SPECIES DIFFERENCES IN OVIPOSITOR INSTINCTS WITHIN THE VERMILEONINAE (DIPTERA BRACHYCERA, RHAGIONIDAE = LEPTIDAE)

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1. INTRODUCTION

The senior author (A.M.H.) is responsible for the completion of the project as a whole and for most of the work involved. The junior author (B.R.N.) shared from June 1967 in the planning and carrying out of many experiments and undertook the filming of the ovipository behaviour in the two species Lamprocrypta canariensis and L.fortunata and also participated in the treatment of data and final preparation of figures.

Observations on the ovipository behaviour of Vermileo species have been made by Wheeler (1931, p. 215) on the Nortli American Vermileo comstocki Wheeler, 1918, and by Hafez & El-Moursy (1956b) and Le Faucheux (1961) on Egyptian...
and French populations, respectively, of what they assigned to *Vermileo vermileo* (L., 1758).

This report concerns the differences in stereotyped instinctive ovipository behaviour exhibited by 3 Mediterranean and 3 Canarian species of *Vermileo* reared in Denmark from larvae collected in Tunisia 1961 (*Lampropomia pallida* Macquart, 1835), the Canary Islands 1965-1968 (*L. canariensis* Macquart, 1838, *L. fortunata* Stuckenberg, 1971, and *L. hemmingseni* Stuckenberg, 1971) and the Iberian Peninsula 1965/*L. funebris* Dufour, 1850, and *V. nigriventris* Strobl, 1906). Flies reared from the larvae of *V. vermileo* (L., 1758) collected in Italy in 1961 (cf. Hemmingsen 1968a) copulated but did not oviposit.

We have been very fortunate to profit from the taxonomic advice of Dr. B.R. Stuckenberg, Natal Museum, Pietermaritzburg, South Africa. He has also in a preceding paper (Stuckenberg 1971) described and named the two new endemic species found by A.M.H. in the Canary Islands. *L. canariensis* Macquart, 1838, is the species of the western islands (La Palma, El Hierro, La Gomera and Tenerife). *L. fortunata* Stuckenberg, 1971, lives in the central island, Gran Canaria; and *L. hemmingseni* Stuckenberg, 1971, in the two eastern islands, Lanzarote and Fuerteventura. The latter species is closely related to the Moroccan *L. lecerfi* Séguy, 1928 (Stuckenberg 1971). Dr. Stuckenberg has also checked the identification of all the species on which this paper is based.

The view quoted and held by Stuckenberg in the said 1971 paper that the Canary Islands are vestiges of a former westward extension of Africa is strongly supported for the two eastern islands by the presence of extensive prevolcanic sediments on Fuerteventura and, not least, of fossil ostrich eggs in prevolcanic terrestrial limestone on Lanzarote (Rothe 1964, 1966, 1967 and 1968).

However, according to Rothe (1968), Rothe & Schmincke (1968) and Evers et al. (1970) possibly the other, more western islands may be oceanic in origin.

*Vermileo* larvae (Worm-lions) were collected January-April 1960-69 and altogether 725 flies reared from several localities in all the seven major Canary Islands (Fig. 1). A.M.H. collected at all the localities, except Nos. 28 and 35. In these and Nos. 14, 17, 25-27, 30-33, 36, 37 and 39 Mr. Andreas Lund-Drosvad made for us supplementary collections. But among the resulting images none belonged to the 3 species allegedly occurring in these islands according to early authors apart from *L. canariensis*, viz. *V. vermileo* (L., 1758), *Lampropomia cylindrica* (Fabricius, 1794) and *L. pallida* Macquart, 1835 (see Hemmingsen 1963, p. 238). It is strongly felt that these 3 records should be rejected (cf. Stuckenberg 1971, p. 78).

The larval instincts have been dealt with in previous publications (Hemmingsen 1963, 1968a). In the first of these (1963) their ethological convergence with those of pit-building *Myrmeloiniae* was dealt with, as also in a paper by Hafer & El-Moursy (1964). In the 1963-paper the name *Lampropomia canariensis* Macquart, 1838, should now be corrected to *L. fortunata* Stuckenberg, 1971.

The genus *Lampronotia* was divided by Stuckenberg (1960) into two subgenera. The Mediterranean and Canarian *Lampronotia* species dealt with in this paper fall in the nominate subgenus, *Lampronotiasensu stricto*, but as a matter of convenience this will not be specified every time a species is mentioned. The other subgenus *Vermipardus* remains exclusively South African on present knowledge.

2. TREATMENT OF FLIES

The larvae were fed chiefly on ants, but sometimes other insects were offered, e.g. apterous *Drosophila*, kindly supplied by Dr. O. Frydenberg, Genetic Institute, University of Copenhagen. The pupae were kept at 26°C, and the pupal stage at this temperature lasted about 10 days.

Sometimes one or more pupae were placed at 8°C to delay emergence of imagines until more larvae of the respective species had pupated at the higher temperatures. In this way rather simultaneous emergence of more flies of both sexes.
could be obtained. Pupal durations at different temperatures were tentatively estimated from Hafez & El-Moursy’s data on *Vermileo* (1956b, table II on p. 344) partly by extrapolation.

It was not actually established, however, whether these data are valid in detail for the *Lampronioia* species in question. Our principal concern was with oviposition.

The flies were confined in glass-walled containers (Fig. 2) usually measuring 77 (length) \( \times \) 30 (width) \( \times \) 35 (height) cm or 62 \( \times \) 19.5 \( \times \) 26 cm (rarely 20 \( \times \) 15 \( \times \) 20, see p. 165) with removable wire gauze ceiling and containing a bottom layer of fine sifted sand with particle sizes of 0.4-0.5 mm unless otherwise stated. Small flowers were supplied in vessels with water, as also water and sugar- or honey-water in minute vials.

Previous authors have had difficulties in keeping verinine flies alive because these would not take the sweet liquids offered to them. Yet Buchner (1940) saw *V. vermale* settle on flowers and sip from dew and sweet juices. Wheeler (1931) considered the function of the very long proboscis of *Lampronioia* a complete enigma and suggested that it may be used during oviposition. Stuckenberg (1960, p. 223, and in litt.) refers to lack of mandibles in proboscis, presence of well developed labella, and frequent presence of pollen on body, and surmises nectar-feeding habits.

![Fig. 2. Container used for oviposition studies in Vermileoinae. To the left hygrometer and air-thermometer; in the middle sand-thermometer. Flies seen on the sand. B. R. N. phot.](image)
Both sexes of all the Lampromyia species dealt with in this paper were seen to insert their proboscis into one deep flower after the other (Fig. 3) and they lived up to a week – sometimes even two weeks. The species without a proboscis, Vermileo nigriventris, was also seen to suck (from umbelliferous flowers).

Still, it sometimes seems that there might be some truth in Wheeler’s suggestion, in as much as sometimes the female appears to use the proboscis for extra support during the ovipository process. This might be thought to be especially useful when, as in some species, both fore and middle legs are engaged in covering the egg after it has been laid, so that only the hind legs are firmly resting on the substrate.

A scrutiny of cinematographic pictures taken of two such species, L. canariensis and L. fortunata, reveals, however, that there is no consistency in the position of the proboscis during either phase 1 (digging a pit and laying the egg in it) or phase 2 (egg-covering). Sometimes the proboscis just touches the substrate, sometimes it is gently pressed against it so as to be curved slightly beyond its natural forwardly convex curvature; sometimes it is bored a little into the substrate, e.g. at the termination of egg-covering, or else between substrate and glass wall. But often it does not even touch the substrate, pointing more forward.

III Lampromyia pallida copulation and oviposition, as also the visits to flowers in both sexes, appeared to occur only when the container with the flies was placed either 1) in the sun (but might thereafter continue in the shade) or 2) on overcast
days so common in the Danish climate, or at night — in strong indoor light ("artificial sunlight") produced by a Philips 125 watt bulb mercury lamp emitting 75% white and 25% ultraviolet light (Type 57202 E/21, HP 125 w. 5000 lm; Fin Table I on p. 155). Even at 28-30°C without sun or "artificial sunlight", often nothing happened even though the flies became somewhat more mobile. Only in the sun or "artificial sunlight" at similar or lower temperatures (ca. 26°C) they flew to the flowers and sucked, copulated and performed the ovipository maneuvers. At 20-23°C they were usually inactive.

Perhaps in the sun the insect body is heated above the air temperature, as indicated in experiments by Parry (1951). But the observations in "artificial sunlight" suggest that there is something else in the rays that stimulates the flies.

Later a possibly better imitation of normal sunlight than the above-mentioned 125 watt mercury lamp was established by means of an ordinary white fluorescent tube (Pope FT 40 w/33) in conjunction with a superactinic fluorescent mercury tube emitting 40% white and 60% ultraviolet light (Philips TLA 40 w/05) (C in Table 1).

Eventually, however, it turned out that at least in L. canariensis and L. fortunata oviposition could occur even at such low temperatures as 20-22°C and in the absence of direct or "artificial sunlight".

When in the sun the container must be closed with net and not with a glass lid. Otherwise the flies get overheated and do not survive. In the experiments of which cinematographic pictures were taken and in some other experiments at 20°C, 22°C, 30°C and 35°C, a white incandescent lamp (Philips 500 watt B 220 volt; G in Table 1) was used. In these experiments the substrate (sand) temperature was about 1-2°C above the air temperature in the container; except at 35°C, when on account of the sand being less quickly heated, it was a little below air temperature.

Differences with different sources of heating (central, coke stove, electrical) without thermostat regulation had to be used. All temperatures were measured with mercury thermometers corrected through comparisons with a standard thermometer. They are rounded to the nearest half degree.

An approximate assessment of the illumination was attempted in terms of the international unit of light, lux (meter candle), by means of a selenium cell placed at the sites of oviposition.

The lux unit is based on the spectral sensitivity distribution of the human eye, while the values obtained by the luxmeter used ("Gossen") are based on the spectral distribution of the changes in electrical conductivity of metallic selenium under the action of light.

Comparisons with a luxmeter ("Ljuskultur") with filters corrected for the difference between selenium and human sensitivities showed that while they agreed with incandescent lamps the selenium values would have to be multiplied by the following factors to obtain the correct lux values:
Table 1. Illuminations used.

<table>
<thead>
<tr>
<th>Lamps</th>
<th>Lux (“Gossen” selenium cell)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Ordinary white fluorescent tube (Pope FT 40 w/33)</td>
<td>40-150</td>
</tr>
<tr>
<td>B. Same with additional blue incandescent lamp (Pope 60 w A6 220-230 v)</td>
<td>up to 165</td>
</tr>
<tr>
<td>C. Same tube with additional superactinic tube, (Philips TLA 40 w/05), white and ultraviolet</td>
<td>40-165</td>
</tr>
<tr>
<td>D. Same two tubes with additional blue bulb</td>
<td>up to 285</td>
</tr>
<tr>
<td>E. Same two tubes with Philips HP 125 w mercury lamp, white and ultraviolet</td>
<td>77-750</td>
</tr>
<tr>
<td>F. Philips HP 125 w mercury lamp</td>
<td>&lt;1400</td>
</tr>
<tr>
<td>G. Philips 500 w B incandescent lamp</td>
<td>1900-2600</td>
</tr>
<tr>
<td>H. Philips 500 w B incandescent lamp with Philips HP 125 w mercury lamp, placed immediately above the wire gauze ceiling.</td>
<td>3370</td>
</tr>
</tbody>
</table>

* Measured at sites of oviposition

For the HP mercury lamp 1.85  
For daylight at a window 1.33  
For an ordinary white fluorescent tube 1.25

What is virtually wanted is not the reaction of the human eye but that of the vermilionine eye, and this is unknown, though the insect eye in general is known to be sensitive to shorter wave lengths and to differ in different insect groups as to wave length perceptions. The spectral energy distribution of the light received might serve better. This varies from one source of light to the other, and even in daylight under different conditions. Sources of light giving the same lux values may have quite different energy distributions. It is a complicated matter to calculate this from the lux values measured, especially for the TLA tube.

Therefore, no corrections have been applied, and obviously the values obtained represent but an approximate symbol. Still they will convey a certain impression of the illumination used in the different experiments.

The values measured at the sites of oviposition varied according to position in the container and distance of lamps as in column 2 of Table 1.

On a clear sunny summer day in the open up to 100000 lux or more may be measured; indoors at the window through glass on a clear day, ca. 2000; good electrical illumination 100-1000; in an ordinary lighted room, 15-20. Thus, even if the fraction contributed by the HP lamp in the value of the strongest illumination used (H in Table 1) were corrected by the above factor (maximally (3370-1900) x 1.85 = ca. 2700) the maximal illumination used (2600 ÷ 2700 = 5300) has probably not by far reached the outdoor illumination on a sunny day to which, for instance, as mentioned the container with ovipositing L. pallida was exposed in some cases. Cf. also postscript on p. 202.

For the HP lamp the energy received as calculated from the known energy
distribution of contributiiig wave lengths is for 1400 lux for the white light 334, aid for the ultraviolet fraction 107 microwatt per cm².

However, an undetermined amount of the ultraviolet light will have been absorbed by the glass in the containers. Some part went through the wire gauze cover. And the fraction of ultraviolet light is not niasured by the luximeters. So we can only say that in terms of energy emitted it was 25% of the total emission of light by the HP lamp and 60% for the TLA 40 w tube.

When in some batches of Canarian and Spanish species the females would riot cooperate, the use of extra ultraviolet light (HP 125 watt mercury lamp) in addition to the above-mentioned fluorescent tubes was resorted to (E in Table 1) and was believed to stimulate the females to oviposit. This presumed extra stimulation, if at all real, is believed not to have gone beyond the mere triggering, for we have not been able to find any consistent difference in the effects of the two ultraviolet lamps, superactinic tube and HP 125 w mercury lamp or of their sum. Therefore, what is termed in this paper "artificial sunlight" covers experiments in which one or both of these lamps were used, usually in conjunction with white light from an ordinary white fluorescent tube or an incandescent lamp (C-F in Table 1).

Used in conjunction with the strong light of the 500 w incandescent lamp the direct ultraviolet light of the HP lamp (see H in Table 1) placed immediately above the wire gauze ceiling, seems to have produced an especially stimulating effect (see chapter 11 A). Otherwise, the light intensity discrimination in many insects is known to be poor (references by Wigglesworth 1953, pp. 142-143).

The relative humidity in the containers was not measured in all cases but the values actually measured were 57-85% at 20-22°C, 45-57% at 24-27°C, 50-55% at 30°C and 50% at 35°C. As hair hygronieters were used the values are but roughly approximative.

With some batches of flies no results could be obtained, as they would neither suck nor mate or oviposit, and some showed signs of nervous disturbances and loss of equilibrium. This would sometimes bring us onto the verge of abandoning the whole project.

No ovipositions were, for instance, obtained with 32 flies of Lamprophania (Verminiparans), a not yet determined species, collected as larvae on May 7th, 1967, by Dr. Stuckenegg at Giants Castle, Drakenberg Mountains, South Africa, aidkiidly sent to us. Imagines emerged in July and August 1967 and May 1968; that is, the larvae have presumably been stimulated to pupate by the increasing day length in spring-summer of the Northern Hemisphere, the normal flight period of Verminiparans species in South Africa being October-January (Stuckenegg 1960).

In some species causes of the failure were sought in too long confinement of the larvae in too narrow tubes during transport, lack of some vitamins or other nutritional defects, e.g. caused by the little varied diet consisting of worker ants. But no definite conclusions could be drawn as success was attainied in other batches apparently identically treated.
In the attempt to ensure success with at least one female usually a number of flies of both sexes were confined in the same container. Sometimes individual females could be told by their size, but the results were in general based on a fair number of different females of the same species.

When new flies of the species emerged they were added, replacing those that eventually died. Often no distinction was made between flies from different localities within the island or islands of the species.

No matter whether one individual or different females successively are observed it is impossible to focus attention simultaneously upon all the relevant details in the ovipository behaviour pattern. When counting, for instance, the number of forward thrusts in the air of the downward bent abdominal apex during ovipository digging, it is difficult or in many cases impossible at the same time to count the number of scrapings of the legs, or to establish which legs participate, and if and when the wings quiver, etc. This is why the total number of observations of any single trait in a species is not always the same as with other traits under the same conditions.

Only by repetitions can all the traits be established. A virtual repetition was only possible with cinematographic pictures. Such were obtained in some L. canariensis and L. fortunata at 25-27°C and 20-22°C. The film was exposed at a speed of 32 frames (pictures) per second.

In the beginning, and as mentioned especially with L. pallida, about 26°C appeared to be the lowest temperature at which they would work; and sunlight or "artificial sunlight" appeared necessary. Therefore, all the different species later obtained were also studied at about this temperature and in "artificial sunlight". But as this temperature, as well as the extra ultraviolet light (cf. chapter 11 A), may perhahs in some cases be in excess of the conditions in the open, e.g. in caves, and it later turned out to be possible to work at 20-22°C and in ordinary daylight, some check comparisons were made under these presumably less stimulating conditions (chapter 12).

Between experiments the containers with the flies were transferred to a cool room, where the flies would stay inactive.

3. PROCESSING OF DATA

In all the species there is a pit-digging phase concluding with egg-laying in the pit and followed by egg-covering and pit-refilling in one or two phases.

The duration of the various phases or other ovipository processes were in the most extensive experiments measured with a stop watch with double stopper (addition) in terms of hundredths of a minute, for shortness termed in this paper centi-minutes, abbreviated cmin., in analogy with centimeters and centigrams. For uniformity measurements made originally in terms of seconds have been transferred to cmin.
The durations of any phase 1 (digging) might sometimes under given experimental conditions in some flies in the beginning increase from one oviposition to the next; in others, decrease; to eventually vary at random (cf. Table 2 on p. 159), as also often from the outset in most flies.

With regard to the various details studied it must be expected that virtually there will be a somewhat smaller variation within individuals than between individuals. But this is difficult to ascertain without profound statistical calculations.

For instance, in 15 flies of L. fortunata in which a number of measurements of the length of the digging process (phase 1) could be made in each fly (2-33 measurements in each) the maximum range was at 20-22°C 142 min. (6 ovipositions in one fly); and at 24-27°C, 93 min. (33 ovipositions in one fly); whereas within the whole material the range was at 20-22°C 178; aid at 24-37°C, 123 min. But since for mere statistical reasons the range increases with the total number of observations these data do not prove that the variation is virtually greater between than within individuals.

By collecting a large number of observations on different individual flies under each experimental condition it was attempted to obtain an over-all impression of the variation within the species under that particular condition.

There is some evidence that "durations" in general tend to be skewly distributed in a frequency diagram whereas their logarithms are normally, or at least tend to be normally distributed (Henningsen 1938, Williams 1967, own (A. M. H.) unpublished treatments of published or unpublished data, calls of a canary, telephonic calls, hospitalizations, sickness absences in a firm, duration of parturitions, etc.). This applies also to lengths of the ovipository phases 1 and 2 in Vermilioninae. This is why Log scales are used in Figs. 12, 13, 15, 16, 18 and 19.

Though even the frequency distribution of the logarithms of the phase durations appears to retain in some cases a certain skewness (cf. Fig. 13 on p. 173) statistical tests have been made in a few cases assuming the logarithms of phase 1 to be inherently normally distributed (pp. 176 and 188).

Currently used statistical tests of significance assume that the observations are mutually independent, and may be highly misleading if the observations are even slightly correlated (Hald 1957, p. 760). As mentioned there is likely to be some correlation between observations within each of the individual flies whose phases obtained under identical experimental conditions were pooled (as in Figs. 13, 15, 16, 18, 19) so that the tests can be considered merely orientative.

As to phase 2 the shortest phases lasting less than 1 min., and piut at zero, do not fall into line with the approximately normal distribution of the logarithms of the rest. The measurements of phase 3 have, therefore, in no case been subjected to statistical tests, but are discussed at their face values.
**Table 2. Examples of oviposition data in Lampronotia fortunata. 24-27°C. "Artificial sunlight."**

<table>
<thead>
<tr>
<th>Designation</th>
<th>Duration Number of abdominal</th>
<th>Number of</th>
<th>Thrusts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>of appearance</td>
<td>thrusts until</td>
<td>of egg laid</td>
</tr>
<tr>
<td>V. 501</td>
<td>32</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>19</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>20</td>
<td>23</td>
</tr>
<tr>
<td>V. 505</td>
<td>33</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>V. 5931</td>
<td>9.2</td>
<td>15</td>
<td>15$^3$</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7.5</td>
<td>10</td>
<td>12</td>
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<tr>
<td></td>
<td>6.7</td>
<td>11</td>
<td>13</td>
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<td></td>
<td>25</td>
<td>45</td>
<td>45</td>
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<td></td>
<td>29</td>
<td>43</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>55</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>55</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>V. 757</td>
<td>55</td>
<td>35</td>
<td></td>
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<td></td>
<td>59</td>
<td>43</td>
<td></td>
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<td></td>
<td>65</td>
<td>46</td>
<td></td>
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<tr>
<td></td>
<td>70</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td></td>
<td>78$^2$</td>
<td>57</td>
<td></td>
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<tr>
<td></td>
<td>63$^2$</td>
<td>47</td>
<td></td>
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<tr>
<td></td>
<td>68.5</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td></td>
<td>64</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td></td>
<td>69.5$^2$</td>
<td>ca. 50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>73</td>
<td>56</td>
<td>61</td>
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<tr>
<td></td>
<td>59</td>
<td>49</td>
<td></td>
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<td>45</td>
<td>41</td>
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<td>59</td>
<td>47</td>
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<td></td>
<td>70</td>
<td>61</td>
<td>65</td>
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<tr>
<td></td>
<td>76</td>
<td>48.5</td>
<td></td>
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<td></td>
<td></td>
<td>67</td>
<td></td>
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<td></td>
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<td>72</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>90$^2$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>66.5</td>
<td></td>
</tr>
</tbody>
</table>

1) Presumably lamps as H in Table 1, cf. pp. 156, 172 and 184. 2) Moved during digging. 3) A few slight thrusts after egg-laying. 4) Fell on side.
4. COPULATION

In *Vermileo vermileo* from Italy and *L. nigriventris* from Spain the copulation pairs observed were hanging vertically as pictured by Buchiier (1940) and Hafez & El-Moursy (1956b) and as in Fig. 5a, and lasted from at least 1-4 to 13-4 hours. The copulations in the *Lampromyia* species were as in Figs. 4 og 5a-b. They lasted in *L. pallida* up to 3-4 hour; and in the other *Lampromyia* species, from a few to 15 minutes.

In Fig. 4 the male is on the left side of the female. It has been observed on the right side in *L. canariensis*; in *L. funechris*, on either side; and presumably this may happen in all the species.

5. OVIPOSITION AT ABOUT 26°C OF

*LAMPROMYIA PALLIDA* MACQUART, 1835

The flies of this species were reared in Denmark from larvae collected in March and April 1961 in various places in Tunisia. These localities and the durations of development as well as taxonomic argumentation are specified in the previous paper on the larval instincts (Hemmingen 1968a, pp. 290-292, 298-300).

Standing on fore and hind legs, sometimes perhaps also supported by the pro-
Fig. 5a-b. Copulation in Lamproomyia fortunata. In a, female uppermost; in b, to the left. B.R.N. phot.
boscis, the female starts the ovipository process by digging a small pit in the sand by thrusting the middle legs simultaneously downward backward. (This procedure is common to all the Lampronius species treated in this paper and is shown in Fig. 6 for *L. fortunata*).

The apical part of the abdomen is bent sharply below the abdomen and is thrust forward in the air every time the middle legs scrape backward. This is about two times per min., though with a somewhat varying rhythm.

Somewhat later the middle legs may strike a couple of times prior to the backward stroke that is synchronous with the forward movement of the apical part of the abdomen: later there may be several small strokes before every backward scraping.

Sometimes the rhythm is so much accelerated that the abdominal movements lag behind so as to almost cease.

After 1/2-3/4 min. (examples: 75, 62, 70, 55, 65, 73, 47 min: cf. Fig. 13) the egg, which has meanwhile appeared on the tip of the abdomen (Fig. 7), now kept quiet, is laid in the pit. This concludes phase 1. Then the middle legs quiver in the bottom of the pit (phase 2), thereby covering the egg (Fig. 8). This takes about 1/6-1/4 min. (examples: 18, 28, 22, 25, 20, 23, 22, 25 min.). Finally, by inwardly directed much slower movements the middle legs scrape sand or dust down into the pit (phase 3). This takes place in stages or steps, each stage or step consisting
Fig. 7. Lampronyia pallida. Egg appearing on the tip of the abdomen, ready to be laid. A. M. H. phot.

Fig. 8. Lampronyia pallida. Female covering the egg in the pit by quivering the middle legs in the bottom of the pit. A. M. H. phot.
of 3-6 scrapings (examples of this process of refilling the pit: 112 cmin. in 16-17 stages, 107 cmin. in 19 stages, 123 cmin. in 19 stages, 225 cmin. in 54 stages). During all this the apical part of the abdomen is kept curved forward below the abdomen; but during the closing of the pit, often more vertically. The whole process of digging, oviposition, egg-covering and pit-refilling takes 1.5-4 min. After a little rest the fly flies about, for instance for 2 cmin. or sometimes more, to settle on another spot and start digging again. This is repeated in different places, one egg being laid each time.

The pit may be so long that only the foreniest part of it is filled by the inward scrapings. In addition, in dust, these may produce on the sides two depressions, so that after the whole process there are three small pits often with a small hill between the pits produced by the inward scrapings (Fig. 9).

Sometimes the egg is laid too far in front so that it is not covered. On the first day of oviposition the whole phenomenon may be characterized by lack of practice: To begin with, the pit may be forked in front, each of the two legs creating its own branch of the fork. But usually the partition between the fork branches breaks down during the last part of the digging. Or, the fly places herself head against the glass wall or near to it, with side to it, two pits are made, one with each middle leg. The two legs are always thrust backward simultaneously. Only sometimes the pits coalesce behind; and the egg may be laid in one of them, apparently most often the left one; or it comes to lie on the ridge separating the pits or (3 cases) it sticks to the proboscis. The fly may in such abnormal cases continue the whole show on one spot, where thus several eggs are deposited, usually poorly covered. The rhythmic movements of the abdomen during digging are in such cases not pronounced and sometimes the fly quivers her wings. The proboscis may also in such abnormal cases bore into the sand. Once it penetrated as far as to the head.

When the process is quite normal the two digging legs are kept close together in the middle so that an undivided hollow results.

The pattern of ovipositor behaviour established in the flies emerged in 1961, especially the duration of some of the phases, the total duration of the oviposition behaviour including covering of the egg and the use of only the middle legs in egg- and pit-covering differed so much from what was seen a few years later in the other vermineon species that the wish arose to have the observations on L. pallida repeated and checked.

It was fortunate, therefore, that progeny of the first batch of flies had been reared from eggs laid in captivity in 1961 so that corroborative observations could be made on imagines emerged in 1965.

The above-mentioned extra strokes of the middle legs during digging, the refilling of the pit in stages and the vestiges afterwards (Fig. 9) were observed in the "artificial sunlight" on dust (1965) and had not been expressly noted but may have been present in the behaviour in the sun on sifted sand (1961). On the other hand, the abnormal dippings of two pits were not seen in "artificial sunlight". But the
observations are too few to exclude the possibility that these differences, if at all consistent, may be individual or due to non-controlled factors. There was no indication in the few direct measurements made that the digging phase or the total process lasted longer in sand than in dust but a much larger number of observations would have been necessary to decide the point. The observations in "artificial sunlight" were in this species made in 1965 in much larger containers than those in the sun 4 years before (20 (length) x 15 (width) x 20 (height) cm).

Between ovipositions a male may suddenly copulate with the female. The flies have a humming flight, lower in pitch in the males.

All observations on this species were made at about 26°C.

6. OVIPOSITION AT ABOUJ 26°C OF
LAMPROMYIA CANARIENSIS MACQUART, 1838

Observations were made in the last half of June 1965 and 1967 in "artificial sunlight" at 25.5-27.0°C on females from the island of La Gomera mated with males from La Gomera and Tenerife, on a female from Tenerife mated with a male from La Gomera, and on females from El Hierro and La Palma mated with males from their own island. Finally, in 1967 and 1968 cinematographic pictures were taken in June or July of the oviposition of females from La Palma mated with males from
El Hierro and La Gomera and females from Tenerife mated with males from the same island. All were reared in Denmark from larvae taken in March-April in the respective islands (cf. Fig. 1).

The ovipository behaviour includes a pit-digging phase 1 as in *L. pallida* but egg-covering and pit-refilling have merged into one phase, which we will call phase 2.

The digging (phase 1) by backward directed rapid movements, some of them in far-reaching throws or scrapings, lasts only 9-36 cmin. as against 47-75 cm in *L. pallida* (cf. Fig. 13 on p. 173).

The digging movements are too quick to be counted. The far-reaching backward throws or scrapings which occur at irregular intervals and with varying strength could be counted. Their rate was at about 27°C 1-2, average 1.5 per cm. (7 obs.).

The occasional acceleration of the digging rhythm in *L. pallida* leading to cessation of the forwardly directed abdominal thrusts has become in *L. canariensis* a normal trait. The shorter duration of phase 1 in *L. canariensis* is apparently correlated with quicker digging movements which the abdominal movements seemingly try in vain to follow, so that the abdomen is either moved so quickly (and slightly) that counting is impossible; or the female gives up the movements. Consequently the abdomen is kept practically still during phase 1, yet gradually and slowly bending more and more down until egg-laying.

In one particular fly (at 26°C) an attempt to count the abdominal movements gave the minimum figures 50, 76, and 50 for three successive phases 1 of durations 17, 18 and 14 cm. corresponding to minimum rates of 2.9, 4.2 and 3.6 thrusts per cm. This is quicker than the 2 thrusts per cm. in *L. pallida* and also quicker than for the following two species, *L. fortunata* and *L. hemmingseni* (cf. Tables 2, 7, 8 and 11, and Fig. 17). It is, however, not certain, that the quicker movements are the only reason for the reduction of abdominal thrusts in *L. canariensis* (see chapter 12B).

The actual laying of the egg is so quick that the pause during which the legs do not move is almost indiscernible.

The covering of the egg and pit (phase 2) takes usually about 1-10, average 2.9 cm. (44 obs.) as against 18-25 cm. (8 obs.) for egg-covering plus 75-225 (8 obs.) for pit-refilling in *L. pallida*.

The shorter duration of phase 1 aids the coalescence of egg-covering phase and pit-refilling phase into one short phase 2 result about the same temperature in the much shorter total duration of usually 0.1-0.4 min. of the process from the moment the female settles until it quickly flies away after the covering, as against 1.5-4 min. in *L. pallida*.

In contrast to the use of solely the middle legs in covering egg and pit by *L. pallida*, both middle and fore legs are used in quivering movements by *L. canariensis*. Due to the short duration of this phase and the quivering movements the single movements are difficult to ascertain. But it seems that the middle legs move
preponderantly inward and the fore legs preponderantly backward, and both simultaneously.

A few times it may seem as if the fore legs are not moved. Sometimes at the start of pit-refilling the proboscis may be thrust forward and down, and the fly or only the middle legs may be moved a little forward. This may sometimes be exaggerated so that a "fake pit-refilling" is carried out in a place away from where the egg was laid.

The vibrations of fore and middle legs during pit-refilling are quicker than those of the middle legs during digging.

After each oviposition there is usually a pause of e.g. 2 1/4 min. In one fly it gradually increased during the more than 2 hours of observation. When during the pause the fly rests on plants or on the sand the egg is seen moving inside the tip of the abdomen which takes shape after it. This is also seen in other species (cf. Fig. 6) including *V. nigriventris*. The flight before she settled to dig again varied (examples: 8, 3, 2, 3 cmin.).

In contrast to what is the rule in the following species this species starts digging immediately after settling from interovipository flight and flies away immediately after phase 2. Only in one out of 56 normal oviposition processes in different flies of this species at 25.5-27.0°C a female remained on the spot after phase 2. She exhibited two jerks of fore and middle legs, just as it commonly occurs in *L. fortunata* and *L. hemmingseni*, the only instance of such jerks seen in this species.

![Fig. 10. Sleeping posture of Lampromyia canariensis. A.M.H. phot.](image)
The wings as a rule quiver during the whole process. But some exceptions were recorded, one presumably rare case even simulating what is the rule in *L. fortunata*, viz. absence of quivering in phase 1, presence in first part of phase 2.

The peculiar "sleeping posture" of this and other species is shown in Fig. 10. It is uncertain, however, whether this is an entirely normal phenomenon. "Sleep" or akinesis in insects has been reviewed by Sogaard Andersen (1968).

The influence of temperature (20-27°C) on oviposition in this species is studied in chapter 11 (Fig. 15).

### 7. OVIPOSITION AT ABOUT 26°C OF *LAMPRomyia fortunata* STUCKENBERG, 1971

Experiments with this species were made in "artificial sunlight" at 24-27°C on flies emerged in spring-summer in 1966, 1967 and 1968 as reared from larvae collected in various localities on Gran Canaria (cf. Fig. 1).

In the Gran Canaria species 3 phases may be distinguished: 1) digging of the pit with backward directed strokes of both middle legs simultaneously followed by quick egg-laying in the pit, 2) covering of the pit by vibrations with fore and middle legs, 3) a number of apparently useless jerks with fore and middle legs.

While in *L. pallida*, at least in the beginning of digging (see p. 162) the downward bent rear part of the abdomen is thrust forward in the air every time the middle legs scrape backward, in *L. fortunata* the digging movements are much (perhaps about 10 times, or more) quicker than the abdominal forward thrusts of the downward bent apex of the abdomen, but they are difficult to count. Figures of 6.7 and 7.2 digging movements per cmin. were obtained in cases when they slowed down after appearance of the egg at the tip of the abdomen.

Farther reaching, backward throws or scrapings like those seen in *L. canariensis* varied in rate from 1.1-2.7, average 1.7 per cmin. (12 obs.).

The forwardly directed thrusts of the downward bent apex of abdomen are not made at strictly regular intervals, and are usually somewhat or entirely halted toward the end of the phase. They may cease before, simultaneously with, or after the appearance of the egg. In the latter case the thrusts after the egg has appeared are of less extension and the abdomen is in a lower position than in many thrusts in the earlier part of phase 1. However, also in the beginning of phase 1 and perhaps especially immediately before appearance of the egg, the thrusts take place in a lower position of the abdomen.

The participation of not only the middle legs but also the front legs was expressly noted both in the sun and in "artificial sunlight".

Table 2 shows within single flies examples of the variations in 1) duration of phases 1 and 2; 2) number of abdominal thrusts in phase 1 until the egg appears, and until it is laid (in these cases they were not halted at the end of phase 1);
Fig. 11. The relation of number of abdominal thrusts in the air to total length of phase 1 in Lampronyia fortunata. All filled circles: 24-27°C. Filled circles with a bar below: Thrusts until appearance of egg. Filled circles with a bar pointing obliquely upward to the right: Last part of phase 1 without thrusts. Filled circles with two bars: At least Philips 500 w B incandescent lamp (illumination G in Table 1 on p. 155); in some, most likely in all, cases with especially strong illumination by Philips HP 125 w mercury lamp (illumination H in Table 1). All open circles: 20-21°C. Open circles with a bar: Last part of phase 1 without thrusts. At 20-21°C no "artificial sunlight" (G in Table 1).

3) number of jerks in phase 3. The table shows also that irregularities such as shifting site of digging during phase 1 and falling on the side in phases 2 or 3, may occur. Such irregular phases are excluded from the data used in constructing the diagrams for any of the species.

The number of abdominal thrusts are related to the length of phase 1 as in Fig. 11. It will be seen that data obtained with illumination G or most likely H (Table 1 on p. 155) fall at a higher level, doubtlessly owing to the direct ultraviolet light from the HP lamp (cf. pp. 172,184). Also it is seen that the data obtained at 20-21°C fall at a lower level than those obtained at 24-27°C. From the relation in Fig. 11 the rates of thrusts (thrusts per cmin.) can be calculated (see p. 184 and Fig. 17). At 20-21°C "artificial sunlight" (ultraviolet light) was not used (G in Table 1).

The variation in length of phases 1 and 2 and their relation to one another in the whole material of data in many different flies can be read from Fig. 12 (log length of phase 2 plotted against log length of phase 1, cf. p. 158). There seems to be some slight tendency to an average increase in length of phase 2 with increas-
ing length of phase 1. But the inclusion of zero values and the possibility of association between values from individual flies as well as the considerable scatter do not invite statistical tests of correlation.

In any particular fly at 24-27°C the jerks (phase 3) may be present in all ovipositions observed (e.g. in up to 10 in one fly), or absent in all (e.g. in up to 7 in one fly), or absent only in some (up to 33 examples). These differences were not related to particular localities of origin. In 37 out of a total of 149 ovipositions in different flies, in which the presence or absence of phase 3 was explicitly noted, phase 3 was absent (25%). The experiments with particle sizes 0.5-1.5 mm (chapter 11B) are here included.

Instead of jerks a few slow movements up and down of the abdomen may be seen in some cases (as also in some cases during phase 2).
The jerks have apparently no particular function. An obvious question is whether they represent a sort of "atavism" equivalent to phase 3 in the ovipository process of *L. pallida*.

The fact that in *L. hemmingseni* (at 24-27.5°C) the jerks appear in many cases to merge with phase 2 (see next species), and their absence in *L. fortunata* in so many cases (25%) at 24-27°C and in most cases at 20-22°C (cf. chapter 11A), suggest that they constitute an abortive part of phase 2.

If so, one would expect the length of phase 2 to be shorter when jerks are present than when they are absent.

Table 3 confirms this expectation, at least as far as the trend is concerned. Still, the average difference in length of phase 2 with and without jerks (in Table 3, last column: 0.5 or 0.8 cmin.) is much smaller than the duration of phase 3 (jerks) as measured from cessation of phase 2 in the cases given in Table 4. This may merely mean that when an abortive part of phase 2 occurs the whole length of phase 2 (i.e. including the jerks) is protracted.

The number of jerks in phase 3 shows no correlation with the length of either phase 1 or 2.

The idea that the jerks represent an abortive part of phase 2 is not necessarily incompatible with the possibility that they may be considered (though perhaps a bit speculatively) equivalent to phase 3 in *L. pallida*. For, phase 2 in *L. fortunata* covers both phases 2 (egg-covering) and 3 (pit-refilling) of *L. pallida*.

In contrast to *L. canariensis* as a rule this species does not start digging immediately after settling from the flight between ovipositions and does not fly away immediately after phase 2 (or 3, which is practically absent in *L. canariensis*) but remains on the spot for a while. Only in 1 or 2 cases out of more than 200 ovipositions did a female of *L. fortunata* fly away immediately after phase 2, presumably on account of some disturbance.
in Lampromyia fortunata at 26.0-

<table>
<thead>
<tr>
<th>Number of jerks</th>
<th>cm/min.</th>
</tr>
</thead>
</table>

It is perhaps not without significance that in the singular cases when *L. canariensis* remained on the spot or *L. fortunata* flew away after phase 2, the former exhibited a few jerks; the latter, not.

The short pause after settling in *L. fortunata* makes it much easier to obtain cinematographic pictures of the whole of phase 1 in this species than in *L. canariensis*. The latter species cannot be "caught" by the camera until the digging has already started (cf., however, postscript on p. 202).

Another consistent difference between the two species concerns the duration of phase 1 which, excluding the four aberrantly low durations in *L. fortunata*, is evidently on the average much longer in this species than in *L. canariensis* (Fig. 13). This is presumably correlated with 1) slower digging movements in *L. fortunata* than in *L. canariensis* and 2) the presence of forward thrusts of the downward bent apex of the abdomen in *L. fortunata* and their practical absence in *L. canariensis*.

The four aberrantly low durations in *L. fortunata* (Fig. 13) may perhaps be ascribed to excessively strong direct ultraviolet illumination from the HP 125 watt lamp placed above the wire gauze ceiling (H in Table 1; cf. chapter 11A, p. 184). They were exhibited consecutively by one female. The durations in her succeeding ovipositions also all measured by filming, were not aberrantly low, so she may have moved to less exposed sites or have accommodated (V. 593 in Table 2).

The four low durations in point fall so far outside the range of the other durations of phase 1 in *L. fortunata* at the same temperature that from a mere statistical point of view they are extremely unlikely to rank with the same frequency distribution. It might thus seem warranted to discard them altogether. As, however, we have no other reason to think that some unnoticed error may have crept in just in the filming of these four durations we have felt obliged to retain them.

Phase 2 (or 2 plus 3 in some *L. fortunata*) is of similar short length in both species (cf. Table 5). Thus the total duration of the whole oviposition process is also longer in *L. fortunata* than in *L. canariensis* (Table 6).

Moreover, while as a rule *L. canariensis* quivers her wings during the whole
process (see exceptions under the species), *L. fortunata* as a rule quivers her wings only at the egg-laying proper at the end of phase 1 and during the first part of phase 2 (example: the first 3 min. of a phase 2 of 5 min.). Several exceptions were, however, recorded, such as twitching of the wings during phase 1, sometimes even to the extent of a short quivering in the beginning of phase 1, or even (rarely) more
<table>
<thead>
<tr>
<th>Species</th>
<th>Particle size in substrate mm</th>
<th>Phases included</th>
<th>No. of obs.</th>
<th>cmin. Min.</th>
<th>Mnx.</th>
<th>Average</th>
<th>Temperature °C</th>
<th>&quot;Artificial sunlight&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. pallida</em></td>
<td>0.02-0.4 and 0.4-0.5</td>
<td>2-3</td>
<td>&gt;22</td>
<td>239 1</td>
<td>253 1</td>
<td>151 1</td>
<td>25-26</td>
<td>+ 8</td>
</tr>
<tr>
<td><em>L. hemmingseni</em></td>
<td>0.4-0.5</td>
<td>2-3</td>
<td>27-8</td>
<td>28-1</td>
<td>17</td>
<td>11.9</td>
<td>24.0-27.5</td>
<td>+</td>
</tr>
<tr>
<td><em>L. fortunata</em></td>
<td>0.5-1.5</td>
<td>2-3</td>
<td>27-8</td>
<td>28-1</td>
<td>17</td>
<td>11.9</td>
<td>24.0-27.5</td>
<td>+</td>
</tr>
<tr>
<td><em>L. juncebris</em></td>
<td>0.4-0.5</td>
<td>2-3</td>
<td>27-8</td>
<td>28-1</td>
<td>17</td>
<td>11.9</td>
<td>24.0-27.5</td>
<td>+</td>
</tr>
<tr>
<td><em>L. cunnriensis</em></td>
<td>0.4-0.5</td>
<td>2-3</td>
<td>27-8</td>
<td>28-1</td>
<td>17</td>
<td>11.9</td>
<td>24.0-27.5</td>
<td>+</td>
</tr>
<tr>
<td><em>V. iigriventus</em></td>
<td>several</td>
<td>very short</td>
<td>27-8</td>
<td>28-1</td>
<td>17</td>
<td>11.9</td>
<td>24.0-27.5</td>
<td>+</td>
</tr>
</tbody>
</table>

1) cf. p. 162 f. 2) If 13 phases 2 with short immeasurable lengths are put at 0 and included, the average is 2.0. 3) Illumination H (Table 1 on p. 155) excluded. If 20 phases 2 with short immeasurable lengths are put at 0 and included, the average is 3.3. 4) If 1 very short phase 1 is put at 0 and included, the average is 5.6. No “artificial sunlight”. 5) “Artificial sunlight”. 6) Ordinary daylight. 7) 5. and 6. pooled. 8) Or sun. 9) Ordinary daylight or illumination G in Table 1. 10) Illumination G in Table 1.

or less faintly during the whole of phase 1, e.g. increasing toward egg-laying proper or with a short pause at egg-laying. Also in phase 2 exceptions occur, e.g. quivering not until after egg-laying, or during the whole of the phase or not at all during phase 2.

Like *L. pallida* *L. fortunata* may sometimes in the beginning display a very awkward inexperienced oviposition behaviour, digging slowly with the middle legs spread so that two pits result. In the first of a series of such cases the fly remained for 2-3 minutes with the apical part of the abdomen moving up and down, eventually flying away without finishing off with egg-laying. By and by through repetitions of the oviposition attempts the two holes reach one another and the processes become of shorter duration. The data from such abnormal behaviour are not included in the processing of data.

The influence on oviposition in this species of temperature (20-35°C), light and substrate particle size are studied in chapter 11 (Figs. 16-18).
### Table 6. Total length of ovipository process.

<table>
<thead>
<tr>
<th>Species</th>
<th>Particle size in substrate, mm</th>
<th>Phases included</th>
<th>No. of obs.</th>
<th>cmin.</th>
<th>Minutes ca.</th>
<th>Temp. °C</th>
<th>&quot;Artificial sunlight&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Min.</td>
<td>Max.</td>
<td>Average</td>
<td>Min.</td>
</tr>
<tr>
<td><em>L. pallida</em></td>
<td>0.02-0.4 and 0.4-0.5</td>
<td>1-3</td>
<td>&gt;22</td>
<td>150</td>
<td>400</td>
<td>ca. 260</td>
<td>1.5</td>
</tr>
<tr>
<td><em>L. hemmingseni</em></td>
<td>0.4-0.5</td>
<td>1-2</td>
<td>12</td>
<td>29, 30</td>
<td>65.5, 103.5</td>
<td>50</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1-3</td>
<td>29</td>
<td>26, 38</td>
<td>95, 112</td>
<td>61</td>
</tr>
<tr>
<td><em>L. fortunata</em></td>
<td>0.5-1.5</td>
<td>1-2</td>
<td>55</td>
<td>35, 37</td>
<td>215, 219</td>
<td>91</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>0.4-0.5</td>
<td></td>
<td>26</td>
<td>22, 29</td>
<td>74, 76.5</td>
<td>48³</td>
<td>0.25</td>
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<td></td>
<td></td>
<td></td>
<td>19</td>
<td>35, 37</td>
<td>91, 104</td>
<td>56</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>109</td>
<td>8.4, 9.2</td>
<td>98, 135</td>
<td>47³</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21</td>
<td>33, 36</td>
<td>69, 76</td>
<td>52</td>
<td>0.33</td>
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<td></td>
<td></td>
<td></td>
<td>23</td>
<td>17, 18</td>
<td>53, 118</td>
<td>35</td>
<td>0.2</td>
</tr>
<tr>
<td><em>L. junebrisi</em></td>
<td></td>
<td>6</td>
<td>28</td>
<td>40</td>
<td>35</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td><em>L. canariensis</em></td>
<td></td>
<td>27</td>
<td>15</td>
<td>60</td>
<td>32</td>
<td>0.15</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>54</td>
<td>12, 12.5</td>
<td>39, 40</td>
<td>20</td>
<td>0.1</td>
</tr>
<tr>
<td><em>V. nigrovittata</em></td>
<td></td>
<td>several</td>
<td>5</td>
<td>0.05</td>
<td>24.27</td>
<td>0.05</td>
<td>24.27</td>
</tr>
</tbody>
</table>

1) If 6 phases 2 with short immeasurable lengths are put at 0 and included, the average is 46.2) If 9 phases 2 with short immeasurable lengths are put at 0 and included, the average is 46.3) Or sun. 4) Ordinary daylight or illumination G in Table 1 on p. 155.5) Illumination G in Table 1. 6) Ordinary daylight.
8. OVIPOSITION AT ABOUT 26°C OF LAMPROMYIA HEMMINGSENII STUCKENBERG, 1971

Feinales of this brownish, hairy species reared from larvae from both Lanzarote and Fuerteventura (cf. Fig. 1) were studied 30. IV, 1. V. 1967 and 20. VI. 1968 at 24-27.5°C in "artificial sunlight".

Phase 1 was much the same as in L. fortunata, the middle legs throwing the sand back to form a pit, and the apex of the downward bent abdomen being thrust rhythmically forward in the air.

The relation between number of abdominal thrusts and length of phase 1 is shown in Fig. 14.

The thrusts ceased during the last part of phase 1 (a few examples in Table 7 and Fig. 14). This may be a general rule in this species. Durations of phase 1 and corresponding number of thrusts until thrusts ceased are compared in Table 7 with the few available data from L. fortunata. The data are too few to reveal any possible difference between the two species.

The rates of thrusts are plotted in Fig. 17 on p. 185 and are seen to fall more into line with the relation between rates and temperature for L. fortunata 'artificial sunlight' at 20-21°C, 30 and 35°C than with the rates of the latter species in "artificial sunlight" at about the same temperatures.

In two observations the egg was seen to appear at the 20th and 30th thrust (total 35 thrusts in the latter case).

From Fig. 13 it will be seen that the duration of phase 1 is practically within the range of durations found in L. fortunata, but clearly longer than phase 1 of L. canariensis.

The average log duration is higher in L. hemmingsenii than in L. fortunata, corresponding to a difference of 12% of the lower average; but the difference is not statistically significant. This confirms the impression formed by a mere inspection of Fig. 13, viz. that if there is a difference at all it is but a slight one.

The egg is quickly laid in the pit.

During phase 2 the egg was covered by the fore and middle legs, in small jerks which were few and made at increasing intervals, so that the duration of phase 2 becomes difficult to measure.

Thus while phase 1 was practically as in L. fortunata, phase 2 was reminiscent of phase 3 of the Gran Canarian species, though functioning as phase 2 of the latter (covering the egg).

In cases in which it was attempted to distinguish in L. hemmingsenii phase 2 from phase 3, phase 2 lasted 2-8, average 4.4 cmiii. (15 obs.), phase 3 consisting of 3-11 jerks (22 obs.). In most cases (35 obs.) phase 2 and 3 merged lasting 8-17, average 11.9 cmii. (cf. Table 5). The abdomen may move slightly during phases 2-3.
thrusts in the air to total length of phase 1 in *Lampromyia hemmingseii*. "Artificial sunlight" (C or D + F in Table 1 on p. 155). 23-27.5-C. Open circles: The examples from Table 7 of thrusts ceasing toward end of phase 1.

*L. hemmingseii* was observed to start digging immediately after settling from interovipository flight.

Like *L. fortunata* but unlike *L. canariensis* *L. hemmingseii* does not fly away immediately following phase 2 or 3 but remains on the spot for a while.

The wings appear, at least as a rule, to quiver during the first part of phase 1, until the 10th to 20th abdominal thrust, i.e. not during the whole process as is the rule in *L. canariensis* and not at all in phase 2 as is the rule in *L. fortunata*.

Though *L. canariensis* and *L. fortunata* appear at first sight morphologically and by appearance to be nearer to one another than to *L. hemmingseii*, which is brownish hairy, still the oviposition patterns of *L. fortunata* and *L. hemmingseii* are evidently more similar to one another than to that of *L. canariensis*. This is reflected in hypopygial structures (cf. p. 197).

9. OVIPOSITION AT 26°C OF *LAMPROMYIA FUNEBRIS* DUFOUR, 1850

According to Stuckenberg (in litt.) the name *funebris* Dufour, 1850, should be retrieved from synonymy (cf. Stuckenberg 1960, p. 250) to replace for Spain and South France the name *cylindrïca* (Fabricius, 1794). The latter name should be restricted to the North African populations. Dr. Stuckenberg has kindly checked that our specimens are *L. funebris*.

Females of this dark-winged species reared from larvae collected by A.M. H. in a quarry in Valle de Puerto de Santa Maria between Cadiz and Arcos de la Frontera in South Spain on 29. IV. 1965, mated with males obtained from larvae from the same locality. Ovipositions were obtained in June at 26°C both in the sun and in "artificial sunlight".

The pattern of ovipository behaviour differed in several respects from that of
10. OVIPOSITION OF VERMILEO SPECIES

According to Hafez & El-Moursy (1956b, p. 338) before oviposition the female of *V. vermileo* in Egypt hovers near the surface of the sand while testing it with the hind tibiae. Thereafter, fixed to the sand with her fore and hind legs, she digs a small pit with her middle legs and curves her abdomen downward and anteriorly. The abdomen vibrates rapidly and the egg is thrust into the pit by a rapid stroke. The pit is stated to be filled with sand by help of the fore and middle legs. The site of oviposition assumes the shape of a small heap of sand with a depression in the center.

This description is seen to be similar to the observations on the *Lampromyia* species from Spain and the Canary Islands reported in the foregoing pages. But no mention is made for the Egyptian *Vermileo* of quivering of the middle legs to cover the eggs as in *L. pallida*, or of their inward movements to fill the pit. Also in the use not only of the middle legs but also of the fore legs to fill the pit the Egyptian *Vermileo* deviates from *L. pallida*, and conforms with the others.

According to Le Faucheux (1961) a female of *V. vermileo* from Les Eyzies in...
Dordogne, South France, about to oviposit, alternately flies 1) in all directions about 15 cm above the sand and 2) at the surface of the sand, scratching it with her middle legs. After a final such scratching she settles on the sand with wings spread, curves the abdomen and oviposits without the legs moving but with the abdomen slowly and rhythmically dilating and contracting with corresponding changes in its curvature. Finally one egg is laid, but no trace at the sand surface reveals where.

In own (A.M.H.) observations on 5 females of Vermileo nigriventris Strobl, 1906 (kindly determined by Dr. Stuckenberg) reared from larvae collected (by A.M.H.) at Camino de la Nieve, Arcos de la Frontera, in South Spain on 29. IV. 1965 and mated with males reared from the same locality, ovipositions were obtained in “artificial sunlight” at 24-27°C. The whole process of oviposition was very quick (duration about 5 cm). The shortest among the species dealt with in this paper (cf. Fig. 13). The female flies about thrusting her long down-hanging hind legs against the sand (as in the Egyptian observations); by and by with the hind legs resting on the sand she throws herself forward in jerks, along the sand, and with a final jerk immediately starts digging. This was seen to be performed on bobbing fore and hind legs by backward movements of the joined middle legs – and the egg was seen being laid. But in no case was it possible to ascertain with certainty whether or not the fore legs were involved in covering. Sometimes it seemed as if there was hardly any covering, or as if all legs were involved in a quick scraping to cover the eggs. There were pauses after each oviposition and flights before the next.

The yellow colour of the legs made it additionally difficult to follow their movements. A black powder substrate was tried but even then the movements were too quick to follow.

Also in this species abortive “ovipositions” occurred: with vibrating wings the female lay with head against glass, kicking with the hind legs, performing some awkward digging movements, bent the abdomen, might or might not lay an egg. No covering pit-refilling movements.

From the Egyptian record the observations in southern France are seen to differ in a number of details (specified by Le Faucheux 1961, p. 140), as also from ours on Spanish flies.

Two suspicions or possibilities emerge from this. One is that all the populations in question may be more or less genetically different, even perhaps at a species level. It seems likely that the Egyptian population is Vermileo niloticus Edwards, 1935; and the French, V. vermaleo (L., 1758); as said ours from Spain is V. nigriventris Strobl, 1906 (cf. Stuckenberg 1965, p. 495).

The other suspicion arises out of the apparent lack in the French observations of coordination between the scratching of the sand with the middle legs and the actual oviposition. In the Egyptian and own observations on Vermileo the movements of the middle legs are closely associated with the digging of a pit for the egg.
and the flies test the sand during flight with the hind legs; not, the middle legs. 

Own observations as recorded in the foregoing pages, esp. pp. 164, 174, 178 and 179 show that both in V. nigriventris and in the Lampronymia species the female may perform a number of quite atypical, or rather abnormal, ovipositions until she has become accustomed to the artificial environment of the container. The question emerges, therefore, whether the French flies may not have performed atypical ovipositions.

Also Buchner (1940, p. 130) described for V. vermileo (from Ischia) how the female which is about to oviposit, in flight scratches the surface of the soil with her legs; which pair is not specified. Buchner interprets this as probing of the consistency of the soil before oviposition, but does not describe the latter.

The results recorded in chapter 11 A invite experiments on Vermileo species at lower temperatures, say 20° C, at which the movements would be slower, so that details of digging and duration of phases could be more accurately studied and compared with the other species.

It seems possible that at least some of the palaearctic Vermileo species oviposit at lower temperatures than the palaearctic Lampronymia species, in as much as the genus Vermileo extends more to the North (Northern France, Bavaria, Northern Austria, cf. Hemmingsen 1968, p. 291).

The description by Wheeler (1931, p. 215) of the oviposition of the North American V. conzstocki Wheeler, 1918 (taxonomic details by Pechuman 1938), shows essential departures from the patterns of oviposition discussed above: The females thrust the extensible tip of the abdomen 3 mm down into the soil, standing on their hind legs, with the anterior pair of legs stretched out into the air and the tips of the delicate wings so forcibly applied to the sand that they are often broken or torn. All the eggs, more than fifty in number are extruded at one time, and the female dies soon after withdrawing the tip of the abdomen.

Although Wheeler in this connection speaks of females (i.e. in the plural) it is not quite clear in how many females the actual act of oviposition was observed in detail. On the background of the discussion above regarding abnormal ovipositions it seems desirable to have Wheeler's deviating observations checked, both as to behaviour and as to number of eggs laid. All the other above-mentioned observations on Vermileo and species of Lampronymia agree in normally one egg being laid at each oviposition, and, apart from those of Le Faucheux, in a pit being dug by the middle legs for the eggs.

It is true that within another group of Diptera, the Tipulinae, while most species lay one egg at each of the rather superficial ovipositions, two subgenera (Vestiplex and Odonatisca) which are especially adapted to inserting the whole of the abdomen into the substrate at oviposition, applying the wings to the substrate, lay the eggs in batches (Hemmingsen 1952, 1956a, b, 1965, pp. 136-139). But the wings are not applied so forcibly that they are broken and the female oviposits more than once and does not die soon after.
to temperature in Lampromyia canariensis. Filled circles: "Artificial sunlight" (C-E in Table 1 on p. 155). Open circles: Ordinary daylight in room without sun. Open circles with a bar: 500 watt incandescent lamp (G in Table 1).

11. THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS ON THE OVIPOSITION PATTERN

The oviposition behaviour of the various species as recorded in the preceding chapters was studied at about the same environmental temperature, 26°C (24.0-27.5°C), in "artificial sunlight", and (except in some observations on L. pallida) on the same substrate, Danish sifted blown sand with particle sizes of 0.4-0.5 mm.

Some of the differences found between species are differences in durations or rates of the movements especially in phase 1, and it might be theorized that the optimal temperature of the different species might be different, the durations or rates being the same in different species at their respective optimal temperatures. Similar arguments might apply to illumination and particle size.

A sufficient number of flies were obtained only in Lampromyia canariensis and L. fortunata for inter- or intraspecific comparisons at different temperatures, different illumination and different particle sizes.

A. The influence of temperature and light

As substrate sifted blown sand with particle size of 0.4-0.5 mm was used.

In Fig. 15 the lengths of phase 1 at 25.5-27.0°C in L. canariensis (already plotted in Fig. 13) are compared with the lengths at 20.0-21.5°C. Though the scatter is
great the average and range of lengths are clearly seen to lie higher at the lower temperatures. This apparently becomes even more accentuated if only the data obtained in the absence of "artificial sunlight" (specially marked) are compared. However, there is not much to suggest that if more observations had been made phase 1 would virtually be on a statistical basis significantly shorter without than with "artificial sunlight" (cf. lines 3-5 from below on this page).

The rates of the quickest digging movements were difficult to count but the rate of those that reached farther backward in throws, as counted in cinematographic pictures, was somewhat lower at the lower temperatures (1.1-1.5; average 1.23 per cmin. (6 obs.)) without "artificial sunlight" than at the higher temperatures (1.0-2.0, average 1.5 per cmin. (7 obs.)) with "artificial sunlight".

Also phase 2 lasted longer at the lower temperatures without "artificial sunlight", viz. 1-17 (38 obs.), average 5.6 cmin. as against 3.5-7, average 5 cmin. (6 obs.) without "artificial sunlight" or 1-10, average 2.9 cmin. (44 obs.) with "artificial sunlight" at the higher temperatures (cf. Table 5). Thus of course also the duration of the whole ovipository process is greater (Table 6).

These differences in rate of throws and length of phase 2 may be due to the difference in either temperature or light or both.

At the lower temperatures just as at the higher temperatures as previously reported, after flying about the fly started digging immediately after settling; and the abdomen, apparently in trying to follow the rhythm of the diggings, either moved so quickly (and slightly) up and down that counting was impossible or it gave up the movements and hardly moved the abdomen at all.

Also, the female flew away immediately after phase 2, no jerks being made. There was only one exception to this at the higher temperatures as previously stated (two jerks being made and the fly thereafter remaining on the spot as is the rule in L. fortunata and L. hemmingseni). At the lower temperatures there were no cases of jerks; but in 4 cases, 2 of which with other irregularities, e.g., abnormal long phase 1 without egg-laying (therefore not included in the diagram), the fly did not fly away after phase 2.

In L. fortunata experiments without "artificial sunlight" (ultraviolet light) were made at 20-22, 27, 30, and 35 C.

Results are shown in Fig. 16, in which the logarithm of the length of phase 1 is plotted against temperature, and in Fig. 17 in which the rate of abdominal thrusts during phase 1 is plotted against temperature. In the experiments at 27° without ultraviolet light (Fig. 16) the thrusts had not been counted. In both diagrams other experiments at 24-27 C in "artificial sunlight" are included.

It will be seen from Fig. 16 that no significant difference can be established between phase lengths with ultraviolet light (in "artificial sunlight") at 24.0-26.5° C and without ultraviolet light at 27 C, and that between 24 C and 30 C there is no appreciable change in phase length with temperature. This might be thought to represent largely the temperatures at which oviposition is carried out in nature
Fig. 16. The relation of length of phase 1 to temperature in Lampronia fortunata. Filled circles: “Artificial sunlight” (C-E in Table 1 on p. 155). Filled circles with a bar: At least Philips 500 w B incandescent lamp (illumination G in Table 1); in some, most likely in all, cases with especially strong illumination by Philips HP 125 w mercury lamp (illumination H in Table 1). Open circles: At 20°C ordinary daylight in room without sun. At 27°C no ultraviolet light (illumination A or B in Table 1). Open circles with a bar: 500 watt incandescent lamp (G in Table 1). Experiments with particle sizes 0.5-1.5 mm not included.

(still cf. postscript on p. 202). It seems more reasonable to assume that there is virtually a gliding decrease in average and range of lengths of phase 1 all the way from 20°C to 35°C, the uncertainties inherent in the great scatter or a slight decrease in the phase length by artificial sunlight at 24.0-26.5°C, being responsible for the apparent lack of relation between 24 and 30°C.
The 4 exceptionally low durations at 27°C may perhaps be due to the direct illumination of the especially strong ultraviolet light (H in Table 1 on p. 155; cf. p. 172).

It will be seen both from Fig. 15 and from Fig. 16 that at 20-22°C there is no difference in length of phase 1 with and without the use of the 500 watt incandescent lamp. The calculated averages are practically the same, though the difference in luminosity must have been about 2000 lux (cf. Table 1 on p. 155).

As regards the relation of the rate of abdominal thrusts to temperature in Fig. 17 there is obviously a gradual rise in the rate with temperature when comparable conditions of illumination (no ultraviolet light, G in Table 1) are instituted as at 20-22, 30 and 35°C. There is no other difference between the experiments at these temperatures and those at 25-27°C than the use of “artificial sunlight” at the latter temperatures.

The high rates falling above the 20-30-35°C relation at 25-27°C must, therefore, doubtlessly be ascribed to the ultraviolet radiation in the “artificial sunlight”. The excessively high rates when, most likely in all these cases, the strong illumination from the 500 watt white incandescent lamp was combined with the especially strong ultraviolet emission from the 125 watt bulb (H in Table 1 p. 155) strengthens this supposition.

These very high rates were entirely unexpected and not discovered until processing the data after conclusion of all experiments on this species.

As just mentioned the 500 watt incandescent lamp induces no stimulating effect in excess of that of ordinary indoor daylight. But in at least some, most likely all, the filming experiments giving the excessively high rates in Fig. 17 the HP lamp was placed at a short distance above the wire gauze ceiling so that no ultraviolet light was absorbed through the glass walls of the container. This direct illumination with strong ultraviolet light is perhaps what caused the 4 short durations of phase 1 at 27°C in Fig. 13 and 16 and the excessively high rates at 25-27°C in Fig. 17 (cf. pp. 156, 159 and 172).

Rates obtained with L. hemmingseni with “artificial sunlight” at 26.5-27.5°C are included in Fig. 17. They are seen to fall more into line with the gradual 20-30-35°C relation for L. fortunata than the data of the latter species at 24-27°C, though perhaps also a little above it due to the use of ultraviolet light. But why they fall at a lower level than the rates of L. fortunata under similar conditions, is not evident.

Whereas in L. fortunata at 24-27°C the forward thrusts in the air of the downward bent apex of the abdomen as a rule continued, though with decreasing rate, until egg-laying (cf. Table 2); at 20-22°C, at least in ordinary daylight and at least in some ovipositions at about 26°C studied explicitly as to this trait, the thrusts ceased a considerable time before egg-laying (Table 8).

The rates plotted in Fig. 17 are for all temperatures calculated as average rates during the whole period of phase 1, thus including for each oviposition the slower rates or absence of thrusts toward the end of the phase.
The digging movements in *L. fortunata* were both at 20-22°C and at 24-27°C usually too rapid to be counted. Attempts to count them in cinematographic pictures gave at 20°C (without "artificial sunlight") as minimum values 8, 10 and 8.7 per cmin. In other cases at this temperature they were slow enough to be counted, viz. 6, 3.7, 3.7, 3 and 3.1 per cmin. At 27°C (in "artificial sunlight") minimum rates could not be assessed, except that figures of 6.7 and 7.2 were obtained in

Fig. 17. The relation of rate of abdominal thrusts in the air to temperature in *Lampropyia fortunata* and *Lampropyia hemmingseni*. Filled circles without a bar or with an angled bar: *Lampropyia fortunata*, "artificial sunlight" (C-E in Table 1 on p. 155). Filled circles with a bar: *Lampropyia fortunata*, at least Philips 500 w incandescent lamp (illumination G in Table 1); in some, most likely in all cases, with especially strong illumination by Philips HP 125 watt mercury lamp (illumination H in Table 1). Filled circles with an angled bar: *Lampronzyia fortunata*, particle sizes 0.5-1.5 mm (all other data 0.4-0.5 mm). Open circles with a bar: *Lampropyia fortunata*, 500 watt incandescent lamp (G in Table 1). Inverted T's: *Lampropyia hemmingseni", "artificial sunlight" (C or D + F in Table 1).
<table>
<thead>
<tr>
<th>Species</th>
<th>Duration of phase 1, cmin.</th>
<th>Number of abdominal thrusts until they ceased</th>
<th>Duration of phase 2, cmin.</th>
<th>Number of jerks in phase 3</th>
<th>Number of abdominal thrusts per cmin.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Until thrusts ceased</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L. hemmingseni</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>25</td>
<td>20</td>
<td></td>
<td></td>
<td>0.82</td>
</tr>
<tr>
<td>40</td>
<td>45</td>
<td>31</td>
<td></td>
<td></td>
<td>0.67</td>
</tr>
<tr>
<td>27</td>
<td>27</td>
<td>18</td>
<td></td>
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<td>0.17</td>
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<tr>
<td>30</td>
<td>30</td>
<td>31</td>
<td></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>30</td>
<td>2</td>
<td></td>
<td>some</td>
<td>0.74</td>
</tr>
<tr>
<td>28</td>
<td>38</td>
<td>3</td>
<td></td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>60</td>
<td>1</td>
<td></td>
<td>11</td>
<td>0.52</td>
</tr>
</tbody>
</table>

Table 8. Average rates in *L. fortunata* at 20-22°C in daylight (room, no sun) of forward thrusts in the air of the downward bent apex of the abdomen in phase 1 (digging) for 1) only the first part of phase with thrusts and 2) whole phase including thrust-less period.

<table>
<thead>
<tr>
<th>Durations, cmin.</th>
<th>Number of thrusts</th>
<th>Rates: Thrusts per cmin.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First period:</td>
<td>Total</td>
</tr>
<tr>
<td></td>
<td>With thrusts</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Without thrusts</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>10</td>
<td>23</td>
</tr>
<tr>
<td>45</td>
<td>21</td>
<td>24</td>
</tr>
<tr>
<td>175</td>
<td>49</td>
<td>126</td>
</tr>
<tr>
<td>95</td>
<td>30</td>
<td>65</td>
</tr>
<tr>
<td>57</td>
<td>32</td>
<td>25</td>
</tr>
<tr>
<td>52.5</td>
<td>32.5</td>
<td>20</td>
</tr>
<tr>
<td>56</td>
<td>35</td>
<td>31</td>
</tr>
<tr>
<td>53</td>
<td>37.5</td>
<td>15.5</td>
</tr>
<tr>
<td>97</td>
<td>68</td>
<td>29</td>
</tr>
</tbody>
</table>

cases when the niovenents slowed down after the egg had appeared on the abdominal apex. Thus lower minimum values and lower countable values were obtained at 20°C than at 27°C. But as the rates are usually too high at either temperature to be counted, rational comparisons could not be made. To this comes the paucity of countings and differences in light.

The rates of far-reaching backward throws during digging were measured in
Table 9. The relation of length of phase 2 to temperature in L. fortunata.

<table>
<thead>
<tr>
<th>Tenperature C</th>
<th>No. of obs.</th>
<th>Phase 2, cmin.</th>
<th>&quot;Artificial sunlight&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Min.</td>
<td>Max.</td>
</tr>
<tr>
<td>20-22</td>
<td>69</td>
<td>1.5</td>
<td>1</td>
</tr>
<tr>
<td>24-37</td>
<td>175</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>24-27</td>
<td>129</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>30</td>
<td>22</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>35</td>
<td>24</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

1) Including experiments with substrates of 0.5-1.5 mm particle size and others with strong ultraviolet light under filming conditions ([H in Table 1 on p. 155]). If 20 very short phases 2 are included as zero values, the average becomes 3.6. 2) Excluding experiments with substrates of 0.5-1.5 mm particle size and others with strong ultraviolet light under filming conditions (H in Table 1). If 20 very short phases 2 are included as zero values, the average becomes 3.3. 3) Ordinary daylight or illumination G in Table 1. 4) Illumination G in Table 1.  

cinecinematographic pictures, and were at 20-22°C without "artificial sunlight" 0.64-1.33, average 0.93 per cmin. (5 obs.); and at 24-27°C in "artificial sunlight", 1.1-2.7, average 1.7 per cmin. (12 obs.). These differences may be due to differences in temperature or light or both.

The lengths of phase 2 were as shown in Table 9.

Evidently the same trend exists as with phase 1.

As mentioned before, at 24-27°C the rule is that phase 2 is followed by a number of jerks (phase 3), so that only 25% of the ovipositions terminate without jerks.

At the other temperatures this is—at the face values of the data—reversed. Most ovipositions have no phase 3, only 4 out of 99 (4%) exhibiting jerks at 20-22°C; 4 out of 24 (17%) at 35°C; and 9 out of 22 (41%) at 30°C.

The difference between each of these 3 percentages and the 75% (112 out of 149) at 24-27°C are statistically significant on the assumption that they represent random samples. This assumption is to some extent supported by the fact that some individual flies after some ovipositions exhibit jerks; after others, not (cf. p. 170). In other words the occurrence or non-occurrence of jerks is not associated with certain individual flies. Still, the percentage of ovipositions with jerks might be individual.

The uncertainty of the percentage 41 (but not of the 4% and 17%) involves the possibility that the true percentage may exceed 50, so that at 30°C the apparent reversion is uncertain.

That a reversion is nothing to do with the use of ordinary daylight at these temperatures ("artificial sunlight" being used at 24-27°C) is evident from the fact that also all 34 ovipositions at 27°C without "artificial sunlight" closed with 2-4 jerks, except 4 which had no jerks.

Presumably the delay in start of digging after settling and staying on after phase 2, as seen in L. fortunata at 24-27°C, were experienced also at 30 and 35°C.
but we did not focus attention to these details. At 20-22°C we did (see p. 191) and found them to occur. During jerks, of course, the females stay on but apparently also with few exceptions for a while after they have ceased.


**B. The influence of particle size in substrate**

Four different substrates were used, classified as in Table 10 according to particle sizes:

Though the larvae thrived in substrate I and though this substrate had also served for some ovipositions of the Tunisian and Spanish species it appeared for some reason or other noxious to the imagines of some species, e.g. _L. fortunata_ and _L. hemmingseni_ (perliaps through clogging the spiracles ?). Therefore, comparisons between the behaviour in blown sand substrate (II) and dust substrate (I) could not be made in the species _L. fortunata_, of which sufficient females were available (still cf. postscript on p. 202). But the behaviour on substrate II could be compared at about 26°C with that on substrates III and IV.

The particle sizes in IV were evidently too large. For, in two experiments with 4 and 5 mated females of _L. fortunata_, respectively, made under the usual conditions in "artificial sunlight" at about 26°C, no ovipositions occurred. A female settled to start digging, but immediately flew a little away and tried again, and this was repeated 5-6 times. Then she gave up.

With 4 females on substrate III similar repeated attempts at digging were seen in some cases but the flies eventually carried through the whole ovipositionary process, also in some cases at the first attempt. The delay in digging after settling, otherwise specific of _L. fortunata_, was not expressly noted in these cases, and presumably did not occur, at least not with the repeated attempts.

It will be seen from Fig. 18 that the length of phase 1 may be slightly greater with III than with II.

The average difference, corresponding to a 15% rise in length of phase 1 with the coarser substrate, is, however, not statistically significant. We can conclude

| Table 10. Classification of particle sizes in substrate. Approximate diameter in mm. |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| 1 Dust (colloidal clay substance) | II Sifted blown sand | III Coarsely sifted sand from gravel bank | IV Coarsely sifted sand from gravel bank |
| 0.02-0.4, a few 0.5 ; many 0.02-0.05 | 0.4-0.5 | 0.5-1.5 | 1.5-2.0 |
that if the length of phase 1 is at all greater with substrate III than with substrate II, it is but slightly greater.

The data on III have been in some treatments pooled with other data obtained under similar experimental conditions; in others, kept apart (examples Tables 3, 5, 6, 9, Fig. 17) or not included at all.

Also the length of phase 2 is numerically somewhat greater (cf. Tables 5 and 9), viz. 2-7.5, average 5.1 cmin. (35 obs.) as against 1-7, average 2.0 cmin. (60 obs.) with sifted blown sand (II) within the same temperatures (26.0-26.5°C) or against 1-14, average 3.3 cmin. (149 obs.) within 24-27°C.

Furthermore, the rate of abdominal thrusts (with rather irregular rhythm) is greater, viz. 0.73-1.16, average 0.94 thrusts per cmin. (13 obs.) as against 0.50-0.95, average 0.80 thrusts per cmin. (15 obs.), in both cases at 26.0-26.5°C. Here only the ovipositions were included for which no cessation of the thrusts was noted towards the end of phase 1 (cf. Fig. 17).

Out of 31 ovipositions on III, 19 (61%) had a phase 3 (jerks); 12, not. The number of jerks was 1-8, average 3.9 (18 obs.). On II at the same temperatures (26.0-26.5°C) out of 49 ovipositions 38 (78%) had jerks; 11, not. And the number of jerks was 1-9, average 2.3 (30 obs.). These are hardly differences of any importance.
As on 11 the flies did not fly away immediately after phases 2 or 3, and the wings at least sometimes vibrated at the egg-laying at the end of phase 1.

It might seem natural if the lengths of phase 1 and 2 were increased due to the extra exertion imposed by the coarser substrate; perhaps also that the rate of abdominal thrusts were increased.

In the preceding pages an opposite association was found, higher rates of thrusts being associated with shorter lengths especially of phase 1 (effect of temperature, of strong direct ultravioletlight*, differences between *L. canariensis* and *L. fortunata*).

While the difference in length of phase 1 in these latter cases were distinct and relatively great, the slight and statistically insignificant rise in length of phase 1 with substrate III over II does not encourage speculations on the apparent discrepancy.

12. COMPARISON BETWEEN *LAMPROMYIA CANARIENSIS* AND *L. FORTUNATA* AT 20-22°C

A. Ordinary daylight

The fear that the use at 24-27°C of "artificial sunlight" may have stimulated the flies beyond a mere trigger effect led to the institution of check comparisons at the lower temperatures 20-22°C in natural daylight (in a room in the absence of sun) between the two species of which a sufficient number of flies were available, viz. *L. canariensis* and *L. fortunata*.

Fig. 19 shows that also under these conditions the duration of phase 1 is distinctly shorter in *L. canariensis* than in *L. fortunata*.

As regards phase 2 it is apparently opposite, the duration being in *L. canariensis* 2-12, average 6.9 cmin. (10 obs.) and in *L. fortunata* 2.5-11, average 5.3 cmin. (36 obs.) but this may be due to too few observations in *L. canariensis*. Jerks are absent in *L. fortunata* under those conditions, so these do not add to the length of phase 2.

And, anyway, the length of phase 2 being only a minor fraction of the length of phase 1, the total duration of the ovipository process remains distinctly shorter in *L. canariensis* (17-45, average 27.5 cmin. in 9 obs.) than in *L. fortunata* (42-215, average 94 cmin. in 35 obs.).

Just as at the higher temperatures the female *L. canariensis* after flying about started the digging movements immediately after settling, showed no abdominal thrusts during phase 1, quivered her wings throughout the two phases and flew away immediately after phase 2; whereas *L. fortunata*, just as at the

* Yet perhaps not of the ultraviolet light in mere "artificial sunlight" which though in *L. fortunata* it distinctly enforces rate of thrusts (Fig. 17), may not or only slightly decrease length of phase 1 (Fig. 16).
higher temperatures, started digging a short while after settling, showed rhythmic abdominal thrusts during phase 1, quivered her wings only at egg-laying proper and perhaps in the beginning of phase 2 (though perhaps with more exceptions than at 24-27°C), and stayed on for a while after finishing phase 2. But in contrast to the observations on *L. fortunata* at 24-27°C only in 1 out of 47 ovipositions was a single jerk with the front legs seen following phase 2 (cf. p. 170).

The specific differences in ovipository behaviour between these two species are thus the same at 20-22°C in natural daylight as at 24-27°C in "artificial sunlight", with the exception that at 20-22°C in natural daylight practically no jerks (phase 3) are exhibited by *L. fortunata*.

The reduction of the jerks seems to be an effect of the lower temperature, not of the absence of ultraviolet light, as they are present in fair proportions at higher temperatures (27, 30, 35°C) in the absence of extra ultraviolet light (cf. p. 187, where a similar reduction is noted at 20-22°C with illumination G).
B. Filming conditions

In cinematographic pictures taken at the same temperatures, 20-22°C, and also without “artificial sunlight”, but with illumination from a 500 watt incandescent lamp (G in Table 1 on p. 155), it was attempted to compare the rate of movements in the two species. The rate of the motion pictures was 32 frames (pictures) per second.

At about 26°C (24-27°C) it is impossible to decide whether the digging movements are quicker in _L. canariensis_ than in _L. fortunata_, as at this temperature they are too quick to be counted in either species, even in motion pictures produced at half rate. The rate of the farther-reaching backward throws or scrapings at about 26°C is apparently not greater in _L. canariensis_ (1-2, average 1.5 per cmin. in 7 obs.) than in _L. fortunata_ (1.1-2.7, average 1.7 per cmin. in 12 obs.).

At 20-22°C the rates of digging movements of _L. fortunata_ in motion pictures at half rate were in many cases low enough to be counted, e.g. (transferred to normal rate) 3 and 8 per cmin., whereas in _L. canariensis_ they were still too great to be counted. So at 20-22°C doubtless the rates are quicker in _L. canariensis_ than in _L. fortunata_. Also the farther-reaching backward scrapings were at 20-22°C quicker (1.1-1.5, average 1.23 per cmin. in 6 obs.) in _L. canariensis_ than in _L. fortunata_ (0.64-0.99, once 1.33, average 0.93 per cmin. in 5 obs.).

It is, however, not certain that difficulty or impossibility for the rate of abdominal thrusts to follow the higher rate of digging movements in _L. canariensis_ is the only reason why abdominal thrusts are strongly reduced or absent in this species. If this were the only reason the rate of digging movements in _L. fortunata_ at about 26°C, where this species exhibits pronounced abdominal thrusts, should be lower than that of _L. canariensis_ at 20-22°C, where this species still retains the practical absence of abdominal thrusts. And this could not with certainty be decided even in the motion pictures produced at half rate.

Also, while rate of thrusts and length of phase 1 vary inversely under the action of temperature or (at least in some cases) strong direct ultraviolet light, this is not so convincingly the case with mere “artificial sunlight” (Figs. 16 and 17).

The above comparisons of digging rates were made on flies digging away from the glass walls of the containers. The ovipositions with the front end in contact with the glass wall would usually have slower often countable digging movements, but this position being abnormal they were discarded.

Just as at 25-27°C in “artificial sunlight” (Table 2) the abdominal thrusts in _L. fortunata_ under the filming conditions in point might continue after appearance of the egg until egg-laying (2-7 minor thrusts in 7 obs.) in contrast to observations at 20-22°C in ordinary daylight, in which the thrusts ceased a considerable time before egg-appearance and egg-laying (Table 8). In 2 out of 26 normal ovipositions under the above mentioned filming conditions the female _L. canariensis_ exceptionally remained on the spot after phase 2.
OVIPOSITORY INSTINCTS IN VERMILEONINAE

Table 11. Forwardly directed thrusts in the air of the downward bent abdomen during phase 1 in Lampromyia fortunata at 35°C. Illumination G (cf. Table 1 on p. 155).

<table>
<thead>
<tr>
<th>Phase 1, cmin.</th>
<th>Number of thrusts</th>
<th>Phase 2, cmin.</th>
<th>Phase 3 (jerks)</th>
<th>Thrusts per cmin.</th>
</tr>
</thead>
<tbody>
<tr>
<td>42</td>
<td>40</td>
<td>3</td>
<td>–</td>
<td>0.95</td>
</tr>
<tr>
<td>46</td>
<td>41</td>
<td>4</td>
<td>–</td>
<td>0.89</td>
</tr>
<tr>
<td>50</td>
<td>35</td>
<td>3</td>
<td>+</td>
<td>0.70</td>
</tr>
<tr>
<td>36</td>
<td>25</td>
<td>3</td>
<td>+</td>
<td>0.70</td>
</tr>
<tr>
<td>28</td>
<td>27</td>
<td>2</td>
<td>–</td>
<td>0.97</td>
</tr>
<tr>
<td>26</td>
<td>25</td>
<td>2</td>
<td>–</td>
<td>0.96</td>
</tr>
<tr>
<td>33</td>
<td>35</td>
<td>2</td>
<td>–</td>
<td>1.06</td>
</tr>
<tr>
<td>29</td>
<td>26</td>
<td>2</td>
<td>–</td>
<td>0.90</td>
</tr>
<tr>
<td>28</td>
<td>23</td>
<td>3</td>
<td>+</td>
<td>0.82</td>
</tr>
<tr>
<td>33</td>
<td>20</td>
<td>3</td>
<td>–</td>
<td>0.61</td>
</tr>
<tr>
<td>91</td>
<td>24</td>
<td>3</td>
<td>–</td>
<td>0.26</td>
</tr>
<tr>
<td>15</td>
<td>14</td>
<td>3</td>
<td>–</td>
<td>0.93</td>
</tr>
<tr>
<td>19</td>
<td>18</td>
<td>2</td>
<td>–</td>
<td>0.95</td>
</tr>
<tr>
<td>14</td>
<td>12</td>
<td>3</td>
<td>–</td>
<td>0.86</td>
</tr>
</tbody>
</table>

13. COMPARATIVE REMARKS ON THE OVIPOSITORY INSTINCTS OF THE DIFFERENT SPECIES

The species under consideration may be arranged in three groups according to the specialization and total duration of the ovipository process, all considered in “artificial sunlight” at about 26°C (24-27.5°C) (cf. Table 6). All species dig the hole for the egg with the middle legs. Usually the insertion of the abdomen into the soil is quick; the withdrawal, which presumably represents the actual extrusion of the egg, slightly slower. Body lengths below include both sexes (proboscis not included).

1) *L. pallida* (10-15 mm): Total duration 150-400 cmin. (1.5-4 min.). A special quivering of the middle legs in the bottom of the pit (egg-covering) is being inserted between egg-laying and pit-refilling. Pit-refilling with middle legs takes place in stages. Fore legs do not participate in pit-refilling.

2) *L. canariensis* (8.5-13.5 mm), *L. fortunata* (8.0-11.5 mm), *L. hemmingseni* (7.5-12.4 mm), and *L. funebris* (7.5-10 min): Total duration roughly 10-140 cmin. (0.1-1.4 min.). No quivering phase between egg-laying and pit-refilling. Fore legs participate with middle legs in pit-refilling.

3) *Vermileo nigrientris* (8.5-10 mm): Total duration 5 cmin. (0.05 min.). Participation of fore legs in pit-refilling reported in the Egyptian observations presumably on *V. niloticus*.

The most specialized and slowest species *L. pallida* is the largest (10-15 mm) and presumably the most thermophilous; and the least specialized and quickest,
**V. vermileo**, is one of the smallest (8.5-10 mm) and presumably the least thermophilous. Also in the possession of the long proboscis the genus *Lampromyia* is more specialized than *Vermileo*. However, *L. canariensis* which is the quickest among the rest (shortest phase 1), is not the smallest among them. Evidently the above-mentioned trends should be checked and supplemented by studying other species. There is not in the species under consideration any special adaptations of the middle or fore legs such as expansion of legs or sweeping hairs as seen in some other digging insects.

It will be evident from the foregoing sections that the stereotyped instinctive ovipository behaviour pattern differs substantially from species to species. The most extensive comparisons were made between the three Canarian species.

In *L. canariensis* both at 20.0-21.5°C and at 25.5-27.0°C and in *L. hemmingseni* at 24.0-27.5°C the female starts digging immediately after settling from interovipository flight. In *L. fortinata* at the same temperatures (20-22°C and 24-27°C) the female does not start digging until shortly after settling (still cf. postscript on p. 202).

In *L. canariensis* at both ranges of temperatures the abdominal forward thrusts of the downward bent apex of the abdomen in the air during digging (phase 1) are so rapid that either they cannot be counted with the naked eye, or they simply merge, i.e. they are practically absent during phase 1. In *L. fortinata* (20-35°C) and *L. hemmingseni* (24.0-26.5°C) the abdominal thrusts can be easily counted and are produced at a slower rate than the digging movements. As shown for *L. fortinata* the rate increases with temperature and with ultraviolet light.

The length of phase 1 is on the average at a certain temperature much shorter in *L. canariensis* than in *L. fortinata* (shown at 20-22°C and 24-27°C) and *L. hemmingseni* (shown at 24.0-27.5°C) (cf. Figs. 13 and 19). In the latter two species the length of phase 1 is at a certain temperature, as studied about 26°C (24-27.5°C), nearly the same, or perhaps on the average a little greater in *L. hemmingseni*.

As a scrutiny of Table 5 will show there is no clear-cut, let alone great, difference in length of phase 2 between *L. canariensis* on the hand, and *L. fortinata* and *L. hemmingseni* on the other hand. At about 26°C (24-27.5°C) it is on the face value of the averages actually - like the length of phase 1 - a little shorter in *L. canariensis* than in *L. fortinata* and *L. hemmingseni*. This would be accentuated by adding the duration of jerks (phase 3) to phase 2 in *L. fortinata* and *L. hemmingseni*, though the discrepancy between Tables 3 and 4 makes it uncertain how much should in *L. fortinata* be added. But at 20-22°C the difference between *L. canariensis* and *L. fortinata* taken at its face value, goes slightly in the opposite direction; and there is no average duration of jerks to be added in *L. fortinata* in which jerks are practically absent at these temperatures.

Like phase 1, phase 2 is perhaps at about 26°C (24-27.5°C) a little longer in *L. hemmingseni* than in *L. fortinata*. 

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In *L. canariensis* both at temperatures 20-22°C and 25.5-27°C the female flies away immediately after phase 2. When as a rare exception it remains on the spot, a few jerks may be seen of fore and middle legs. In *L. fortunata* and *L. hemmingseni* the fly does not fly away immediately after phase 2 but stays on for a while. In *L. fortunata* phase 2 is in some cases followed by a number of jerks of fore and middle legs (phase 3). At 24-27°C jerks occurred in 75% of the cases; at 20-22°C, in 4%; at 30°C, 41%; and at 35°C, 17%. In *L. hemmingseni* phases 2 and 3 tend to merge.

In *L. canariensis* at 20-22°C and 25.5-27°C the wings usually quiver during the whole process, whereas in *L. fortunata* they usually quiver at egg-laying proper at the end of phase 1 and during phase 2. In *L. hemmingseni* the wings appear, at least as a rule, to quiver during the first part of phase 1 until the 10th-20th abdominal thrust, i.e., not during the whole process as in *L. canariensis* and not at all in phase 2 as in *L. fortunata*.

The reduction in *L. fortunata* at 20-22°C, 30°C and 35°C of phase 3 (jerks) mentioned on p. 187 – an approach to the practical absence of jerks in *L. canariensis* – poses the question as to whether there may be also in other respects an approach with change in temperature.

As is evident from Fig. 13 the length of phase 1 is at about 26°C on the average considerably shorter in *L. canariensis* than in *L. fortunata*. By raising the temperature for *L. fortunata* or lowering it for *L. canariensis* it should be possible to obtain the same lengths of phase 1 in either.

A comparison between Figs. 15 and 16 shows that actually the lengths are about the same at 20-21.5°C in *L. canariensis* and 35°C in *L. fortunata*.

Thus at 35°C *L. fortunata* approaches *L. canariensis* in reduction of jerks and reaches it in length of phase 1.

Phase 2 is perhaps a little shorter in *L. canariensis* than in *L. fortunata* at 24-27°C (Table 5). In as much as there is a shortening of phase 2 with rising temperature in *L. fortunata* (Table 9) there may perhaps be said also to be an approach to *L. canariensis* in length of phase 2 with rising temperature. But the figures are very far from being so convincing as for phase 1.

As regards the rate of abdominal thrusts there may be said to be an approach to *L. canariensis* in as much as the rate increases from 20°C to 35°C (Fig. 17). But it is very far from being an approach to the extent of increasing the rate so much as to practically stop the movements as in *L. canariensis*. Not even the aberrant high rates at 25-27°C (Fig. 17) reach the minimum rates 2.9-4.2 attained in *L. canariensis* (cf. the species, p. 166).

Doubtless owing to the increase in rate of thrusts at 25-27°C in comparison with the rates at both lower and higher temperatures in Fig. 17, presumably due to the stimulation with ultraviolet light at 25-27°C no approach at all is seen by comparing the last columns in Tables 2 (25-27°C) and 11 (35°C).

We are pretty sure that also the start of digging shortly after settling from flight
and the staying on after phase 2 (or 3 when present) were at 35°C as at 24-27°C. At least this was so in some experiments at 20-22°C, but attention was concentrated on other details in the other temperature experiments.

It might similarly be asked if there are approaches to *L. canariensis* in the experiments on *L. canariensis* at 20-21.5°C, apart from practical identity in length of phase 1.

Also phase 2 increases in length in *L. canariensis* with decreasing temperature (Table 5) but again the data are less clear because the difference in length of phase 2 between the species at about 26°C is not clear-cut.

As already mentioned also at the lower temperatures *L. canariensis* started digging immediately after settling, the abdomen still could not follow the rhythm of digging and with a few exceptions the female flew away immediately after phase 2, phase 3 being absent.

In other words, the length of phase 1 presumably also of phase 2, and in *L. fortunata* the percentage occurrence of jerks are species characteristics only if temperature is allowed for, whereas the other specific differences in ovipository behaviour persist with changes in temperature (with above-mentioned assumptions as regards the experiments at 35°C): start of digging immediately after (*L. canariensis*) or shortly after (*L. fortunata*) settling, presence (*L. fortunata*) or absence (*L. canariensis*) of pronounced abdominal thrusts in the air, staying on (*L. fortunata*) or flying away (*L. canariensis*) after phase 2, (cf. postscript on p. 202).

There seems to be no reason to believe that in nature *L. canariensis* preferably oviposits at 20-21.5°C and *L. fortunata* at 35°C, so that presumably the temperature-susceptible specific differences established at 24-27°C will obtain in nature, as well as the non-temperature-susceptible differences.

It seems natural to suppose that in nature oviposition takes place in the ordinary habitat of the larvae. This is generally in smaller or larger caves, or under overhanging cliffs, sometimes in small niches or close to walls (e.g. *L. fortunata*, see Hemmingsen 1963, p. 238). In general the conditions described by Hafez & El Moursy (1956a, e.g. pp. 284-286) for *Vermileo* presumably holds more or less for other species of worm-lions.

In Fuerteventura A.M.H. found the larvae (*L. hemmingseni*) commonly near walls and fences entirely in the open. Presumably in this island they are not so much in need of shelter from rain, because it sometimes does not rain for a whole year. Wet substrates are too hard for the larvae to work in.

The worm-lions are capable of leaping a considerable distance (cf. Hemmingsen 1968a, p. 291) and of wandering (cf. loc. cit., pp. 292-293), so that it is not a priori certain that the eggs were laid exactly where larval pits are found.

No direct observations have been made of the site, time of day and months, temperature or other conditions for oviposition in nature in any of the species (except for the presumptive evidence of flying periods and general activity), but
would be desirable in order to check the above suppositions (cf. postscript on p. 202). Also temperature preference of the imagines of the different species might give clues.

The senior author (A.M.H.) has found larvae in the Canary Islands on suitable spots from about sea level throughout the low dry zone, but does not know the exact upper limit. He found them up to ca. 900 m altitude (below Aguamansa in the Orotava Valley and above Chío, west of Tenerife: Nos. 19 and 20 in Fig. 1). Reports of adult flies are strikingly scarce compared with reports on the larvae. The senior author has seen flies of *L. fortunata* collected by Mr. J.M. Fernandez in the open from April (El Rincón, Gran Canary) and of *L. canariensis* in May-June (Santa Cruz de Tenerife and Puerto de la Cruz, Tenerife). Frey (1937, p. 43) reports 40 flies flying in July in front of the opening of a depression in a rock wall at Orotava, Tenerife. Hafez & El Moursy (1956b) found three females and one male of the Egyptian *Vermileo* on 22.IV. and found that reared flies were inactive at 16°C and distinctly active at 22°C. But there is nothing in these various facts to establish ecological differences as regards the temperature at which oviposition takes place in the open in the different species (cf. postscript on p. 202).

The closer affinity as regards ovipository behaviour between *L. fortunata* and *L. hemmingseni*, as contrasted with *L. canariensis*, (cf. p. 177) - despite the outward similarity between *L. canariensis* and *L. fortunata* - is borne out by the study of the male hypopygia (Stuckenberg 1971).

We have here a case of relationships being expressed, as it seems, just as clearly by similarities and differences in stereotyped (instinctive) behaviour as by the more commonly used corporeal characteristics. It thus seems that such ethological data should be consulted in taxonomical and evolutionary arguments. This has been pointed out and stressed by quite a number of previous authors for different animal groups (e.g. Whitman 1899, 1919, Heinroth 1910, 1930, Petrunkevitch 1926, Lorenz 1941, Delacour & Mayr 1945, Adrianse 1947 and Baerends & Baerends-van Roon 1950; for references to all these see Lelirmann 1953, p. 346; further Michelsen 1963, 1966a, b, Church 1967 and Hemmingsen 1968b, p. 26).

But, alas, as the present work amply testifies, the use of ethological data in taxonomy is unavoidably restricted by the work and practical difficulties involved in obtaining the data.

Moreover, there are cases in which ethological evidence appears to run counter to structural evidence.

According to the viewpoints just advanced the distict difference in ovipository behaviour between *L. pallida* and the other species should be expected to be reflect-ed in the structure of the male genitalia.

According to Stuckenberg (1960, p. 247) in genital characters *L. canariensis* is closest to the South African *L. pilosula*-group, while *L. pallida* and *L. cylindrca* are more distantly related though close to one another. This apparently does not reflect the differences in ovipository behaviour. For, as the preceding section show,
the females of *L. funebris* (from Spain), by Stuckenberg in 1960 still referred to *L. cylindrica*, behaved much more like *L. canariensis* (and thus the other two Canarian species) than like *L. pallida* (from Tunisia).

However, the species which Stuckenberg in 1960 referred to as *L. pallida* was based on a specimen from Spain, and seems to be different morphologically to the North African *L. pallida* Macquart, type locality Oran, and will need a new name (Stuckenberg in litt. 1968). So though presumably this new species and the North African true *L. pallida* are closer morphologically to one another than to *L. funebris* the apparent discrepancy between ethological and morphological evidence in this case cannot be postulated definitely until it has been established whether also the genital characters of the true North African *L. pallida* are closer to *L. funebris* than to *L. canariensis*.

A similar discrepancy is seen in the fact that the ovipository behaviour pattern of our Canarian-Spanish *Lampronyxia* species is more close to that of *Verniileo* species, of a different genus, without a proboscis (use of both fore and middle legs in one short egg-covering pit-refilling phase), than to *L. pallida* of their own genus with proboscis (use of only middle legs in two long phases, the first egg-covering, the second pit-refilling).

Fig. 13 presents a comparison at 24.0-27.5°C between the lengths of phase 1 in the 6 species under study in this paper. It will be seen, and a statistical test corroborates, that if phase 1 lasts longer in *L. hemmingseni* than in *L. fortunata*, this is only slightly so.

The marked difference between, on the one hand, the length of phase 1 in these two species and, on the other hand, in *L. canariensis* needs no statistical test. It is evident that *L. canariensis* has a much shorter average length of phase 1 than the other two Canarian species (cf. also Fig. 19). And phase 1 of *V. nigriventris* is shorter than that of any of the other species.

Judging from the relatively few data on *L. pallida* and *L. funebris* the former species has the largest average length of phase 1; and the latter, an average intermediary between that of *L. hemmingseni* or *L. fortunata* and that of *L. canariensis*.

The length of the phases following phase 1 have already been discussed for the three Canarian species.

In *L. pallida* there is an egg-covering phase 2 and a pit-refilling phase 3, both carried out by the middle legs only. They are, so to speak, merged into one egg-covering and pit-refilling phase in the other species, which use both fore and middle legs. Phase 3 (jerks) in the other species can only with difficulty be homologized with phase 3 in *L. pallida*. It appears to be virtually part of phase 2, as is especially evident in *L. hemmingseni*, in which phases 2 and 3 often merge. The combined length of phases 2 and 3 in *L. pallida* exceeds manifold the length of phase 2 or 2 plus 3 in the other species (Table 5). In the two remaining species, *L. funebris* and *Verniileo nigriventris* too few direct measurements on phase 2 are available for comparison. The total lengths in the different species of the whole process until
the egg has been covered (i.e. excluding phase 3: the jerks) are compared in Table 6. In *L. hemmingseni* the cases in which phase 2 and 3 (jerks) merged are treated separately.

A close study of Tables 5 and 6 will show that the trends in length of phase 2 and total length of the ovipository process are the same as in Figs. 13 (specific phase 1 lengths), 15 and 16 (phase 1 at different temperatures) with the qualifications already discussed in the case of phase 2.

The addition to phase 1 of *L. pallida* of the long lasting egg-covering and pit-refilling phases (Table 5) in this species is seen from Table 6 to result in a distinctly much larger duration of the whole process than in any of the other species.

### 14. ACKNOWLEDGEMENTS

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### 15. SUMMARY

All the six species of Vermileoninae studied dig a pit in loose substrate with the simultaneously backward moved pairs of middle legs (phase 1), and lay an egg in the pit.

*Lampromyia pallida* covers the egg by the vibrating middle legs (phase 2) and thereafter refills the pit (phase 3) by inward strokes only of the middle legs in stages.

All the other species cover and refill the pit in one stage (phase 2) by both fore and middle legs. In *L. fortunata* the fore and middle legs may make some jerks (phase 3) after the pit has been refilled. In *L. hemmingseni* the jerks often constitute part of phase 2.

The duration of the whole process is longest (1.5-4 min.) in *L. pallida*, shortest (0.05 min.) in *Vermileo nigriventris*.

Phase 1 which in all the species is considerably longer than phase 2, is at a defined temperature distinctly longer (and practically equal in length) in *L. fortunata* and *L. hemmingseni* than in *L. canariensis* (Fig. 13). The same appears to apply to phase 2.

The length of phase 1 is at a defined temperature among all six species in *L. pal-
_*lida*_ apparently on the average the longest; and in *L. finebris*, apparently intermediary between *L. fortunata* and *L. canariensis* (Fig. 13).

During phase 1 the downward bent apex of the abdomen is thrust rhythmically forward in the air in *L. pallida* (synchronously with the digging movements), *L. fortunata* and *L. hemmingseni* (in the latter two species less frequently than the digging movements, which are quicker than in *L. pallida*). In *L. canariensis* the thrusts and the digging movements are still quicker, and the thrusts appear to attempt in vain to follow the digging movements so as to apparently cease at all. Whether or not such thrusts occur in *L. finebris* and *Vermileo nigriventris* was not noted.

In *L. canariensis* and *L. hemmingseni* the female starts digging inmediately after settling from interovipository flight. In *L. canariensis* it flies away immediately after phase 2 without exhibiting any jerks with fore and middle legs (with rare exceptions). In *L. fortunata* the fly does not start digging until a short while after settling (still cf. postscript on p. 202), and in this species and *L. hemmingseni* she stays on for a while after phase 2 (or 3 when present).

In *L. canariensis* the female quivers her wings throughout the whole process; in *L. fortunata*, only at the egg-laying proper at the conclusion of phase 1 and during phase 2; and in *L. hemmingseni*, during the first part of phase 1. Exceptions occur.

There is a clear-cut shortening of phase 1 and 2 with rising temperature as shown in Fig. 15 and Table 5, respectively, for *L. canariensis* (20-27°C), and in Fig. 16 and Table 9, respectively, for *L. fortunata* (20-35°C); and in *L. fortunata* a rise in rate of abdominal thrusts (with non-ultraviolet light at 20-22°C, 30°C and 35°C in Fig. 17).

By lowering the environmental temperature for *L. canariensis* to 20.0-21.5°C and raising it to 35°C for *L. fortunata* an approach to practically identical ranges of the duration of phase 1 (ovipository digging) were attained.

*As* regards phase 2 the results were too contradictory for an approach to be postulated. But somewhat of an approach to the practical absence of phase 3 (jerks) in *L. canariensis* can be obtained in *L. fortunata* by the rise to 35°C. There is also an apparent approach in rate of thrusts, but not to the extent of eliminating them. The following stereotyped behavioral characteristics in which *L. fortunata* differs from *L. canariensis* were not substantially affected by the rise to 35°C: presence of abdominal thrusts and presumably starting of digging a short while after settling and staying on for a while after phase 2 or 3.

In *L. canariensis* no approach to *L. fortunata* was observed by lowering the temperature from about 26°C to 20-21.5°C apart from the approach in length of phase 1.

Thus, the duration of phase 1 and in *L. fortunata* the percentage occurrence of jerks are specific only with defined temperatures, whereas the other specific differences in stereotyped (instinctive) ovipository behaviour are independent or presumably independent of temperature within the limits studied (20-35°C).
The closer affinity in ovipository instinctive behaviour between *L. fortunata* and *L. hemmingseni*, in contrast to *L. canariensis* (in spite of the outward resemblance between *L. canariensis* and *L. fortunata*) confirms the conclusions of Stuckenberg (1971) based on the hypopygal differences of the species.

Apparently *L. pallida* and *L. funebris* and the *Vermileo* species do not conform to a parallelity between ovipository behaviour and corporeal structures.

16. REFERENCES


— 1956a: Convergent methods of oviposition in short-horned grasshoppers (Acridiidae) and some crane-flies (Tipulidae) compared with other types of convergent evolution. — Int. Congr. Zool. 1953: 177-178.


17. POSTSCRIPT

(cf. pp. 155, 172, 183, 188 (twice), 194 and 196)

After completion of this paper ca. 50 ovipositions of Lampronyxia fortunata were studied throughout May 1971 in the caves of Ceioibia de Vaieron, Gran Canaria, by A. M. H. jointly with Mr. Jorgen Frederiksen. The ovipositions were seen only in dust and in the shade (385-9000, usually 1600-3300 lux), at 18-21°C and relative humidity of 50-70% As the Canarian species are largely inactive below 18° these observations imply that this species does not consistently ovipo-
sit at higher temperatures than *L. canariensis* (cf. p. 196). The lengths of phases 1 and 2 and number and rates of abdominal thrusts were found to practically coincide (phases) or at least to coincide for the largest part of their ranges (thrusts) with the observations recorded at 20-22°C in Figs. 11, 16, 17 and 19 and Tables 8 and 9. Oviposition in sifted sand (II in Table 10) and dust thus appears to be much the same. There were, however, more exceptions to the short delay in start of digging after settling but very few to the staying on after phase 2. Details including ecological data will be published later.

Correction to p. 156, lines 14-16: In order to simplify disposition, experiments in which illumination G (see Table 1) at least in some, most likely in all, cases was combined with F, as H, have been without qualification in the text considered, and in the tables listed, under "artificial sunlight".

Correction to Fig. 16 on p. 183: Insert 2 phases of 28 cmin. and 1 of 29 cmin. at 35°C.