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Breeding of an F_2 of *Hyles* hybrid *vespertilioides* (Boisduval, 1827) after induction with ecdysone of metamorphosis in diapausal pupae

E. A. Loeliger* & F. Karrer**

* Hofdijck 48, NL-2341 ND Oegstgeest, The Netherlands
** Rebbergstrasse 5, CH-4800 Zofingen, Switzerland

Summary

After synchronisation of the emergence of male and female adults of *Hyles* hybrid *vespertilioides* Bdv. by means of ecdysone injected into four of the six female pupae, pairing took place quickly. Oviposition was abundant and survival was normal. Fertility of the eggs averaged 50 per cent. Ovipositing females as well as about 65 per cent of the larvae preferred *Epilobium dodonaei* Vill. as host. Phenotypically, F_2-larvae and F_2-imagines varied markedly : from the typical *H. vespertilio* (Esper, 1779) to the almost classical *H. hippophaes* (Esper, 1793). There was, however, a striking correlation between host preference and phenotype : caterpillars displaying typical grandparental aspect choose the grandparental host and transformed into imagines strongly resembling the respective grandparent. Particularly notable among larvae raised on *Hippophae rhamnoides* L. and/or *Elaeagnus angustifolia* L. were those mimicking the uncommon recessive variety of *H. hippophaes* displaying rubiginous colouration and among imagines those closely resembling the rare ab. *flava* Blach. of *H. vespertilio*.

Résumé

Après synchronisation de l'éclosion des adultes mâle et femelle de *Hyles* hybride *vespertilioides* Bdv. au moyen d'ecdysone injectée en quatre des six chrysalides femelles, l'accouplement eut lieu rapidement. La ponte était abondante et le degré de survie normal. La fertilité des œufs était d'environ 50 pour cent. Les femelles qui pondaient ainsi qu'approximativement 65 pour cent des chenilles préféraient *Epilobium dodonaei* Vill. comme plante-hôte. Le phénotype des chenilles F_2 et des imagos F_2 variait de façon marquée : de *H. vespertilio* (Esper, 1779) au *H. hippophaes* (Esper, 1793) presque classique. Il y avait néanmoins une corrélation frappante entre la préférence de l'hôte et le phénotype : des chenilles arborant l'aspect grandparental typique choisissaient la plante-hôte grandparentale et se transformaient en imagos ressemblant fortement au grand-parent respectif. Particulièrement remarquables

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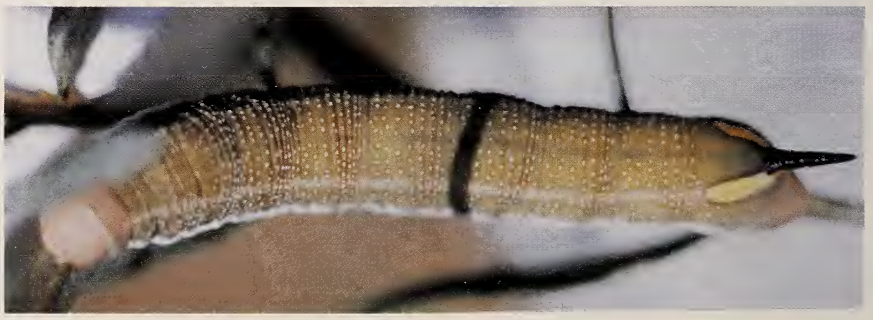
a

b



c

Fig. 1. Three L_5 caterpillars, 1 a and 1 b being specimens of F_2 *H.* hybrid *vespertilioides*, 1 a closely resembling *vespertilio*, and 1 b that of 1 c which is the propositus of the rare rubiginous variety of an *hippophaes* L_5 found in the field (Loeliger, 1996).

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Fig. 2. L_5 caterpillars of F_2 *H.* hybrid *vespertilioides* displaying uncommon appearance, 2 a, 2 b, and 2 c grown on *H. rhamnoides*/*E. angustifolia* and 2 d, 2 e, and 2 f on *E. dodonaei*/*angustifolium*.

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parmi les chenilles élevées sur *Hippophae rhamnoides* L. et/ou *Elaeagnus angustifolia* L. étaient celles imitant la variété récessive rare de *H. hippophaes* arborant une coloration rougeâtre et parmi les imagos ceux ressemblant de près la rare ab. *flava* Blach. de *H. vespertilio*.

Introduction

Hyles hybrid *vespertilioides* (Boisduval, 1827) is the product of crossing a *Hyles hippophaes* (Esper, 1793) male with a *Hyles vespertilio* (Esper, 1779) female, two closely related species of the sphingid family which are practically monophagous and highly ubiquitous in the riverine valleys of the northern Mediterranean region. Hybridization must occur regularly under field conditions since hybrid caterpillars have been found repeatedly along the Rhône River (Boisduval, 1827 ; Feisthamel, 1827 ; Denso, 1909 ; Wenczel, 1983). Hybridization has also been obtained in captivity (Benz, 1952 ; Baumgartner, 1971, pers. comm. ; personal experience on repeated occasions in the eighties). Reports on a second generation (F_2), i.e., the cross *vespertilioides x vespertilioides*, have not yet been published although an F_2 has been obtained at least once (Benz, 1962, unpublished). The adults produced and diary records are in the possession of one of us (FK).

Our interest in an F_2 generation arose from observations of the hereditary transmission of grandparental peculiarities, such as the complete lack of the caudal horn of *H. vespertilio* caterpillars or the conspicuous colouration of adults of the two species involved. Investigation of a possible correlation between host preference and phenotype of the caterpillar and/or ovipositing adult also seemed worthwhile. In addition, the possible de novo appearance of rare varieties of the grandparental species continues to be one of the incentives to undertake hybridization experiments.

The attempt to breed an F_2 generation of *vespertilioides* was complicated by the fact that metamorphosis of the females is known to be markedly retarded (Baumgartner, 1971, pers. comm ; personal observations in 1971 and 1973), although it may occur simultaneously with that of the males (Benz, 1962).

In this paper the achievement of successful synchronization of the emergence of male and female adults of *vespertilioides* by means of the injection of ecdysone into female pupae is reported and our observations during the breeding of an F_2 generation of this hybrid are described.

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Materials and methods

Experimental animals : the male imago of the hybrid vespertilioides cross was an exceptionally strong specimen of *H. hippophaes,* grown in 1993 as the offspring of the mating of a *H. hippophaes caucasica* (Denso, 1913) male, the caterpillar of which was found on *Elaeagnus angustifolia* near Bogazkale (TR) in October 1992, with a *H. hippophaes* hippophaes female originating from the Swiss part of the Rhône Valley (courtesy F.Weber, Riehen, CH). This female had produced 680 mainly fertile eggs (dissection revealed that only eight eggs had remained *in situ*). The mother of the *vespertilioides* cross was one of the many *H. vespertilio*-specimens grown in 1993 under field conditions (the F_1 female lived for $4^1/_2$ weeks and laid all of its 250 eggs, exclusively on *Epilobium dodonaei* Vill., the vast majority being fertile). The grandparental *vespertilio* caterpillars were found near Les Baux in southern France (courtesy C. Czipka, Fürth-Erlangen, D).

Flight cages : the rectangular wooden floor, 30 x 50 cm, is capped with a tunnel of gauze, e.g., surgical Tubinette™, stretched over the floor and three aluminium arches which have a maximum height of 30 cm and are attached at regular intervals to the floor along its length.

A cage generally does not contain more than one or two females plus two to three males. The long side is exposed to daylight and, if possible, there is some circulation of fresh air. With sprigs of the host along the bright side of the cage, the cages also serve as receptacles for oviposition.

Preparation and injection of the ecdysone solution : one milligram of commercially available alpha-ecdysone crystals is dissolved in 0.12 ml ethanol or isopropanol. To obtain the full sterilizing capacity of the alcohol, 0.08 ml of water are added. Ten minutes later, 0.8 ml of water are added to obtain the final alcohol concentration of 12 per cent and the final ecdysone concentration of 0.1 per cent. The ingredients are mixed thoroughly and the solution is aspirated with a 30 G Microlance™ needle (Beckton, Dickinson & Comp.) into a one-ml-syringe subdivided into 0.02 ml portions (e.g. a Jecton-S™ syringe), each portion thus containing 20 mg ecdysone and amounts of diluted alcohol too small to damage pupal tissue.

The optimum amount of hormone to be injected, as assessed from the results of treatment of more than 300 specimens, is approximately six mg per gramme pupa. Before injection, the vertex of the head of

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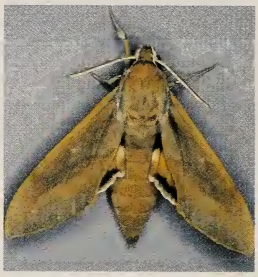
a



b

Fig. 3. Five imagines resembling *H. vespertilio* ab. *flava* Blach., the specimen shown in Figure 3 a grown by EAL, and the four displayed specimens shown in Figure 3 c belonging to the collection of FK. The specimen presented in Figure 3 a is the same as that on display to the bottom left in Figure 4 c; the bottom right specimen in Figure 3 b is the same as that among the months shown in Figure 4 b.

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Fig. 4. (a) presents two imagines resembling *hippophaes* (top) and *vespertilio* (bottom). L_5 of the latter is presented in Figure 1 a.
(b) shows the four imagines of the 1994 breeding by FK. The two smaller bottom specimens are samples of the Benz collection.
(c) Overview of the nine imagines of the 1994 breeding by EAL (the 10th, a specimen of the *flava* variety with coiled forewings is not shown).

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the pupa is iodinized. To prevent abdominal movement of the pupa, which would increase internal pressure such that blood loss from the puncture site would be heavy, the pupa is anaesthetized by exposure for 30 to 40 minutes to CO_2 ; for this purpose, the pupa is placed in a container on a two to three cm thick layer of linen covering small pieces of dry ice. Before the injection, the pupa is laid on the middle finger and fixed with the thumb. The needle is inserted along the sagittal axis through the iodinized vertex of the head deep into the thorax/ abdomen. The predetermined amount of the ecdysone solution is then injected slowly. The needle is kept in situ for about 10 seconds. After withdrawal of the needle, the puncture site is covered with collodion and the pupa is placed on fine peat or sand to avoid unnecessary movements which may be caused by coarse underlying material. Twenty-four hours after injection the pupa can be handled normally.

Rearing the larvae : before use the containers, mainly Petri dishes, were thoroughly washed and sterilized with formaldehyde. Every 24-48 hours the leaves were changed. Larvae, twigs and leaves were only handled after thorough hand-washing ; they were deposited on clean sheets of paper.

Results

The hybrid *vespertilioides* : on June 20th, 1994, shortly after midnight, copulation took place between a *H. hippophaes* male (two males had been in the cage) with a *H. vespertilio* female (one adult in the cage only). Room temperature was 22°C. Oviposition on *E. dodonaei* Vill. started the day after pairing. By June 30th, a total of 284 eggs had been deposited exclusively on the host. Subsequent dissection of the female revealed that no eggs were left in the abdomen. The caterpillars first grew on *E. parviflorum* Schreber, until stage L_4. Stage L_5 were fed *E. angustifolia* L. and exposed to a constant temperature of 35°C.

By July 12th, the first larva prepared for pupation, and by July 28th, there were 13 male and six female pupae. On July 26th, the first and second male pupae exhibited signs of metamorphosis. By August 2nd and 3rd, five male imagines had emerged ; all other males were still in the process of development. The six females remained in diapause. In order to induce their metamorphosis, ecdysone was injected into four pupae on August 5th, the other two pupae were left untreated to serve as controls. The injected pupae were maintained at 35°C. Developing male pupae were kept at the lowest possible room temperature ; emerged males were exposed to continuous light to minimize flying. By August 8th, eye pigmentation, the first sign of metamorphosis,

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was discerned on translucence, and by August 12th, wing pigmentation had become apparent. In the afternoon of August 14th, the four imagines emerged almost simultaneously, the forewings being slightly deformed in three cases after filling with blood and their scaling being more or less defective (unscaled wing patterns display a green glimmer). The probosces were insufficiently coiled in two cases. None of the four females exhibited overt problems as far as flight, oviposition and feeding were concerned.

The two non-treated female pupae remained in diapause.

Pairing of *vespertilioides* : The two first-born females (emergence time about 16.00 h and 18.30 h, respectively) were kept in separate cages together with two males for each. Both copulated on the same day shortly after midnight. Pairing lasted one and three hours, respectively. The other two females (emergence time about 19.00 h and 20.00 h, respectively) copulated with different males the next day, also shortly after midnight, with similar pairing times.

Oviposition : the first egg was deposited during the night of August 15th. After eight hours of incubation at 32°C, signs of embryogenesis could be discerned microscopically. During the night of August 16th, imago I deposited more than 100 eggs mainly on *E. dodonaei.* These eggs were shipped to collectors and used to obtain an appropriate number of caterpillars for observation (n = 50 ; see page seven). From August 18th through August 22th, the possibility of a preference for one of the parental hosts was investigated. For this purpose, each female was kept in a separate cage and the host was changed daily. The first night (August 18th) *H. rhamnoides* or *E. angustifolia* and *E. dodonaei* were presented together (females I and III, Table 1).

Table 1

Number of eggs deposited either on the host or on the gauze of the cage. The numbers in parentheses refer to the four females separately. — : not present during that night.

Host	*E. dodonaei*	*H. rhamnoides* *E. angustifolia*	gauze n	%
Day				
18/8	126 (19, 18, 35, 54)	25 (8, –, 17, –)	55 (21, 16, 10, 8)	27
19/8	—	85 (32, 0, 12, 41)	59 (9, 30, 7, 13)	41
20/8	39 (3, 22, 2, 12)	—	68 (1, 41, 23, 3)	64
21/8	—	39 (18, 7, 11, 3)	129 (2, 63, 53, 11)	78
22/8	94 (17, 25, 19, 33)	—	146 (7, 100, 14, 25)	61
Total n	259 (39, 65, 56, 99)	149 (58, 7, 40, 44)	457 (40, 240, 107, 60)	
%	30	17	53	

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Fig. 5. (a) Overview of the 32 imagines raised by Benz in 1962. The numbers run vertically from top to bottom and left to right. The four vertical columns contain 8 imagines each. Numbers 2, 3, 4, 6, 13, 18, 21 and 31 (together 25 per cent) resemble *hippophaes*, while numbers 11, 12, 16, 17, 20, 22 and 23 (together 22 per cent) are similar to *vespertilio*.
(b) shows the four most *hippophaes*-like specimens (nrs. 2, 3, 13, 18).

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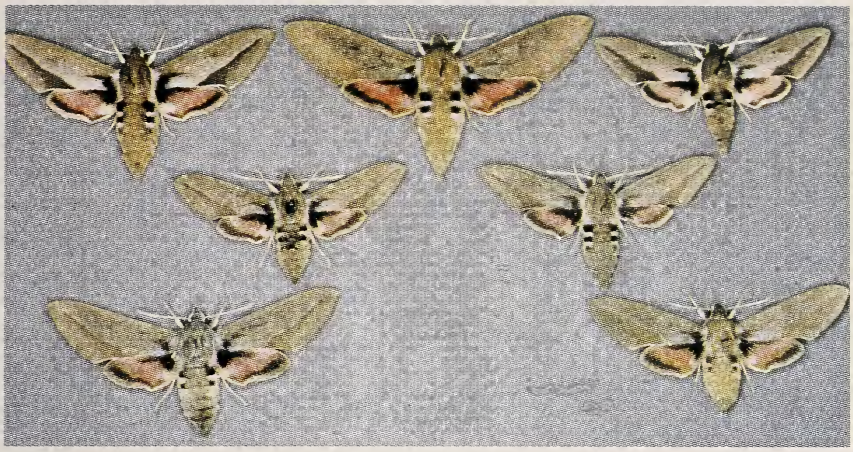

Fig. 6. Adults of the cross *vespophaes* male x *vespertilioides* female. Note the novel phenotype in the centre of the top row. The two adjacent specimens closely resemble *hippophaes* as did their caterpillars.

Fig. 7. The seven adults of *vespophaes* F_2 in the collection of FK. None is typically *vespertilio*-like. Four resemble specimens of *vespophaes* F_1. The two in the mid-row are *hippophaes*-like, the left one with a highly conspicuous right/left difference. The seventh (bottom right) resembles, although only slightly, the novelty shown in Figure 6.

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From the data presented in Table 1 it appears that *E. dodonaei* was preferred for oviposition : the number of eggs deposited on this host was about twice that deposited on *H. rhamnoides* or *E. angustifolia.* Interestingly, the percentage eggs on gauze increased rapidly after the first two days.

The number of eggs deposited separately by the four females was 268, 630, 309, and 296, respectively, or a total of 1503. The imagines died (I) or were killed (II, III, IV) 10, 24, 21, and 15 days after emergence. On dissection, they contained not more than 2, 0, 0, and 3 eggs, respectively. Imago I, which died spontaneously 10 days after emergence, had deposited 2/3 of her eggs within three days of pairing. In contrast imago II (the female which deposited the most eggs and lived the longest) slowly increased the number deposited up to 125 during the night of day seven (22/8). The antipathy of this female for *H. rhamnoides* and/or *E. angustifolia* was also striking.

The imagines were fed a 10 per cent saccharose solution every second day.

Peculiarities of larvae and pupae of the F_2 : approximately 75 per cent of the eggs deposited by females I and II were fertile versus 25 per cent of those from females III and IV. When exposed only to *E. dodonaei*, about 50 per cent of the larvae were still alive after a fortnight ; of those exposed exclusively to *E. angustifolia* or *H. rhamnoides*, only 50 per cent were alive after the first week. Unfortunately, some of the L_1 caterpillars escaped from the Petri dishes, thus excluding exact statistics in this respect.

The length of the caudal horn varied greatly, from being non-existent (as in *vespertilio*) to full length (as in *hippophaes*). Observation of more than 200 larvae revealed that, irrespective of the host, 14 per cent had virtually no horn, 36 per cent had a small horn, 36 per cent had a horn of medium length, and the remaining 14 per cent had a horn about as long as customary for *hippophaes* larvae.

Marking and colouration of the caterpillars varied enormously particularly in phases L_3 - L_5, from a close resemblance to *vespertilio* (Fig. 1 a) to almost indistinguishable from *hippophaes*, especially the rare rubiginous variety (Fig. 1 b and c). However, many of the larvae were also similar to the parent hybrid. The majority of the larvae reared on *H. rhamnoides*/*E. angustifolia* clearly tended to resemble *hippophaes*, whereas the phenotype of larvae growing on *E. dodonaei*/*angustifolium* looked much more like *vespertilio*. On several occasions we observed accelerated growth of an insufficiently developed *vespertilio*-like cater-

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pillar when the host was changed from *E. angustifolia* to *E. dodonaei* or *E. angustifolium*. Several caterpillars were striking due to their totally unfamiliar appearance (Fig. 2).

Correlation between host preference, phenotype of the larva and that of the imago: fifty of the eggs deposited by female I on August 16th/17th were chosen for raising and observing F_2 specimens under carefully controlled conditions. They were exposed to 33°C and a mixture of the grandparental hosts. By August 21st, about one day after hatching, 23 larvae had selected *E. dodonaei* as their host, 14 *H. rhamnoides*, and five had not yet made a choice. Eight did not hatch. Three days later, 29 surviving larvae were counted : 19 on *E. dodonaei* and 10 on *H. rhamnoides*. By August 28th, 27 larvae remained : seven L_5, eight L_4 and three L_3 on *E. dodonaei*, and three L_5, five L_4 and one L_3 on *E. angustifolia*/*H. rhamnoides* (due to a shortage of leaves, L_5 were fed on *E. angustifolia* and *E. angustifolium*, respectively). On day 10, the first larva ceased feeding and initiated pupation. Caterpillars on *E. dodonaei* pupated one to two days earlier than those on *E. angustifolia*, mainly because growth of the mature larvae had decreased temporarily when the host was changed. In total 23 larvae pupated : 16 of those grown on *E. angustifolium* (one slightly crippled) and 7 of those on *E. angustifolia*.

Within a fortnight of pupation, 10 of the 23 pupae (four males and six females) underwent metamorphosis, eight having been grown on *E. dodonaei*/*angustifolium* and two on *H. rhamnoides*/*E. angustifolia*. On September 14th, the first imago out of the *vespertilio*-like caterpillars of the *Epilobium* group emerged. After expansion, its forewings remained strongly coiled, and its hindwings were yellow instead of red, fitting the phenotype of *H. vespertilio* ab. *flava* Blach. This *flava*-type variety emerged from four other pupae of this series. The four in the possession of FK are shown in Fig. 3 b, in which the specimen to the left bottom is the same as that of Fig. 4 b. Eight of the nine caterpillars of the flava-type imagines had been fed on *Epilobium*. Of the five raised by and kept in the collection of EAL only two are shown (Fig. 3 a and 4 c). At least five of the caterpillars of the *flava* type had been striking pale yellow tinged green. A conspicuous golden glitter of the grayish or brownish scales of the imago was characteristic of this *de novo* variety as was particularly obvious in one case (Fig. 3 a, which is the same as the left bottom specimen in Fig. 4 c). Of the remaining five caterpillars raised by EAL on *E. dodonaei*/*angustifolium*, the one that resembled *vespertilio* the most as caterpillar (Fig. 1 a) gave rise to a slate-grey moth conspicuously similar to its grandmother

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(Fig. 4 a, and Fig. 4 c, top left). The other four had many features in commom with their parents, i.e., *vespertilioides* F_1. Of the two *H. rhamnoides*/*E. angustifolia*-fed larvae, the one resembling *hippophaes* the most yielded a moth which closely resembled a pale specimen of *hippophaes* (Fig. 4 a, and Fig. 4 c, bottom right) its larva having been olive-green with two pairs of orange ocelli, one at the base of the small caudal horn ; it also displayed an orange midline, as so often observed on the L_5 of *hippophaes* caterpillars. The other imago resembling *hippophaes* (Fig.4 c, midst specimen) emerged from a caterpillar which had been green, too, with orange ocelli from head to horn, the latter having been of intermediate length.

Figs. 4 b and 4 c depict F_2 imagines from the collection of FK and EAL, respectively, the FK specimens exclusively grown on *E. dodonaei*. The two *vespertilioides*-like bottom imagines in Fig. 4 b belong to the much smaller specimens of the Benz-collection. The three top specimens shown in Fig. 4 c resemble *vespertilio* as did their caterpillars.

Mendelian type distribution of the grandparental imaginal phenotype among specimens grown exclusively on E. dodonaei : the F_2 imagines raised by Benz in 1962 were never reported on, probably because of insufficient documentation of the breeding. As a supplement to our results, however, their presentation may provide additional evidence of Mendelian type inheritance of grandparental phenotypes, particularly since all of his imagines were from larvae reared exclusively on *E. dodonaei*. (From the records we know that only a few of the freshly hatched caterpillars temporarily accepted *H. rhamnoides* as their host). If one studies Figure 5 a , one might be tempted to divide the 32 imagines very roughly into three categories : one *hippophaes*-like (25 per cent), another *vespertilioides*-like (53 per cent), and a third one *vespertilio*-like (22 per cent). In Figure 5 b, the four most *hippophaes*-like specimens are presented.

Discussion

The present paper is the report of successful breeding of an F_2 of the hybrid *vespertilioides* in numbers large enough to assess (1) hereditary transmission of grandparental morphological and biological peculiarities as well as specific markings and colouration ; (2) the possible correlation between larval and adult phenotypes ; and (3) the occurrence of *de novo* varieties. Imagines of an earlier successful breeding of this hybrid (Benz, 1962, unpublished ; Fig. 5) underscore our findings.

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The success of our breeding is attributable primarily to the excellent health of the animals : the grandfather *hippophaes* was one of the numerous "fresh blood" offspring of the mating between a male specimen from Anatolia and a female specimen from Switzerland ; the grandmother *vespertilio* was raised in the field, its parents were found in southern France. Success would, however, not have been achieved without ecdysone-induced synchronization of the emergence of the parental males and females. In spite of the fact that the caterpillars were exposed to high temperatures, none of the females underwent metamorphosis shortly after pupation together with the males. This well-known disparity is not necessarily a hybrid-bound phenomenon since preferential subitaneous development of exclusively male imagines in pupae of *H. euphorbiae deserticola* caterpillars grown at elevated temperatures has also been observed (FK, 1973 ; not published).

As soon as it became evident that the females would remain in diapause, appropriate amounts of ecdysone were injected into four of the six female pupae. From large experience we knew that it would take about 10 days to complete metamorphosis if the injected pupae were stored at 35°C. This time it took 11 days. The accuracy of the hormone dosage had been such that the four females emerged almost simultaneously. Only one displayed no flaws. But the slight distortion and incomplete scaling of the forewings of the other three did not perceptibly interfere with their biological activities although flying might have been hampered slightly, which would explain the rapid drop in the percentage eggs deposited on the host relative to the gauze. The excellent vitality of the ecdysone-treated females was demonstrated by the rapid and uncomplicated pairing as well as the abundance and completeness of oviposition.

To evaluate the mode of inheritance of grandparental morphological characteristics, caudal horn length seemed to be the most appropriate factor. Interlarval differences were gradual, from non-existent to full length. There was no clear host dependence, although some of the caterpillars with complete absence of the horn looked like typical *vespertilio* (Fig. 1 a) and those with the longest horns often resembled *hippophaes* (Fig. 1 b and c).

Hereditary transmission of grandparental biological behaviour, such as feeding at night or hiding during daytime, which is so typical of the L_5 of *vespertilio*, or open sunning in the L_5 of *hippophaes*, would have been difficult to investigate. A much easier factor to assess was imaginal and larval host preference for oviposition and feeding, respectively. According to the figures presented in Table 1, the preference for *E.*

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dodonaei for oviposition was obvious : twice as many eggs were deposited on this host compared to *H. rhamnoides*/*E. angustifolia*. On days when only the latter plants were available, about 20 per cent more eggs were deposited on gauze than on days when *E. dodonaei* was available.

About two-thirds of the caterpillars selected *E. dodonaei* out of a mixture of the grandparental hosts. Among those confronted with only one type, the percentage acceptance was initially high ; but the 50 per cent survival time for those on *E. dodonaei* was about twice that for larvae on *H. rhamnoides*. Unfortunately, exact figures cannot be presented since an unknown number of freshly hatched caterpillars escaped from the Petri dishes.

Hereditary transmission of marking and colouration was fascinating. Among caterpillars (Figs. 1 and 2), diversity was almost infinite, such that a classical Mendelian type of grouping into grandfather, parental, and grandmother larval phenotypes would have been a mere fabrication, although many specimens displayed the rather vague markings and beige-greyish colouration exhibited by the parent caterpillars and the resemblance of quite a number of larvae with the grandparental phenotype was conspicuous (Fig. 1 a and b). There was a preponderance of olive-green and ochreous brown in larvae grown on *H. rhamnoides*/*E. angustifolia*. Several exceptions to this rule exhibited retarded growth, which accelerated after switching hosts.

Among adults, phenotypic identification was easier. About half resemble the parent *H.* hybrid *vespertilioides*. Of the remnant, some are very similar to *hippophaes*, others to *vespertilio*. Most interesting is the fact that the more the imago resembles the grandparental phenotype, the closer the caterpillar had done the same. This is beautifully illustrated by the imagines presented in Figure 4 a : the caterpillar of the upper moth had displayed all features typical for *hippophaes*, while the caterpillar of the lower specimen looked very much like an L_5 of *vespertilio* (Fig. 1 a). Among the excellently preserved imagines of *vespertilioides* F_2 grown by Benz in 1962 (see Fig. 5 a) about 25 percent each resembled the two grandparental phenotypes. The four most resembling *hippophaes* are presented separately in Figure 5 b. The rest was *vespertilioides*-like. It is noteworthy that Mendelian segregation appears to be independent on the host caterpillars had been fed with, since Benz had all raised on *E. dodonaei* exclusively. Unfortunately, Benz had made no attempt to correlate larval with original phenotype. Our observation of such a correlation, therefore, must be considered novel. It contradicts observations and interpretations made earlier with F_2 hybrids (Fischer, 1931).

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Most interesting, finally, was the occurrence of specimens which closely resembled rare varieties of the grandparental species. Among the caterpillars, there were the diffusely rubiginous ones, i.e., those whose colour was complementary to the classical olive-green of *hippophaes*. Caterpillars with such colouration are very rarely found in the field. Experimentally, it proved to be an autosomal recessive trait (Loeliger, 1996). Among the adults, those with yellow hindwings are striking. Whether these specimens are identical to the ab. *flava* Blach. of *vespertilio* referred to in handbooks remains to be detected. Specimens found in the field might, at least in part, be the offspring of primary or secondary hybrids occurring under natural circumstances.

A thorough study of the reports of the first hybrid caterpillars of *vespertilioides* observed near Grenoble (Boisduval, 1927 ; De Feisthamel, 1827) reveals that those found by Boisduval might, at least partly, have been secondary bastards or perhaps even F_2 *vespertilioides* (Kysela, 1908). This is not a far-fetched supposition since at the end of the 19th century, primary and secondary bastards of *Hyles* hybrid *epilobii* have been found in the field (Mory, 1901 and 1903 ; Lippe, 1902).

ADDENDUM

In 1995, we were successful with the breeding of *H.* hybrid *vespophaes* (Denso, 1909 ; Benz, 1948) and its F_2 , and with that of the cross of a *vespophaes* male with one of the two non-injected females of *vespertilioides*. Of both these broods, the results were closely similar to those described above, confirming our conclusions. There were two differences, however.

First, not a single specimen of the *flava* variety was observed among the 10 and 16 adults obtained from these F_2 hybrids, respectively. Second, an apparently novel phenotype emerged, particularly obvious among the seven adults obtained by EAL of the *vespophaes* x *vespertilioides* hybrid, the large specimen in the centre of the top row presented in Fig. 6. On closer inspection, the forewings of this novelty appear to resemble those of the *flava* variety of the F_2 of *vespertilioides*. Particularly notable is the white instead of darkbrown spot. The specimen to the bottom right displays resemblance to this novel-type variety, as does the bottom right specimen of the seven F_2 adults of *vespophaes* grown by FK (Fig. 7). Among the latter, note especially the highly uncommon right/left colour difference presented by the mid-left specimen.

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For the two additional references and the two additional figures see under the respective headings.

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The Checklist is intended to demonstrate our current state of knowledge of the Australian fauna of Lepidoptera. It therefore includes a large number of nomenclatural changes formally published for the first time ; new synonymies, new combinations, changes of status and reinstatements are clearly indicated as new in the Checklist. A complete index of all names is included together with a CD-rom containing all the actual Checklist files in ASCII format. The Checklist is multi-authored with one or more authors responsible for each family with contributions by A. Atkins, I. F. B. Common, E. D. Edwards, K. D. Fairey, M. Horak, F. Komai, T. Kumata, M. S. Moulds, P. B. McQuillan, E. S. Nielsen, G. S. Robinson, M. Shaffer and G. Tarmann. The family classification adopted in this work is that developed by I. F. B. Common and E. S. Nielsen for Moths of Australia (Common, 1990) and the treatment of Lepidoptera in The Insects of Australia (Nielsen & Common, 1991), with minor changes. The editors are to be congratulated for the high professionalism of the present achievement. This work presents a wealth of information in concise form and is absolutely indispensable to anyone working on Australian Lepidoptera.

Alain Olivier

Errata in and acknowledgement to *Nota lepidopterologica* Vol. 19, 1996

E. A. Loeliger

Hofdijck 48, NL-2341 ND Oegstgeest, The Netherlands

In the articles of Loeliger & Karrer, published 21.XI. and 21.XII.1996, pages 113-128 and 243-260, respectively, quantities of ecdysone injected into pupae are erroneously presented a thousand times too high in most instances, i.e. in mg instead of in µg. Correct figures are given in the first publication under Material and Methods, Table 3 and Figure 2, and the French Summary, on pages 113, 117-120 and 123, resp. ; and in the second article under Material and Methods on page 247.

The first author's address is also incorrectly given. In The Netherlands two capitals separate the numbering and wording of the domicile (vide supra).

As the author responsible for reviewing the proofs I apologize for the flaws.

Delightful news is the approval, just before publication, of our request for financial support by the Uyttenboogaart-Eliasen foundation in Amsterdam. Its gift satisfactorily compensates the costs of the colour printing of the figures 1-7, illustrating the results of our cross breeding experiments published in volume 19 (3/4) of *Nota lepid.*

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