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LEPIDOPTERA FEEDING AT PUDDLE-MARGINS, DUNG, AND CARRION

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Butterflies are often seen feeding at the margins of small puddles, sometimes in considerable numbers, and it is known also that certain species are found at dung and at carrion. In the summers of 1970 and 1971, in the course of other field work, I was able to make some observations on these habits, and came to the conclusion that they are closely related expressions of the same phenomenon. I also found that these feeding sites are well frequented not only by day but also at night, by moths of at least five families. The observations were made at Black Lake in North Burgess Township, some fifteen miles south of Perth, Ontario, along field tracks through former pasture land and the adjacent mixed hardwood and swampy areas.

Observations by Day

A list of species observed feeding at the margins of puddles by day is given below. For every specimen involved, it was clearly established that the proboscis was extended in the feeding position. Perhaps, in all, twice as many species were seen beside the puddles, but many individuals could not be approached for critical examination.

NYMPHALIDAE. Speyeria cybele Fab.; Boloria bellona Fab.; Phyciodes tharos Drury; Polygonia comma Harris; Vanessa virginiensis Drury; Limenitis archippus Cramer.

LYCAENIDAE. Harkenclenus titus Fab.; Feniseca tarquinius Fab.; Lycaena phlaeas L.; Celastrina argiolus L.

PIERIDAE. Colias philodice Godt.; Pieris rapae L.

HESPERIIDAE. Erynnis lucilius Scudder and Burgess; Polites themistocles Latr.; P. peckius Kirby; P. mystic Scudder; Wallengrenia otho A. and S.

PYRALIDAE. Pyrausta orphrisalis Wlk.; Desmia funeralis Hb.

Fifty-two individuals of these species were examined for sex; all were males with the exception of 2 (out of 5) specimens of *Lycaena phlaeas*.

The probing butterflies were found, with few exceptions, around four small groups of puddles situated at intervals of a quarter mile or so along the field road. At three of these stations a swampy ditch with open water ran along one or both sides of the track for a considerable distance, and all along the roadway there were patches of thick grassy vegetation where dew might remain throughout the forenoon. Often many butterflies were congregated at the puddles for several hours before the dew had dissipated. Thus it seemed unlikely, from the outset, that the basic function of puddle-visiting was to obtain water, which was usually in ample daily supply on a wide scale.

The butterflies probed, typically, at the moist soil around the margins of the puddles, not at the free water itself. They avoided standing on the moister regions, and the skippers in particular often perched on a dry pebble or twig and, working their way towards the edge, probed with the tongue at the damp mud below. The mud remained attractive, through not so strongly, even as it dried and ceased to be visibly moist; and on occasion *Lycaena phlaeas* and several of the nymphalids and skippers were seen probing industriously at normally dry soil more than a week after any visible puddle had disappeared. (It is always important, in these situations, to establish that the butterfly is engaged in feeding, and not merely in sunning—the more so as nymphalids, when they are feeding on the ground, usually hold the wings open.) On one occasion *Vanessa virginiensis* was encountered probing steadily among dry duff and topsoil beneath pine trees; and *Feniseca tarquinius* often probed for long periods over slightly moist rotten wood lying on the ground.

Nevertheless, the presence of the puddle clearly increased the attractiveness of the site, and a depression visited only by an occasional individual in dry weather became a centre of interest for six or eight species when water was again available. The puddles, of course, all lay in depressions, and were filled from time to time by water seeping or draining down the pathway on either side. Probably they represented areas of concentration of organic debris and solutes, and it seems likely that this was the real source of their attractiveness. The decaying organic material probably gave off odorous substances, able to attract or arrest passing insects, especially when moist; and its attractiveness would decrease as it became dry.

As already mentioned, butterflies are sometimes observed also on dung and on carrion. When horse dung, and still more when recently killed frogs or turtles or small mammals were added to a puddle, the numbers

of insects visiting it and probing increased very considerably. The individuals probing directly at the dung or carrion were remarkably stable -especially those on carrion, which were so intent on probing that they could usually be approached and picked up with the fingers. Specimens of Harkenclenus titus, Celastrina argiolus, Feniseca tarquinius, Phyciodes tharos, Vanessa virginiensis and Limenitis arthemis were collected in this way from a dead frog. At an ordinary puddle, the butterflies move around fairly readily, probing repeatedly with the proboscis as they gradually shift their position near the margin. On encountering a piece of dung they are at once stabilized, and continue feeding there for a considerable period; and still more so on encountering carrion. It seems that the ordinary but inevitably somewhat enriched puddle, the horse dung, and the dead animals represent successively higher levels of the same stimuli. The order of preference was the same for all species present in significant numbers, but no additional species, not found at the ordinary puddles, visited the dung or carrion.

Just as some butterflies probed at dry mud that could scarcely have yielded any significant amount of liquid, so also, occasionally, they visited and probed at desiccated pieces of dung. A specimen of *Polygonia* (? *interrogationis* Fab.) explored a dry gunny sack that had contained horse manure for upwards of 20 minutes, all the time probing between the fibres with the proboscis. *Lycaena phlaeas* also was seen at dry horse dung; and *Erynnis* sp. landed and probed repeatedly on a dry bird dropping on a bare rock exposed to the sun. The lepidopteran proboscis is adapted for taking up liquids only, and it seemed therefore of interest to make some closer observation of these attempts to feed on dry materials.

Specimens of Lycaena phlaeas $(3 \& \&; 1 \Leftrightarrow)$, Phyciodes tharos, and Polygonia comma, held in glass vials were offered dry clippings of skin and muscle from a dead frog, and in direct sunlight they probed readily with the extended tongue. The manner in which Lepidoptera feed on dry sugar-containing materials is being described elsewhere (Downes, in prep.), and the feeding process on other dry materials is very similar. Briefly, the tongue is extended and the anterior (dorsal) face of the apical region—the only part used for food intake; the main length of the proboscis merely enabling the insect to probe at a distance—is applied closely to the surface of the skin clipping. The seam between the two galeae that make up the tongue opens slightly and a pulse of saliva is released along the whole length of the apical region where it is applied to the food. The saliva penetrates among the shrivelled skin and muscle for a distance of perhaps five tongues' width all around. It is then quickly

withdrawn into the tongue, by suction exerted by the muscles of the cibarium. At a satisfactory feeding point the cycle of outflow and withdrawal of saliva may be repeated 10-20 times in as many seconds, and the tongue then probes again nearby. Thus the surface of the food is repeatedly washed with saliva, and soluble materials liquefied and imbibed. There can be little doubt that this is what happens in nature when butterflies probe at dry mud or horse dung. Somewhat similarly, individuals of Feniseca tarquinius and Danaus plexippus (L.) have been observed salivating and re-imbibing on the skin of the hand, at dry sweat and on areas that had earlier been lightly painted with sodium chloride. It thus appears that Lepidoptera may obtain not only sugars but also other nutrients from dry deposits, by washing them out with saliva. [Unfortunately none of the skipper butterflies were observed in detail when feeding on dry materials. There are several records in the literature of hesperids moistening the food by a droplet of liquid from the anus, and then imbibing (see Norris, 1936). I think, however, that this represents a special case.]

The requirement that is satisfied by feeding at puddle-margins and the related sources remains unknown. The obvious first suggestion is a need for protein or amino acids. There seems, however, to be no indication in the literature of the occurrence of proteinases in the digestive system of Lepidoptera; and it would, moreover, be remarkable that a requirement for nitrogen should be almost restricted to the male sex. Other possibilities are a requirement for salt, or some trace substance for which the male, with his probably greater flight activity, has more need. The same puddles were visited also by many kinds of small bees and bombyliid flies; perhaps, therefore, a number of specialized nectar feeding insects have certain requirements that floral nectar does not supply.

A few observations were made on the discovery of the puddle and the choice of the feeding point. The puddle area seemed to be encountered by accident during general flight and then, probably at rather close range, the increase in concentration of odorous substances led to settling on the ground in the general vicinity of a feeding area. A satisfactory feeding point was discovered by random walking, probing meantime at the surface with the proboscis; and similar random movements, as already noted, led eventually to the feeding points on dung or carrion where the insect became more fully stabilized. The discovery of the feeding point, of whatever grade of stability, seemed to be mainly 'accidental,' by unoriented questing.

More specific stimuli may sometimes be involved. The skippers, both

Erynnis and *Polites*, often landed directly onto small whitish patches of bird droppings (which are evidently a favourite feeding site in this family), and sometimes also onto horse dung. The precision of landing suggested an element of visual control as the approach was completed. Occasionally *Celastrina argiolus* also was seen to land directly on bird droppings. The sulphur butterflies often landed within inches of other individuals, evidently recognising them by sight; and in this way, probably, the familiar aggregations of puddle-feeding butterflies are built up.

Observations at Night

As noted above, two species of Pyralidae were occasionally seen feeding with the butterflies at the puddles. The puddle-visiting habit has seldom been recorded except for the Rhopalocera, and this observation suggested that it would be interesting to visit the sites by night. On the first night, 8 July 1971, about an hour after dark, upward of fifty moths, mostly Geometridae and Pyralidae but also a few Noctuidae, Pterophoridae and Tortricidae, were seen at the puddles. It was curious and striking to encounter six or eight conspicuous white or yellow pyralids and geometrids perched on the shell of a crushed turtle, busily probing with the proboscis between the fractures in the carapace. Good numbers were seen also on two occasions later in the month, but few or none on four other nights.

The moths also were stabilized more strongly by carrion than by the normal damp margin of the puddle. Except for a few of the pyralids, the moths were generally much more quiescent while feeding than the daytime butterflies and usually could be collected directly into individual vials. All the geometrids, except for *Hydria prunivorata*, sat with the wings closed, butterfly fashion, above the back. Most of the species encountered were long-tongued forms that are probably also nectar feeders, except for the tortricids, which perhaps feed on honeydew, and the large noctuid *Euthisanotia grata*. This latter species has, for a noctuid, a quite short tongue, and to feed it crouched close to the mud with the wings widely spread out to the sides; in this position it evidently mimics a large variegated bird dropping.

As with the daytime visitors, the moths were very predominantly males; the single specimen of *Tarachidia erastrioides* and one of the two *Blepharomastix ranalis* were the only females among 63 specimens collected and sexed. All these specimens had been clearly observed, before capture, with the proboscis extended and probing at the mud or carrion. The list of species represented is given below; but again other species were seen in apparent feeding situations but were not collected because the observation could not be satisfactorily completed. NOCTUIDAE. Leuconycta diphtheroides Gn.; Euthisanotia grata Fab.; Tarachidia erastrioides Gn.;

GEOMETRIDAE. Xystrota rubromarginaria Pack.; Scopula ancellata Hlst.; S. enucleata Gn.; Euphyia centrostrigaria Woll.; Eupithecia misturata frostiata Swett.; Lygris diversilineata Hb.; Hydria prunivorata Ferg.; Euchlaena johnsonaria Fitch; Itame exauspicata Wlk.; Xanthotype urticaria Swett.; V. sospeta Drury; Sicya macularia Harr.; Nematocampa limbata Haw.; Anacamptodes vellivolata Hlst.

PYRALIDAE. Argyria nivalis Drury; Crambus sp.; Blepharomastix ranalis Gn.; Acrobasis sp.; Tetralopha sp.; Mecyna submedialis Grt.; Herpetogramma pertextalis Led.; Pantographa limata G. and R.; Pyrausta orphrisalis Wlk.; Desmia funeralis Hb. PTEROPHORIDAE. Platyptilia pallidactyla Haw.

TORTRICIDAE. Sparganothis sp. nr. putnamana Free.; Argyrotaenia quadrifasciana Fern.; Argyrotoxa semipurpurana Kft.; Choristoneura rosaceana Harris.

Conclusions from Observations

The chief results that emerge from these observations are as follows.

1. The habit of feeding at puddle-margins is not, basically, related to water requirements, though it may of course often be the way the need for water is supplied. Puddle-visiting occurs even when ordinary water is plentiful nearby, and the same species may (a) sometimes probe also at the dry sites of former puddles, and (b) prefer dung and carrion to the ordinary puddle-margin. The tested species fed from dry materials by washing them with repeated pulses of saliva discharged from the apical region of the proboscis and then re-imbibing.

2. Representatives of most of the main groups of butterflies found in the study area were observed at the puddles/dung/carrion. At night the same feeding sites were visited by moths, principally Geometridae and Pyralidae but also a few Noctuidae, Tortricidae and Pterophoridae. Both the day- and night-time visitors were very predominantly (approx. 96%) males.

3. The nutritional requirement satisfied by probing at puddles/dung/ carrion is not known, but is unlikely to be a requirement for protein. The habit is presumably quite distinct from the sugar-feeding habit general in Lepidoptera, and probably represents a secondary development related to a specialized need in certain families or under certain circumstances.

4. The feeding areas are discovered probably by a response to odour while in flight. The precise point of feeding is apparently reached, after landing, by random questing. There may also be visual responses to already established insects, this tending to build up aggregations, and sometimes perhaps to special feeding sites, such as bird droppings.

Discussion

Many notes have been written on these aspects of the feeding habits of adult Lepidoptera, but they are widely scattered and mostly brief.

An extensive review was published by Norris (1936), and that paper remains the basic reference. Initially Norris treats the puddle-visiting habit as water drinking; but numerous instances of feeding at dung, sweat, salt, the moisture exuding from the eyes of cattle, and such like, are then assembled, and it is pointed out that many puddle and riverside drinking places are contaminated with animal excreta. It is noted that the excreta or soil that the insects visit is sometimes quite dry; and that drinking areas are often restricted to contaminated sites even when cleaner water is abundantly available. Norris concludes, "The problem of water-drinking in the Lepidoptera is [thus] inextricably confused with that of their attraction to dung and sweat . . . There is reason to believe that practically all water-drinking may be primarily due to such attraction." My own observations emphasise even further the significance of dung and carrion, which are more powerful attractants (or arrestants) than lightly contaminated moist soil. The insects probed at such materials even in the dry state and the significant substances were presumably extracted by the saliva that they were seen to discharge and re-imbibe. It seems clear that decaying animal materials must have a significance, and presumably supply a nutritional need, over and above any requirement for water as such.

Norris' records nearly all show a great preponderance of males, similar to that noted above. Females are well represented (about one third of the total) only among the Noctuidae feeding at sweat-impregnated clothing in Collenette's study (1934) in Brazil. The usual great inequality itself suggests that some additional, though perhaps minor, nutritional requirement is obtained, since it is unlikely that water would be required in very different quantity in the two sexes.

The habit of probing at contaminated soil and decaying animal refuse is known throughout the Rhopalocera. The families Papilionidae and Satyridae, lacking, presumably by chance, from my own observations, are mentioned on many occasions by Norris, and latterly by Payne & King (1969). The Riodinidae were mentioned by Bates (1863). Several authors have noted a few day-flying Pyralidae, Geometridae or Thyrididae along with the butterflies, but only Collenette (1934, Brazil) appears to have observed a substantial night-time fauna comparable to that recorded above. A few records are given also by Payne & King (1969). Outside the Rhopalocera the habit seems to be limited mainly to certain systematic groupings. Pyralidae, Geometridae and Noctuidae are the most frequent, with several observations also of Sphingidae; most of the remaining records refer to families related to one or another of the above (Thyrididae; Uraniidae; Arctiidae, Agaristidae, Notodotidae). The present records of Tortricidae and Pterophoridae, and the old record of Psychidae quoted by Norris (p. 81), stand rather apart.

The strikingly gregarious habits of many puddle-frequenting butterflies receives considerable attention from Norris; and some fine photographs of dense groups, chiefly in the tropics, are given by Klots (1958). Collenette & Talbot (1928), in experiments with *Catopsilia* involving paper models, have shown that the group is built up by visual recognition of the already established individuals. The gregarious habit is especially conspicuous in Pieridae. In Nymphalidae and Hesperidae, however, a response to odour is highly developed, and the insects tend to respond individually to the feeding sites and often do not form notable aggregations. Many Nymphalidae likewise find their sources of sugar mainly by smell, and tend to feed at ripe fruit rather than at conspicuously coloured flowers.

In discussing the various forms of the habit of feeding at animal excreta and refuse, Norris refers to Shannon's observations (1928) in Argentina that certain moths probe at the secretions and pus around the eves of mammals. More recently considerable attention has been given to the eve-frequenting moths, in studies in tropical Africa and Asia (Reid, 1954; Büttiker, 1967; Bänziger & Büttiker, 1969). Irritation and pain are caused as the moth probes under the evelid with its proboscis, and the possibility of transmission of infections has been raised. The ingested material includes lachrymal secretions and pus, and sometimes also blood from accidental sores or wounds. About 30 species of eve-frequenting moths have been recorded. The great majority belong to the Noctuidae. Pyralidae and Geometridae, in somewhat similar numbers; and in addition there are two records of Notodontidae and one of Sphingidae (and one record also of a lycaenid butterfly). Thus the eye-frequenting moths belong to exactly the same array of families as the other excreta feeding forms. The relationship between the two groups is sometimes much closer still. The genus Arcyophora (Noctuidae) which includes several of the most important eye moths, includes also a species taken on the carcass of a bullock (Reid, 1954). Pingasa chlora crenaria Guen. (Geometridae) is recorded both from the eves of ungulates (Büttiker, 1967) and from dung and contaminated soil (Bänziger, 1971); the genus Scopula contains an eye-frequenting species in Thailand (Büttiker, 1967) and puddle-margin and carrion species in Ontario (above); and Semiothisa, again with eye-frequenting species in Thailand, is represented by the very closely related genus Itame in the present work. The genus Purausta figures in Shannon's (1928) list of eye moths in Argentina and

in the present work. Thus Norris is almost certainly correct in making the association.

The sex ratio of the eve-frequenting moths is adequately recorded in only two cases, the noctuids Arcyophora sylvatica Büttiker and Lobocraspis griseifusa Hampson. In the former, males and females occur in similar numbers, and in the latter females exceed males by about three to one. This is very different from the usual sex-ratio of puddle-margin and dung feeding Lepidoptera, though roughly similar to the particular case of the Noctuidae recorded on sweat-impregnated clothing by Collenette (1934). Collenette's itemized list of the sex-ratios of the various species shows that this habit, in the Noctuidae, requires a much more detailed study. It is clear, however, that the usual preponderance of males at animal excreta is not an absolute phenomenon; it does not indicate a radical difference in the physiology of the two sexes such as is found in the mosquitoes and other bloodsucking Diptera, but a more quantitative difference that might vary with circumstances. Thus the sex-ratios of the eve-frequenting noctuids do not tell seriously against the derivation of the habit from excreta-feeding.

Bänziger (1968, 1971) has found recently that the noctuid, *Calpe* eustrigata Hamps., is a true bloodsucker, able to pierce the skin of mammals with its apically armoured proboscis. Another species of *Calpe*, *C. minuticornis* Guen., is recorded as a eye-moth, and yet another eye-moth, *Mocis undata* Fabr., falls into the same sub-family (Catocalinae) (Büttiker, 1962, 1967). It is very likely therefore that this bloodsucking represents an extreme case of the group of feeding habits under discussion. No information as to sex is given in the work on these insects.

Bänziger, however, suggests that blood-sucking is a derivative of the fruit-piercing habit. Fruit-piercing is well known among this section of the Noctuidae, and many of the moths have an armoured proboscis approaching that of *C. eustrigata* (Hargreaves, 1936; Büttiker, 1962; Bänziger, 1971). The suggested relationship of the two habits appears, nevertheless, to be very improbable. Fruit-piercing, like flower-visiting, provides the insect with sugar; the mud-, dung-, and carrion-visiting habits, from which eye-frequenting and blood-sucking have apparently evolved, provides the insect with nutrients of an entirely different kind. The latter requirement, whatever its nature may be, is typically characteristic of the male sex; and occurs only in certain families, for the most part highly specialized ones and frequently ones in which the sugarfeeding habit is also highly developed (e.g. Rhopalocera, Noctuidae). Indeed, fruit-piercing has been observed in the blood-sucking *Calpe eustrigata* itself (Bänziger, 1968, 1971), in the eye-visiting *C. minuticornis*,

in other species of *Calpe*, and in many other genera of the sub-family. Thus the two types of habit are by no means alternatives, one of which has evolved from the other; rather sugar-feeding is a basic (plesiotypic) habit of the Lepidoptera that has been maintained in the majority of the component groups, while the 'animal excreta' group of habits appears to be a development *sui generis* that exists alongside sugar-feeding in a limited range of forms. (Bänziger is further mistaken in drawing a comparison with the mosquitoes. Here again there are two kinds of feeding habit, sugar feeding and blood sucking; but they exist side by side in many species and are indeed both plesiotypic features of the order Diptera. In no sense are they alternatives one of which has evolved from the other (see Downes, 1958).) There is however only one feeding organ and one mode of food uptake in Lepidoptera; and it would not be unexpected that a modification of the proboscis associated with a change in the manner of taking sugar (from probing at floral nectaries or rotting fruit to piercing the rind of sound fruit) might elicit a change in the other feeding habit also (from absorbing liquid in contaminated mud or dung to probing under the eyelid and finally to piercing the skin). This is what appears to have taken place in *Calpe eustrigata*.

General Summary

An accessory feeding habit, that of feeding at contaminated liquids and decaying animal material, is found in several groups of Lepidoptera, especially Rhopalocera, Noctuidae, Geometridae and Pyralidae. The habit is usually almost restricted to the male sex. Its significance is not known but it is probably not related to a need for protein and almost certainly not, in essence, a requirement for water; well dried materials can be utilized by repeated salivation. Its most common expression is the habit of feeding at the margins of contaminated puddles, but dung and carrion are preferred if available. In the tropics various noctuids, geometrids and pyralids probe at the exudates of the eyes of mammals, and it seems likely that this is a specialized form of the same habit; it is proposed also that the blood sucking of the noctuid *Calpe eustrigata* is a further specialization of the same nature.

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A NEW GENUS AND SPECIES OF OECOPHORIDAE FROM TROPICAL AMERICA

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The species described below is so striking, and such an unusual oecophorid, that its presence in the Neotropical fauna should be recorded. It is nearly related to the genus *Filinota* Busck and adds another link in the growing classification of the South American fauna.

The drawings for this paper were made by Mrs. Elsie H. Froeschner, staff artist, and the photograph was produced by Victor Krantz, both of the Smithsonian Institution.