908, loc. cit. 51: 121. Type locality: Williams, Arizona. Type male in U.S. National Museum.

The only additions to synonyms previously published are “species A” and “species B” of Miller (1939). Through the courtesy of Dr. Miller 31 specimens of *Lucilia “species A”* were made available for examination. Most of these were bred specimens of about half normal size, probably caused by inadequate food in the larval stage. Except for coloration, the characters of “species A” are the same as those of *L. sericata*. The lighter coloration of “species A” may be partly due to the fact that the specimens were pinned shortly after emergence and before hardening and darkening had been completed. This is suggested not only by their colour but also by the fact that their relatively light-coloured legs are collapsed and twisted, as often happens when unhardened flies are killed.

“Species B”* is also typical morphologically of *L. sericata*, although its coloration is somewhat lighter. This again may have resulted from the specimen having been pinned before it had hardened and darkened. In Dr. Miller's

* The single “type” specimen was available for examination. This specimen has no locality label and Miller says that it may have been collected in Europe, Australia, or New Zealand. It cannot, therefore, be referred to New Zealand.
collection there are two additional males labelled "species B" which were not mentioned in his 1939 paper. These are two typical male \textit{L. sericata} having normal \textit{sericata} coloration. An examination of many specimens of \textit{L. sericata} from New Zealand indicates that they normally have the metallic bluish green coloration typical of this species from other parts of the world and not the "peculiar coppery colour" recorded by Aubertin (1933).

<table>
<thead>
<tr>
<th>Characters</th>
<th>\textit{L. cuprina}</th>
<th>\textit{L. sericata}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Occipital bristles (Figs. 1 and 2)</td>
<td>1 on each side</td>
<td>6 to 8 on each side</td>
</tr>
<tr>
<td>2. Clypeus (Figs. 3 and 4)</td>
<td>Black</td>
<td>Light amber</td>
</tr>
<tr>
<td>3. Frontal stripe (Figs. 3 and 4)</td>
<td>About as wide as a parafrontal</td>
<td>About twice as wide as a parafrontal</td>
</tr>
<tr>
<td>Thorax</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. (i) Humeral calli (Figs. 5, 6, and 7)</td>
<td>2 to 4 hairs</td>
<td>6 to 8 hairs</td>
</tr>
<tr>
<td>4. (ii) Notopleura (Figs. 5, 6, and 7)</td>
<td>3 to 5 hairs</td>
<td>8 to 16 hairs</td>
</tr>
<tr>
<td>5. Second pair of presutural acrostichals (Fig. 5)</td>
<td>Do not extend to first pair of postsutural acrostichals</td>
<td>Extend at least as far as insertions of first pair of postsutural acrostichals</td>
</tr>
<tr>
<td>6. Scutellar bristles (Fig. 5)</td>
<td>Dorsal bristles slightly smaller than, or equal to, lateral hairs</td>
<td>Dorsal bristles distinctly smaller than lateral hairs</td>
</tr>
<tr>
<td>7. Colour of fore femora</td>
<td>Metallic green</td>
<td>Dark metallic blue to black</td>
</tr>
<tr>
<td>Abdomen</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Hairiness of 2nd, 3rd, and 4th abdominal sternites (only for males)</td>
<td>Hairs longer than on hind femora and tibiae</td>
<td>Hairs about the same length as on hind femora and tibiae</td>
</tr>
<tr>
<td>9. Contour of last abdominal tergite</td>
<td>Generally smooth</td>
<td>Collapsed</td>
</tr>
<tr>
<td>10. Male genitalia (Figs. 8 and 9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) Terminal claspers</td>
<td>Long and slender, outer margins of apical third parallel</td>
<td>Broader, tapering regularly, outer margins converge and are not parallel</td>
</tr>
<tr>
<td>(ii) Subterminal claspers</td>
<td>Slender, similar and parallel to terminal claspers</td>
<td>Semicircular and much broader than \textit{cuprina}, particularly at basal half. Widely separated at tip</td>
</tr>
</tbody>
</table>
STATUS OF TWO SPECIES OF LUCILIA

(b) Distinguishing Features of L. cuprina and L. sericata

(i) Adults

In the past, L. cuprina and L. sericata have generally been separated by differences in coloration of the fore femora (Hardy 1940; Joint Blowfly Committee 1933). Although this is a valuable character, it is not always reliable if the specimens have been killed before they have hardened and darkened properly or if they have been exposed to high temperatures or become fouled by animal or plant juices. The only additional characters available are the differences in male genitalia, readily visible only after dissection, and differences in the hairiness of the male abdomen (Aubertin 1933; Hardy 1940; Malloch 1927).

Ullyett (1945) states that, in L. cuprina, the abdomen is green with a bronze sheen, whereas in L. sericata it is a distinct blue-green. Although the distinction holds in a general fashion, exceptions are far too numerous for it to be at all reliable both for Australian L. cuprina and L. sericata and for South African specimens of these species seen by the authors.

As a result of examining many hundreds of well-preserved L. cuprina and L. sericata the following distinguishing features can be listed (Table 1):

Characters on the head

(1) Hairiness of Central Region of Occiput.—The occipital region consists of a central area (the cerebrale) and on either side a lateral area separated from the cerebrale by a distinct suture (Figs. 1 and 2). Whereas the lateral areas carry many hairs, the cerebrale is nearly bare, although on its upper part there are some hairs which provide a means of distinguishing L. cuprina from L. sericata.

In both L. cuprina and L. sericata there is a single pair of “guide hairs” on the upper part of the cerebrale directly behind the ocellar triangle*, the

* Occasionally one or more additional, but smaller, hairs may be present in this region.
distance between these hairs being nearly equal to that between the posterior ocelli. In *L. cuprina* there is, a little lower down the cerebrale, a second pair of hairs separated by a space several times as great as that between the first pair. At times (less than 20 per cent. of individuals) one or both of the hairs of the second pair is accompanied by a second hair which is, however, often smaller than the first.

In *L. sericata* the second pair of hairs is replaced on each side by a group, each group normally consisting of six to eight hairs, although as few as three and as many as fourteen may be present. The number is, however, frequently different on either side of the same insect. Very occasionally the number of hairs is reduced to two on one or on both sides.

A magnification of 20x to 40x is required for the accurate determination of these occipital hairs. They are seen most readily if the head is viewed from above and to one side and only very rarely and in badly damaged specimens are they broken. This character is extremely reliable.

(2) *Degree of Sclerotization of Clypeus.*—On its dorsal surface the proboscis is flexed between the clypeus and the frons, and the clypeus being bounded laterally by the rostrum (Figs. 3 and 4). It is difficult to see the whole of the clypeus unless the proboscis is extended, which is not often the case in pinned specimens. However, if the insect is turned in such a way that the upper part of the mouth cavity is visible, sufficient of the frontal margin of the clypeus can almost always be seen to enable determination of the character described below.

In *L. cuprina* the clypeus, which is slightly bifurcated at its frontal margin, is jet black or a very dark brown, in contrast with the light amber coloration of the rostrum. In *L. sericata* the clypeus is not as distinctly bifurcated anteriorly and is often a light amber colour. However, in a high proportion
of individuals (particularly in males), there are all degrees of sclerotization between amber and dark brown. When the clypeus exhibits its darker shades it is noticeable that its upper half (adjoining the frons) is generally lighter in colour than the lower half.

In spite of the variability of this character it is useful for the rapid initial separation of the two species because it can be employed at low magnifications (10x to 20x). When the sclerotization of the clypeus is such that the specimen cannot be assigned immediately either to L. cuprina or L. sericata, one or more of the other characters must be used.

(3) **Width of Frontal Stripe.**—The region between the antennae and the ocelli is divided into three areas, namely a median frontal stripe, on either side of which lie the parafrontals (Figs. 3 and 4). The feature distinguishing the two species is the relative widths of the frontal stripe and parafrontals at a level midway between the base of the antennae and the anterior ocellus.

In *L. cuprina* the frontal stripe at this level is equal to, or a little broader than, the width of a parafrontal. In *L. sericata* the frontal stripe is considerably broader (generally at least twice as broad) than either of the parafrontals. Confusion sometimes arises in female *L. cuprina* which occasionally may have the frontal stripe almost twice as wide as a parafrontal. It is, however, a reliable character for males.

**Characters on the thorax**

(4) **Hairiness of the Lateral Areas of the Mesonotum** (Figs. 5, 6, and 7).—The mesonotum consists of a middle region, on each side of which are two lateral areas. The anterior, somewhat semicircular, areas are sometimes known as the "humeral calli" and the posterior triangular areas as the "notopleura."

**Humeral calli.**—Arranged transversely across the humeral calli (Figs. 6 and 7) there are three or four large bristles. On the area posterior to these there are, in *L. cuprina*, two or four (rarely up to eight) hairs, whereas in *L. sericata* there are typically six to eight hairs, although all numbers between four and thirteen may be found. Although these hairs can be seen very easily in well-preserved specimens (magnification 30x to 40x), this portion of the body is often rubbed and the bristles and hairs broken off.

**Notopleura.**—Near the posterior edge of each notopleuron (Figs. 6 and 7) there is a large bristle which can be used to demarcate a narrow region lying between it and the posterior border of this sclerite. In *L. cuprina* there are three to five hairs on this area, whereas in *L. sericata* there are not only eight to sixteen hairs, but these are longer than those of *L. cuprina*. Furthermore, the remaining area of the notopleuron is more sparsely clothed with hairs of shorter length in *L. cuprina* than in *L. sericata*. It is convenient, however, to restrict the area examined to that demarcated above, since this area is less frequently damaged than the remainder of the notopleuron. A magnification of about 40x is required for examination of this character.
(5) **Length of the Second Pair of Presutural Acrostichal Bristles on Meso-notum.**—In *L. cuprina* the second pair of acrostichal bristles (not the dorsocentrals) is much shorter than in *L. sericata*. As a ready means of assessing this, they are, for instance, distinctly shorter than the postvertical bristles (situated lateral to the posterior ocelli (Fig. 2)) and also distinctly shorter than the distance between their point of insertion and the point of insertion of the first pair of postsutural acrostichal bristles (Fig. 5A). In *L. sericata*, the second pair of acrostichal bristles is about the same length as the postvertical bristles and they extend back at least as far as the first postsutural acrostichals (Fig. 5B). This character is very easy to use in well-preserved specimens, but suffers from the disadvantage that the bristles are often broken.

![Diagram of dorsal aspect of thorax of *L. cuprina* (A) and *L. sericata* (B).](image)

(6) **Length of Bristles on the Scutellum.**—On the lateral margin of the scutellum there are a series of stout bristles. Between the two anterior bristles (basal and sub-basal) on either side (see Fig. 5) there are a number of hairs. The feature distinguishing the two species is the relative lengths of these hairs and of those on the dorsal surface of the scutellum. In *L. cuprina* the latter hairs are slightly smaller than, or about equal in length to, the lateral hairs. In *L. sericata* the lateral hairs are considerably longer than the dorsal hairs.
(7) Colour of Fore Femora.—In *L. cuprina* the exterior surface of the femora of the forelegs is characteristically a very distinct metallic green. This is sometimes modified by a coppery or bronzy sheen and less frequently by a bluish sheen. In *L. sericata* the fore femora are dull, with rarely a dark blue metallic sheen.

![Diagrams](image)

Fig. 6.—Diagram of right lateral area of thorax of *L. cuprina*.

Fig. 7.—Diagram of right lateral area of thorax of *L. sericata*.

*a.*, area of humeral calli bearing hairs useful in distinguishing *L. cuprina* and *L. sericata*; *b.*, area of notopleuron bearing hairs useful in distinguishing *L. cuprina* and *L. sericata*; *h.*, humeral calli; *n.*, notopleura.

This is generally a useful and highly reliable character except when specimens of *L. cuprina* have been killed too soon after emergence (when full coloration has not been attained). It is also difficult to use when specimens have been wet with plant or animal juices, or have been exposed to high temperatures. Under these circumstances the colour of the fore femora is duller and darker than in typical specimens and less easy to distinguish from *L. sericata*.

**Characters on the abdomen**

(8) Hairiness of Abdominal Sternites.—This character is of value in separating the males only of the two species. The region involved in this distinguishing character consists of the second, third, and fourth sternites, together with the adjoining margins of the second, third, and fourth tergites. When viewed laterally it can be seen that this region bears a number of stout bristles.

In *L. cuprina* these bristles are much longer than those on the hind femora and tibiae, whereas in *L. sericata* the bristles are about the same length as those
on the hind legs. This character is noteworthy in that it is the only one observed in which there is greater bristle development in *L. cuprina* than in *L. sericata*, but it is not an easy one to use without experience.

(9) *Contour of the Last Abdominal Tergite.*—In dried specimens of *L. cuprina* the contour of the last abdominal tergite is smooth without depressions, whereas in *L. sericata* this tergite frequently has one or more irregular depressions or dints. This character, which is applicable to dried specimens only, apparently depends on the hardness of the tergite and its resistance to distortion after death of the fly. It is unreliable, therefore, in flies which have been killed too soon after emergence and before hardening has been completed.

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Fig. 8.—Posterior (exterior) view of male genitalia of *L. cuprina*.

Fig. 9.—Posterior (exterior) view of male genitalia of *L. sericata*.

*s.t.c.*, sub-terminal clasper; *t.c.*, terminal clasper.

(10) *Male Genitalia* (Figs. 8 and 9).—Three differences can be seen between the two species in the terminal and subterminal claspers when the dorsal surfaces of these structures are compared:

(i) In *L. cuprina* the terminal claspers are long and slender, the outer margins of the apical third being parallel. In *L. sericata* the terminal claspers are broader and they taper regularly, so that the outer margins of the apical third converge and are not parallel.

(ii) In *L. cuprina* the subterminal claspers are slender and similar in shape to the terminal claspers. In *L. sericata* the subterminal claspers are very much broader than in *L. cuprina*, particularly at their basal half.

(iii) In *L. cuprina* the subterminal claspers are nearly parallel to the terminal claspers, whereas in *L. sericata* the subterminal claspers are nearly semicircular.

(11) *General Appearance.*—In general appearance *L. cuprina dorsalis* is typically a metallic coppery-green, *L. sericata* a bluish green without any coppery sheen. However, there are too many exceptions for this to be a reliable
character. For instance, *L. cuprina* specimens exposed after death to high temperatures (e.g. strong sunlight) often become bluish green and, at times, specimens of *L. sericata*, particularly when freshly killed, have a coppery appearance.

In general, *L. cuprina* is a smaller and more slender fly than *L. sericata*. However, size alone may be deceptive since, due to limitation of larval food, small adults of both species are not uncommon.

**Characters of type of L. cuprina cuprina**

Except for general coloration (see earlier) Wiedemann’s type female of *L. cuprina* agrees with Australian *cuprina* in all the above characters which can be used (K. R. Norris, personal communication). Thus, the hairiness of the central region of the occiput is typical; the clypeus is black; the frontal stripe is about 1½ times the width of a parafrontal; there are two hairs behind the bristles on the humeral calli; the notopleural hairs are typical; and the right fore femur is green. The left fore femur, the presutural acrostichals, and the dorsal hairs on the scutellum are missing.

(ii) *Larvae*

Fuller (1932) has described several features whereby *L. cuprina* and *L. sericata* larvae may be distinguished from one another. Although some of these are useful, others do not appear to be valid. For example, the anterior spiracles of *L. cuprina* were stated to have seven or eight finger-like processes and *L. sericata* ten. In larvae available to us, *L. cuprina* has an average of seven processes (range five to nine) and *L. sericata* has an average of eight (range six to ten). Although this feature can be used to distinguish two populations, it is

![Diagram of buccopharyngeal armature](image)

Fig. 10.—Lateral view of buccopharyngeal armature of *L. cuprina*.

Fig. 11.—Lateral view of buccopharyngeal armature of *L. sericata*.

*m.h.*, mouth hooks; *v.c.*, ventral cornua.

clearly of limited value in assigning a single larva to a given species. A number of differences were described in the mouth hooks of the two species, but the only constant difference appears to be that the hooks are slightly more curved in *L. cuprina* than in *L. sericata* (Figs. 10 and 11). An apparently constant difference, which was not recorded, but is readily seen, is in the shape of the posterior edges of the ventral cornua. In *L. cuprina* the ventral border is prolonged posteriorly. In *L. sericata* this edge is relatively straight (Figs. 10 and 11). The shape and degree of sclerotization of the posterior spiracles
of the two species (Table 2) is as described by Fuller (1932) but the differences are apparent only to the practised observer. It is clear, however, from Table 2 that there are recognizable differences between the larvae of the two species.

Patton (1920) records six to eight processes in the anterior spiracles of *L. cuprina* from the Orient, whereas Knipling (1936) states that there are four to six in *Phaenicia pallescens* (*L. cuprina*) from North America.

*L. sericata* is said to have ten to eleven processes in England (Patton and Evans 1929) and five to ten in North America (Knipling 1936).

### Table 2

<table>
<thead>
<tr>
<th>Character</th>
<th><em>L. cuprina</em></th>
<th><em>L. sericata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (fully grown)</td>
<td>12 mm.</td>
<td>14 mm.</td>
</tr>
<tr>
<td>Mouth hooks</td>
<td>Distinctly curved</td>
<td>Rather less curved</td>
</tr>
<tr>
<td>Ventral cornua</td>
<td>Posterior edge prolonged ventrally</td>
<td>Posterior edge relatively straight</td>
</tr>
<tr>
<td>Posterior spiracles</td>
<td>Roughly oval in shape, peritreme wide and dark</td>
<td>Somewhat pear-shaped, peritreme narrow and not heavily sclerotized</td>
</tr>
<tr>
<td>Anterior spiracles</td>
<td>Composed of 7 finger-like processes (av.)</td>
<td>Composed of 8 finger-like processes (av.)</td>
</tr>
</tbody>
</table>

### III. Geographical Distribution of *L. sericata* and *L. cuprina*

*L. sericata* is almost cosmopolitan, having been recorded from all the temperate countries of the world (British Isles, Europe, Africa, Asia, Japan, Australia, New Zealand, North and South America). Hall (1948), however, states that no specimens were collected in Central or South America in 1942 and 1943, nor on any of the islands of the central or south-west Pacific in 1944 and 1945, although over 100,000 flies were collected in these areas. This may be because the regions concerned are unfavourable for *L. sericata* or because this species has not been introduced. It is interesting to note, for example, that Miller (1939) concluded that *L. sericata* has become common in New Zealand only since the closing years of last century. Experience in Australia (see later) suggests that this species occurs principally in the vicinity of homes, which evidently provide suitable requirements often absent elsewhere.

*L. cuprina* occurs in North and South Africa, Madagascar, Mauritius, India, Assam, Malaya, Indo-China, Laos, China, Java, Soembawa, Timor, Australia, Fiji, Hawaii, North and South America (Brazil). It has not been recorded from the British Isles, Europe, or New Zealand. In 1949 some thousands of blowflies were trapped by B. A. O'Connor in the vicinity of Suva, Fiji, but not a single *Lucilia* was taken. In general, *L. cuprina* appears to be restricted to the warmer sub-equatorial regions, whereas *L. sericata* not only
occurs in these regions, but extends also into the cooler regions of the world. *L. cuprina* appears to tolerate semi-arid conditions better than *L. sericata*, which is typically found in habitats of high humidity.

IV. Distribution of the Two Species According to Habitat

Mackerras and Fuller (1937) record that *L. cuprina* is very widespread in Australia. It occurs in all mainland States (Fig. 12), but has not yet been recorded from Tasmania. It reaches its greatest abundance in the subtropical and semi-arid regions of northern New South Wales and southern Queensland, particularly during spring and autumn. However, it is abundant also on the cooler southern New South Wales tablelands, and in mountainous as well as low-lying districts. One of the most important factors limiting its distribution appears to be the presence of susceptible sheep on which to breed (Waterhouse 1947). On the other hand, although *L. sericata* has been recorded from all States, including Tasmania (Fig. 13), it is usually an uncommon fly, except in limited areas, and its distribution has no relation to the distribution of sheep. It is known principally from closely settled districts in the cooler parts of Australia, conditions provided by domestic gardens and associated refuse apparently favouring the maintenance of quite dense populations.
However, it has also occasionally been taken many miles from the nearest permanent habitation.

*L. sericata* occurs commonly in Canberra gardens and *L. cuprina* in the open savannah woodland, characteristic of much sheep-grazing country, which surrounds Canberra. An examination was made, therefore, of the preferences of the two species for these habitats. The method employed was to count the numbers of the two species caught in similarly constructed and baited traps exposed simultaneously in a garden, in open country, and in intermediate situations.

![Map showing known distribution of *L. sericata*.](image)

In the first experiment the catch from a trap exposed in a well-watered garden with luxuriant green vegetation was compared with catches from traps placed in an unwatered orchard on the outskirts of Canberra, and in three traps placed in open grazing country (Table 3). In the garden, *L. cuprina* formed less than 1 per cent. of the *Lucilia* specimens trapped, in the orchard only 11 per cent., whereas in open country 82-94 per cent. of the *Lucilia* specimens were *L. cuprina*. This suggested a definite preference of *L. cuprina* for open country and of *L. sericata* for more humid, vegetated situation.

To obtain further data, a second experiment was carried out in which the catch from the garden was compared with that from a trap situated 85 yards away in a dry, open, conifer plantation and with other traps extending 760 yards in roughly a straight line into open country (Plate 1). Three traps were also exposed five miles from the city on a sheep-grazing property. It can be seen (Table 4) that, whereas only about 1 per cent. of *Lucilia* specimens
caught in the garden were *L. cuprina*, the proportion rose to about 40 per cent. less than quarter of a mile away in open country and to 97 per cent. five miles from the city on a sheep property. This general trend was followed closely during each of the three trapping periods (Table 4). The numbers of *L. cuprina* caught in traps 1 to 6 were not greatly different and the variation in the percentages of this species in the catches was principally due to the fact that far larger numbers of *L. sericata* were caught in the garden and the plantation (traps 1 and 2) than elsewhere. It appears, therefore, that *L. sericata* has a very definite preference for the conditions prevailing in the garden. *L.

### Table 3

#### RESULTS OF TRAPPING *LUCILIA* IN DIFFERENT HABITATS (23.xi.48 TO 25.xi.48)

<table>
<thead>
<tr>
<th>Type of Locality</th>
<th>Number of <em>Lucilia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>L. cuprina</em> (%)</td>
</tr>
<tr>
<td>Humid garden</td>
<td>0.7</td>
</tr>
<tr>
<td>Unwatered orchard adjoining a garden</td>
<td>No sheep in vicinity</td>
</tr>
<tr>
<td>Open grassland near irrigated plots</td>
<td>Sheep near trap</td>
</tr>
<tr>
<td>Lucerne paddock near irrigated plots</td>
<td>Sheep near trap</td>
</tr>
<tr>
<td>Open dry grassland</td>
<td>Sheep near trap</td>
</tr>
</tbody>
</table>

### Table 4

#### RESULTS OF TRAPPING *LUCILIA* IN DIFFERENT HABITATS

<table>
<thead>
<tr>
<th>Trap No.</th>
<th>Type of Locality</th>
<th>Distance from Garden (yds.)</th>
<th>Period 1</th>
<th>Period 2</th>
<th>Period 3</th>
<th>Percentage <em>L. cuprina</em> of total <em>Lucilia</em></th>
<th>Number of <em>Lucilia</em> caught</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>14-21.xi.48</td>
<td>21-23.xi.48</td>
<td>25-28.xi.49</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Humid garden</td>
<td>0</td>
<td>1.5</td>
<td>1.2</td>
<td>1.6</td>
<td>45</td>
<td>3246</td>
</tr>
<tr>
<td>2</td>
<td>Unwatered plantation</td>
<td>85</td>
<td>8</td>
<td>5</td>
<td>17</td>
<td>35</td>
<td>390</td>
</tr>
<tr>
<td>3</td>
<td>Grassland within plantation</td>
<td></td>
<td>150</td>
<td>34</td>
<td>27</td>
<td>40</td>
<td>79</td>
</tr>
<tr>
<td>4</td>
<td>Open grassland</td>
<td></td>
<td>390</td>
<td>37</td>
<td>55</td>
<td>40</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td>Open grassland</td>
<td></td>
<td>610</td>
<td>42</td>
<td>42</td>
<td>40</td>
<td>32</td>
</tr>
<tr>
<td>6</td>
<td>Open grassland</td>
<td></td>
<td>760</td>
<td>44</td>
<td>47</td>
<td>47</td>
<td>22</td>
</tr>
<tr>
<td>7</td>
<td>Sheep-grazing property</td>
<td></td>
<td>96</td>
<td></td>
<td></td>
<td>96</td>
<td>24</td>
</tr>
<tr>
<td>8</td>
<td>Sheep-grazing property</td>
<td></td>
<td>98</td>
<td></td>
<td></td>
<td>98</td>
<td>42</td>
</tr>
<tr>
<td>9</td>
<td>Sheep-grazing property</td>
<td></td>
<td>97</td>
<td></td>
<td></td>
<td>97</td>
<td>34</td>
</tr>
</tbody>
</table>

*STATUS OF TWO SPECIES OF LUCILIA*
*cuprina*, on the other hand, does not exhibit such a clear preference for any of the situations examined.

This is in accord with the work of Gilmour, Waterhouse, and McIntyre (1946) who found that, in the Canberra district at least, the *L. cuprina* population ranged widely and at random over the countryside, individual flies being capable of covering up to about five miles in less than 30 hours. The larger numbers of *L. cuprina* trapped five miles from Canberra than elsewhere (Table 4) are probably due to the presence of sheep in the immediate vicinity of these traps, whereas no sheep were near traps 1 to 6 during, or for some time before, the experimental period. A similar explanation probably holds for the comparatively high catches of *L. cuprina* in the three traps of the first experiment (Table 3) which were exposed in the vicinity of sheep. Because sheep are specifically attractive to *L. cuprina* and particularly to the gravid female of this species (Mackerras and Mackerras 1944), one would expect a somewhat higher density of these flies near sheep than elsewhere. Furthermore, any struck sheep would result, at least temporarily, in a considerable local increase in the numbers of *L. cuprina*.

Cragg (unpublished data) found that, in North Wales, *L. caesar* is present in highest density along hedgerows and that the rate of dispersal of a population is comparatively slow. It may be inferred from the present experiments that in Australia *L. sericata* behaves similarly. In Canada and U.S.A., *L. sericata* frequents urban districts, where it is common on almost any kind of garbage, especially when this contains meats or damaged fruit. It frequently rests on leaves of vegetables and shrubs and is attracted to honeydew (Hall 1948). Its observed behaviour in Australia is similar to that recorded from America.

V. HYBRIDIZATION EXPERIMENTS

Successful crosses between *L. cuprina* and *L. sericata* were made by Mackerras (1933), but no details are given except that a F₁ male and a F₁ female from a male *L. cuprina* × female *L. sericata* mating were both indistinguishable from typical *L. cuprina*. These F₁ hybrids were used in a fertility experiment, one particular female laying 3171 eggs. Since this was considerably more than usually obtained either from pure *L. cuprina* or pure *L. sericata* it was suggested that hybrid vigour might be responsible. The results were not published in any further detail because, by the criteria then available (coloration of fore femora and structure of male genitalia) all flies of F₁ and F₂ generations of this and the reciprocal cross exhibited only *L. cuprina* characters, a result which could not be explained on the basis of any known behaviour of genes. The only other information available on these experiments is that the original species crosses produced few eggs, which seemed to support the idea that this was an unusual cross (M. J. Mackerras, personal communication).

Some of the flies from these crosses are still available for study. These were examined using the characters described earlier. All the flies (Table 5) of the F₁ and F₂ generations are typical *L. cuprina*. 
In an endeavour to check these extraordinary results, pupae from pure *L. cuprina* and *L. sericata* cultures were separated into individual tubes a day or two before emergence and the adults subsequently sexed and set up in cages as shown in Table 6. Fresh liver was provided daily and each cage was supplied continuously with sugar and water. The cultures were kept at about 25°C. and 30 per cent. relative humidity, conditions under which both species breed readily.

### Table 6

**DETAILS OF *L. CUPRINA* AND *L. SERICATA* CROSSES**

<table>
<thead>
<tr>
<th>Parents</th>
<th>Type of Experiment</th>
<th>No. of Tests</th>
<th>No. of <em>L. cuprina</em> per Experiment</th>
<th>No. of <em>L. sericata</em> per Experiment</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. cuprina</em></td>
<td>Single pairs</td>
<td>29</td>
<td>1</td>
<td>1</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>6</td>
<td>6</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>35</td>
<td>3</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>10</td>
<td>9</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>14</td>
<td>10</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>21</td>
<td>32</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>7</td>
<td>14</td>
<td>No larvae</td>
</tr>
<tr>
<td><em>L. sericata</em></td>
<td>Single pairs</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>9</td>
<td>8</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>9</td>
<td>9</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>16</td>
<td>16</td>
<td>No larvae</td>
</tr>
<tr>
<td></td>
<td>Communal cages</td>
<td>1</td>
<td>50</td>
<td>25</td>
<td>290 F1 adults</td>
</tr>
</tbody>
</table>

Eggs were laid in a number of these negative experiments, but failed to hatch. The amount of oviposition was no greater, however, than would have been expected from unfertilized females.

In the only successful cross 25 male *L. sericata* and 50 female *L. cuprina* were kept in a 12 × 12 × 12 in. cage. Although 10 egg masses were laid
over a period of about a month, larvae were produced on only seven occasions, resulting in 151 male and 139 female F₁ hybrids. Since the number of offspring per female from an intra-species cross generally lies between 300 and 500 the small number of progeny (290) obtained indicates that the cross was not a very successful one. Perhaps only one of the 50 females was responsible for laying the fertile eggs.

The reciprocal cross (21 male L. cuprina × 32 female L. sericata) carried out at the same time under identical conditions produced eggs on many occasions, but none hatched.

The 75 parents and 290 F₁ hybrids from the successful cross were examined individually for all characters except male genitalia. All the parents were typical of the particular species to which they belonged (Table 6). The results of the examination of hybrids may be summarized as follows:

Characters in which L. cuprina was usually dominant:

(a) Sclerotization of clypeus (generally black or dark brown).
(b) Coloration of fore femora (about 5 per cent. of individuals had legs which were duller than typical L. cuprina).
(c) Length of ventral abdominal bristles in the male.
(d) Length of bristles on the scutellum.

Characters in which L. sericata was sometimes dominant:

(a) Length of second pair of presutural acrostichal bristles (often nearly as long as in L. sericata, but many intermediates occurred).
(b) Width of frontal stripe in male.
(c) Width of frontal stripe in female (although there were many intermediates).
(d) Contour of the last abdominal tergite.

Characters generally intermediate between the two species (see Table 7):

(a) Occipital bristles (about 10 per cent. indistinguishable from L. cuprina, but less than 1 per cent. indistinguishable from L. sericata).
(b) Hairiness of humeral calli.
(c) Hairiness of notopleura.

About 80 per cent. of the F₁ hybrids had characters or combinations of characters which clearly placed them as intermediates between L. cuprina and L. sericata but generally closer to L. cuprina. About 10 per cent. were indistinguishable from L. cuprina and the remaining 10 per cent. distinguishable only with varying degrees of difficulty. No F₁ hybrids were found that could be confused with L. sericata. Although the "dominant" characters of L. cuprina and L. sericata generally appeared together in the progeny, there did not appear to be any close linkage between any of the characters examined, since any character at times varied independently of any other.

F₂ progeny were obtained from three of the seven batches of F₁ hybrids. One hundred and forty-eight F₂ males and 117 F₂ females from three separate ovipositions of one of these three F₁ batches were examined and all were found
to be indistinguishable from typical *L. cuprina*. On the other hand, of 25 F₂ males and 31 F₂ females from the other two batches of F₁ hybrids that laid eggs, one male and six females were indistinguishable from *L. cuprina*, three males and one female were indistinguishable from typical *L. sericata*, and the remainder were intermediates, although many of the latter only differed from one or other species by a single character.

**Table 7**

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Occipital Hairs</th>
<th>Humeral Calli</th>
<th>Notopleura</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. cuprina</em></td>
<td>Male</td>
<td>1 (0-2)</td>
<td>2 (0-8)</td>
<td>3 (2-5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(5% with 2 on one side)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. cuprina</em></td>
<td>Female</td>
<td>1 (1-3)</td>
<td>2 (0-7)</td>
<td>3 (1-5)</td>
</tr>
<tr>
<td>(parents)</td>
<td></td>
<td>(20% with 2 on at least</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>one side); (1 with 3 on one side)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. sericata</em></td>
<td>Male</td>
<td>6 (4-9)</td>
<td>8 (6-13)</td>
<td>11 (9-16)</td>
</tr>
<tr>
<td>(parents)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. sericata</em></td>
<td>Female</td>
<td>8 (5-14)</td>
<td>6 (4-12)</td>
<td>11 (9-15)</td>
</tr>
<tr>
<td><em>F₁</em></td>
<td>Male</td>
<td>2 (1-5)</td>
<td>5 (1-11)</td>
<td>7 (2-11)</td>
</tr>
<tr>
<td><em>F₁</em></td>
<td>Female</td>
<td>2 (1-6)</td>
<td>3 (1-7)</td>
<td>5 (4-9)</td>
</tr>
</tbody>
</table>

Summing up, it is clear that there is considerable difficulty in obtaining successful matings between *L. cuprina* and *L. sericata*. Most of the F₁ hybrids exhibited characters of both species, although some could not be distinguished from *L. cuprina*. The picture in the F₂ generation is very complicated. Some entire F₂ batches are typical of *L. cuprina*, whereas others are mainly intermediates. Further work is required before an explanation can be advanced for this result and for the results of Mackerras.

General confirmation of our findings comes from some material* of Ullyett’s crossing experiments, which have been outlined earlier (Ullyett 1945). The specimens comprised 12 male *L. cuprina*, 9 female *L. sericata*, which were used as parents, and 7 male and 6 female F₁ hybrids. The male *L. cuprina* were typical, except that the frontal stripe was rather more divergent ventrally than usual (i.e. they tended slightly towards *L. sericata* in this respect). The abdominal coloration was indistinguishable from that of Australian male *L. cuprina* and *L. sericata* and varied from coppery to green. Six of the female *L. sericata* were typical; the wings of the remaining three were crumpled and the ptilinum had not been properly retracted. There was no blue coloration whatever of the abdomen. The hybrids were typical of *L. cuprina* in all our characters except the degree of sclerotization of the clypeus, which was typical of *L.

* Made available by courtesy of the Division of Entomology, Pretoria.
sericata. All must therefore be regarded as intermediates. The abdominal coloration of these hybrids was a deeper bluish green than that of their parents and the first visible segment had a bluish sheen in most specimens, but not all. This may be due to different conditions of drying (they were pinned 11 days after their parents), since the authors have found that specimens tend to become bluish if they are dried at higher temperatures than usual. No support whatever could be found from these specimens for Ullyett's contention that abdominal coloration is useful for distinguishing between L. cuprina and L. sericata.

VI. RELATION OF THE TWO SPECIES TO BLOWFLY STRIKE

(a) Attractiveness of Sheep to the Two Species

There is good evidence from insectary experiments that L. sericata does not lay its eggs on sheep as readily as does L. cuprina (Mackerras and Mackerras 1944). In one experiment eight sheep were exposed for a week in an insectary to gravid L. sericata, eggs being laid on two of the sheep. Some L. cuprina were then added to the insectary, and, within four hours, all eight sheep had eggs laid on them, indicating that the sheep were more attractive to L. cuprina than to L. sericata. Some of the freshly laid eggs were collected from each sheep and allowed to develop. From seven of the eight sheep these eggs produced both L. cuprina and L. sericata and from the eighth sheep only L. cuprina. It is clear, therefore, that oviposition by L. cuprina stimulated L. sericata to lay eggs on sheep which they had previously ignored.

In another experiment three sheep were exposed in turn in a small cubicle to a high density of mature L. sericata. After about five hours, when no eggs had been laid, each was transferred to a similar density of L. cuprina in another cubicle, eggs being laid on each sheep within two hours. When similar sheep were exposed first to L. cuprina, oviposition followed in the first few hours (Mackerras and Mackerras 1944).

Cragg (1950a) has also obtained results with L. sericata in Great Britain under field conditions which indicate that this species and Australian L. cuprina show marked differences in behaviour.

(b) Importance of the Two Species in Causing Strike

Records of the occurrence of the two species in field strikes in Australia (Table 8) show quite clearly that L. cuprina is far more important than L. sericata in producing strike wounds. In the Australian Capital Territory, from which the most strikes were examined, 58.3 per cent. of the L. cuprina strikes contained no other species, while only 3.8 per cent. of the L. sericata strikes contained this species alone. L. sericata was present in significant numbers in one year only. The relatively small number of L. sericata strikes and the small percentage in which this species alone occurs is doubtless due to two factors. One is the comparatively low population density of this species in open country and the second is the fact that it is not as powerfully attracted as L. cuprina. 
to lay its eggs on sheep. Its presence in strikes principally from around Canberra may be a result of the fact that sheep are grazed closer to gardens here than is common in other parts of Australia.

*L. cuprina* is the principal cause of blowfly strike in South Africa (Hepburn 1943; Monnig and Cilliers 1944) and it has also been recorded as attacking sheep in Kenya (Lewis 1933). It is apparently of no economic importance in North America as far as sheep are concerned (Hall 1948), nor is it a serious sheep pest in the Orient, possibly owing to the presence of relatively few susceptible sheep.

**Table 8**

<table>
<thead>
<tr>
<th>State</th>
<th>Number of Strikes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>L. cuprina</em></td>
</tr>
<tr>
<td>Queensland</td>
<td>197</td>
</tr>
<tr>
<td>New South Wales</td>
<td>242</td>
</tr>
<tr>
<td>Australian Capital Territory</td>
<td>696</td>
</tr>
<tr>
<td>South Australia</td>
<td>196</td>
</tr>
<tr>
<td>Western Australia</td>
<td>175</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1506</td>
</tr>
</tbody>
</table>

*L. sericata* is the principal sheep blowfly of the British Isles (Davies 1934; Macleod 1943; Ratcliffe 1934) and is one of the two important sheep blowflies of New Zealand (Miller 1939). Blowfly strike of sheep by *L. sericata* occurs also in South Africa (Hepburn 1943) and in U.S.A. (Bishop 1915), but this species is not a serious pest in either country. *L. sericata* does not appear to attack sheep at all commonly in eastern Europe (Cragg 1950b) or in the Ukraine or in Northern Caucasus (Paramonov 1937), although it is not an uncommon fly in these regions.

**VII. Discussion**

It is abundantly clear from the evidence presented that the flies known in Australia as *L. cuprina* and *L. sericata* are distinct species. Not only are there many constant morphological differences between the adults, but the larvae can also be distinguished; hybridization experiments suggest that there is often considerable difficulty in obtaining successful matings; examination of several thousand wild *Lucilia* failed to reveal any intermediates; ecological studies show that the two species have different habitat preferences and that their geographical distribution is not alike; their degree of attraction to living sheep is very different; and finally there are physiological differences.

One result of these physiological differences is the larger size of both larvae and adults of *L. sericata* when this species and *L. cuprina* are bred in an identical fashion and provided with adequate food. Further, the duration of the developmental period from egg to adult is significantly longer in *L. sericata* (14-15 days at 25°C.) than in *L. cuprina* (12-13 days).
Many interesting problems have arisen in the course of this survey of the two species. What, for example, are the factors which restrict the spread of *L. sericata* from the vicinity of dwellings into the surrounding country, and where do they breed? When one or two hundred *L. sericata* were trapped on each of several consecutive days in the Canberra garden (Tables 2 and 3) there was no apparent fall in the numbers of wild *L. sericata* remaining. In this area there could scarcely have been sufficient dead vertebrates (none were known to exist at all) to maintain a relatively steady population, apparently equivalent to between 500 and 1000 *L. sericata* per acre. It would be interesting to determine whether this species can maintain a high population density by breeding in vertebrate excrement, particularly since it has been recorded in small numbers from pig manure (Thomsen 1938) and both it and *L. cuprina* from fowl manure (Illingworth 1923; Tanada, Holdaway, and Quisenberry 1950). Other possible breeding grounds are small invertebrates (e.g. dead snails or fleshy insects) and vegetable material. *L. cuprina* is thought not to be able to maintain a high population density in the absence of sheep (Waterhouse 1947), and even in typical sheep country near Canberra its population density is comparatively low, densities of 0.3 to 5.7 per acre being recorded at different times of the active sheep blowfly season (Gilmour, Waterhouse, and McIntyre 1946).

Another question which arises is whether or not *L. cuprina* and *L. cuprina dorsalis* are really quite distinct in spite of the fact that there do not appear to be any constant morphological differences which would enable a taxonomist to assign specific status to them. The most striking differences are in general coloration and in the fact that, in North and South America, which are the only important sheep-raising countries falling within its distribution, *L. cuprina cuprina* is not an important sheep pest. The latter might be due to the fact that American sheep are relatively insusceptible to blowfly strike, although this is improbable in view of the common occurrence in some regions of the wrinkly Vermont breed.

From South Africa the bulk of the evidence on habits and behaviour of *L. cuprina* and *L. sericata* and also a morphological comparison of specimens from that country and from Australia suggest that the respective *Lucilia* species are very similar, perhaps even identical, in the two countries. There is as yet insufficient evidence to decide whether or not *L. sericata* from England and Australia are similar in physiology and behaviour as well as in morphology.

Finally, the hybridization experiments indicate a most unusual state of affairs, which does not appear to be at all clear on the basis of simple Mendelian laws. Although the early results of Mackerras could not be substantiated in detail because of difficulties of securing successful crosses, our one fertile mating demonstrated that it was possible to obtain at least some F₁ hybrids which were apparently typical *L. cuprina* and also that the entire F₂ progeny from some (but not all) F₁ hybrids appeared to be typical *L. cuprina*. Mackerras (1933) found that *L. cuprina* characters were dominant even if the original male parent was *L. cuprina* and the female *L. sericata*, a cross which
the authors could not repeat. A comparable result does not appear to have been recorded before, although it is known from mosquitoes that the characters of the female may appear in all offspring. For example, when Aedes albopictus males are mated with A. aegypti females, the F₁ and F₂ progeny have A. aegypti characters (7 features examined) (Downs and Baker 1949; Toumanoff 1937), but if male A. aegypti are crossed with female A. albopictus the F₁ and F₂ progeny are typical of A. albopictus (Hoang-Tich-Try 1939; Toumanoff 1937, 1939). Crosses between L. cuprina and L. sericata appear to be well worthy of further attention by the geneticist.

It has been suggested that L. cuprina was introduced into Australia, and the history of the spread of blowfly strike supports this view (Joint Blowfly Committee 1933). More recent evidence lends further support. For instance, the gradual spread of this species up the coast of Western Australia, which was recorded by Mackerras (1936) and Mackerras and Fuller (1937) is apparently still continuing (Jenkins 1945). Thus strike, believed to be due to L. cuprina, was first recorded at Mt. Anderson (near Derby) in 1942, although at that time properties further east in the Fitzroy basin had experienced no trouble. Furthermore, there are other corroborative reports, such as from Nappamerrie station (extreme south-western Queensland), where sheep were run from 1900 to the late ’twenties with no blowfly trouble. In the late ’twenties, successive severe waves of strike caused sheep-raising to be abandoned in this district. However, as recently as November 1949, L. cuprina was taken at Nappamerrie, so that it is evidently able to maintain a population for 20 years or more in the absence of sheep. It is most unlikely that there would have been some 30 successive strike-free years if L. cuprina had always occurred in this region, as would be expected if it were a native species.

There is now no support for the view (Joint Blowfly Committee 1933) that L. cuprina dorsalis was introduced into Australia from the East (i.e. Eastern Asia, or the islands to the north of Australia), since it is not known to occur in this region. It now appears more probable that it was introduced from South Africa or India during the last century. The fact that there are no records of strike in Australia before 1883 (Joint Blowfly Committee 1933) does not necessarily mean that L. cuprina dorsalis was introduced about that time, since the first strikes were recorded in South Africa about 1900 (Smit 1931), although dorsalis (Robineau-Desvoidy 1830) and argyrocephala (Macquart 1846) had been present for at least 70 years before that time. If L. cuprina cuprina is found to occur in Northern Australia (and this possibility cannot be ruled out without further collections from this region) it would be circumstantial evidence in support of the view that L. cuprina dorsalis is an introduced species.

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Aerial photograph showing the distribution of traps (indicated by white triangles) in the habitat preference experiment.