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SOIL- AND PUDDLE-VISITING HABITS OF MOTHS[1]

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ABSTRACT. Ninety-three species of moths representing ten families were recorded probing at soil and mud puddles over a four year period in central Pennsylvania. Nearly 99% of the 3417 individuals observed were males. Observations of Gracillariidae and Lyonetiidae (97% males) are the first records for these families at soil. The natural history of the soil-visiting habits is described. Special mention is given those species of Geometridae and Notodontidae that pass large volumes of water through their gut as they drink from very wet substrates. Evolution of the soil-visiting habits and their relationship to animal excreta are discussed.

The feeding habits of adult Lepidoptera are extremely diverse yet poorly understood. Gilbert and Singer (1975) stated that adults are more opportunistic and less specific in diet than larvae. The list of adult lepidopteran dietary sources other than floral nectar or extrafloral nectar (Downes, 1968) is extensive. Such sources include mud puddles, soil, and dung (Norris, 1936; Bauer, 1953; Sevastopulo, 1959, 1974; Downes, 1973); urine (Owen, 1971); crushed bodies of conspecifics (Reinthal, 1966); moist campfire ashes (Howe, 1975); carrion (Reed, 1958; Payne & King, 1969; Shields, 1972; Downes, 1973; Nielsen, 1977); saliva (refs. in Norris, 1936); exposed heads of basking turtles (D. L. Pearson, pers. comm.); soap suds (Farrell, 1979); lachrymal secretions and pus (Bänziger & Büttiker, 1969; Bänziger, 1972); perspiration (Collenette & Talbot, 1928); plain salt (Skertchly, 1889); blood (Bänziger, 1971, 1975); frog-hopper larval secretion (Lane, 1960); aphid honeydew (Manson, 1931); nectar gland secretion of lycaenid larvae (Gilbert, 1976); rotten fruit (Young, 1972); sound fruit (Hargreaves, 1936); cocoa seeds (Young, 1979); rotten seeds (Frost, p. 188,

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1959); fermented milk (Howe, 1975); rotten cheese (Norris, 1936); borage plants (Pliske, 1975); tree sap (Tutt, 1897; Scott, 1973); red wine (Gomez, 1977); ink (Poulton, 1913); honey (d'Herculais, 1916); and pollen steeped in nectar (Gilbert, 1972).

The present study surveys the soil- and puddle-visiting habits of moths in central Pennsylvania and presents notes on related feeding habits. Among most families of butterflies this behavior, usually referred to as puddling, is extensively documented. However, only a few papers (Fassnidge, 1924; Collenette, 1934; Downes, 1973) indicate that moths, and particularly the nocturnal contingent, also visit soil and puddles. Norris (1936) and Downes (1973) summarize the families of Lepidoptera in which soil visitation occurs.

In nearly all cases the Lepidoptera that do visit soil, puddles, carrion, and animal excreta are predominantly males (review in Norris, 1936). For example, Collenette (1934) found only 3% females among moths at damp sand in Brazil, and Downes (1973) observed 4.4% females among moths and butterflies at mud puddles in Ontario. One notable exception involves noctuids at perspiration in Brazil, where females represented 31% (Collenette, 1934). Females found at soil are usually old and worn (Clark, 1932).

Arms et al. (1974) showed that the sodium ion stimulated puddling behavior in males of *Papilio glaucus* Linnaeus, and established that amino acids obtained from soil are incorporated into body proteins. Recently, Adler and Pearson (1982) demonstrated a difference in the total body sodium levels of male and female *Pieris rapae* Linnaeus, a species in which they likewise found a positive response to sodium.

Lepidoptera that feed on dry substrates first moisten it with a bead of saliva passed down the proboscis and then reimbibe the solubilized nutrients in the manner described by Downes (1973). On the other hand, individuals that drink from wet substrates may discharge water droplets from the tip of the abdomen as they drink.

As early as 1883, Dukinfield-Jones recorded that the Brazilian geometrid, *Panthera apardalaria* Walker, drank from wet stones in a stream for three hours and passed about 200 times its volume in liquid. Guppy (1952) observed *Venusia cambrica* Curtis drink from a bucket of water and pass the liquid in such a fashion as to resemble a "living siphon." Clench (1957), in his observations of the geometrid, *Dyspteris abortivaria* Herrich-Schaeffer, and the drepanid, *Drepana arcuata* Walker, referred to the activity as "pumping."

The discharging of liquid while at wet soil and puddles has also been observed in the Pyralidae (Welling, 1958); Hesperiidae (Roever, 1964); Papilionidae (e.g., Reinthal, 1963; Welling, 1958; Jobe, 1977); Pieridae (Layard, 1883); and Lycaenidae (Tutt, 1897; pers. obs. of

TABLE 1. Summary of moths that visited soil and puddles during the summers of 1977–1980. Species indicated by D consistently discharged droplets of liquid while drinking. Those marked I infrequently discharged. All others were not observed to discharge. Species are arranged alphabetically within families.

	Males	Females	Discharging behavior
Gracillariidae			
Agrocercops perhaps *striginifinitella* (Clem.)	15	—	
Caloptilia cornusella Ely.	4	—	
C. perhaps *stigmatella* (F.)	4	—	
Leucospilapteryx venustella (Clem.)	4	—	
Parornix sp.	3	—	
Lyonetiidae			
Bucculatrix sp.	—	1	
Gelechiidae*			
Genus, species unknown	1	—	
Tortricidae (including Olethreutidae)			
Ancylis metamelana (Wlk.)	4	—	
Cenopis reticulatana Clem.	—	1	
Grapholita eclipsana Zeller (diurnal)	3	—	
Olethreutes albiciliana (Fernald) (diurnal)	4	—	
Pyralidae			
Anania funebris glomeralis (Wlk.) (diurnal)	8	—	
Argyria nivalis (Dru.)	3	—	
Blepharomastix ranalis (Gn.)	1	—	
Crambus turbatellus Wlk.	2	—	
Desmia funeralis (Hbn.)	29	—	
Mutuuraia mysippusalia (Wlk.)	3	—	
Ostrinia nubialis (Hbn.)	15	—	
Pyrausta pertextalis Lederer	1	—	
Sylepta fluctuosalis (Lederer)	103	—	
Pyralid sp.	1	—	
Pterophoridae			
Oidaematophorus homodactylus (Wlk.)	4	—	
O. monodactylus (Linn.)	1	—	
Drepanidae			
Eudeilinea herminiata (Gn.)	4	—	
Geometridae			
Anacamptodes ephyraria (Wlk.)	4	—	
Anagoga occiduaria (Wlk.)	147	—	D
Anavitrinella pampinaria (Gn.)	4	—	
Antepione thisoaria (Gn.)	5	1	
Biston betularia cognataria (Gn.)	39	—	D
Cepphis armataria (H.-S.)	9	—	
Chlorochlamys chloroleucaria (Gn.)	7	—	D
Coryphista meadii (Pack.)	1	—	
Cyclophora myrtaria (Gn.)	1	2	
C. packardi (Prout)	—	1	
Dyspteris abortivaria H.-S.	672	—	D

TABLE 1. Continued.

	Males	Females	Dis-charging behavior
Dystroma hersiliata (Gn.)	1	—	
Ectropis crepuscularia (D. & S.)	1	—	
Euchlaena irraria (B. & McD.)	7	—	
Euphyia unangulata intermediata (Gn.)	14	—	I
Eupithecia sp.	1	—	
Eusarca confusaria Hbn.	69	—	
Haematopis grataria (Fab.)	1	—	
Heliomata cycladata Grote (diurnal)	2	—	
H. infulata Grote (diurnal)	1	—	
Heterophleps triguttaria H.-S.	44	—	D
Homochlodes fritillaria (Gn.)	—	1	
Hydrelia lucata (Gn.)	11	—	D
Hydria prunivorata (Ferguson)	90	—	I
Hydriomena perfracta Swett.	1	—	
Idaea demissaria (Hbn.)	1	1	
Iridopsis larvaria (Gn.)	12	1	
Itame argillacearia (Pack.)	76	—	
I. pustularia (Gn.)	3	2	
Lobophora nivigerata Wlk.	28	—	
Lomographa semiclarata (Wlk.) (diurnal)	700	25	
Melanolophia canadaria (Gn.)	14	—	
M. signataria (Wlk.)	1	—	
Mesoleuca ruficillata (Gn.)	24	—	
Metanema determinata Wlk.	36	—	I
M. inatomaria Gn.	33	—	I
Metarranthis angularia B. & McD.	10	—	
Nematocampa limbata (Haw.)	19	—	D
Nemoria bistriaria Hbn.	4	—	
N. rubrifrontaria (Pack.)	1	—	
Orthonama centrostrigaria (Wollaston)	57	—	I
Plagodis alcoolaria (Gn.)	16	—	
P. fervidaria (H.-S.)	13	—	
P. phlogosaria (Gn.)	33	—	
Probole alienaria H.-S.	72	—	D
P. amicaria (H.-S.)	91	—	D
Scopula inductata (Gn.)	18	—	
S. limboundata (Haw.)	85	2	
Semiothisa bisignata (Wlk.)	—	1	
Sicya macularia (Harr.)	5	—	
Synchlora aerata (F.)	14	—	
Xanthorhoe ferrugata (Clerck)	58	—	I
X. lacustrata (Gn.)	15	—	
Xanthotype urticaria Swett.	118	—	I
Notodontidae			
Clostera albosigma Fitch	210	—	D
Gluphisia septentrionis Wlk.	227	—	D
Noctuidae			
Bomolocha baltimoralis Hbn.	13	—	
Enargia decolor Wlk.	3	—	

TABLE 1. Continued.

	Males	Females	Dis-charging behavior
Hypena humuli Harr.	5	—	
Hyperstrotia sp.	1	—	
Lithachodia carneola (Gn.)	—	1	
Orthosia sp.	—	1	
Palthis angulalis Hbn.	2	—	
Psychomorpha epimenis Dru. (diurnal)	1	—	
Renia discoloralis Gn.	1	1	
R. factiosalis (Wlk.)	1	—	
R. sp.	—	2	
Tarachidia erastrioides (Gn.)	2	—	
Zale undularis (Dru.)	—	1	

* R. L. Mangan (pers. comm.) commonly observed the pink bollworm, *Pectinophora gossypiella* (Saunders) feeding from soil in irrigated cotton fields of Arizona on very warm days.

Celastrina argiolus pseduoargiolus (Boisduval & LeConte)). Bänziger (1972) and Reid (1954) provide examples of nocturnal Lepidoptera discharging drops of liquid while feeding on the eye secretions of various animals. Certain hesperiids turn their abdomens anteroventrally and expel a drop of liquid in order to moisten a substrate and subsequently imbibe the drop (refs. in Norris, 1936; Hessel, 1966; Jobe, 1977; pers. obs. of *Erynnis juvenalis* Fabricius and *E. baptisiae* (Forbes)).

STUDY AREA AND METHODS

I observed nocturnal Lepidoptera with the aid of a head lamp from June through the third week of August each year from 1977 to 1980 (2130–0130 EDST). All field work was conducted in the Scotia Barrens of Centre County, Pennsylvania (approximately 5.7 km west of State College) along a 2.4 km stretch of gravel-dirt road leading south of Ten Acre Pond. The soil of the Scotia Barrens is characterized as Morrison loamy-sand.

Only those individuals with their proboscis extended to the substrate were counted. Individuals were sexed in the field and several representatives of each species were collected for identification.

RESULTS

During the four years of observation encompassed by this study I recorded 3417 moths, representing 93 species in ten families, at damp soil, puddles, ponds and their edges (Table 1). Observations of Gracillariidae and Lyonetiidae at soil are new family records. Females probing at damp soil comprised 1.3% of all individuals and represented only 16 species. Notably, half of these species were unrepresented by males.

All females in Table 1, with the exception of *Zale undularis* Drury, were old and worn; whereas, many of the males appeared fresh. However, senescent males of some species were common at damp soil. For example, 40% of *Eusarca confusaria* Hübner males (n = 63) were fresh (less than two days old), as determined by the wing condition of marked-recaptured individuals, while 31% were middle-aged and 29% were old (more than seven days old). A mark-recapture study of *E. confusaria* revealed that the same male may visit soil on more than one night.

Although flowers (*Asclepias syriaca* L., *Melilotus alba* Desr., *Achillea millefolium* L., *Spiraea latifolia* (Ait.) Borkh., *Solidago* spp., and *Eupatorium* spp.) bloomed plentifully in the study area, soil visitation was far more frequent than nocturnal flower visitation among males of all species in Table 1, except *E. confusaria.* I observed 303 *E. confusaria* males feeding during July 1977 but only 19.8% of these at damp soil. All 171 *E. confusaria* females found feeding were at flowers.

Some areas of the soil visited by moths were intimately associated with the recent presence of animals. Nocturnal Lepidoptera fed on bird droppings (males of *Heterocampa manteo* Doubleday and *E. confusaria*), dead frogs and rabbits, animal urine, and in the footprints of deer. (Although five males of *Prochoerodes transversata* (Drury) fed on the exudates of a dead rabbit, they were never observed at soil.) Aggregates of nocturnal moths were sometimes associated with animal-related substrates and restricted patches of moisture.

I often found nocturnal moths probing on soil-related substrates such as the damp walls, floors, and ceilings of crumbling cement structures in the abandoned (since the 1920's) community of Scotia. Most species found on the cement also visited soil with the exception of two female *Catocala ultronia* Hübner, one female *C. ilia* Cramer, one female *Euparthenos nubialis* Hübner, and one female *Amphipyra pyramiodoides* (Guenée). Although the observations of the latter four species are unique, it is of note that these species often rested on the cement structures during the day.

The species that visited soil and puddles could generally be characterized as those that passed droplets of liquid as they drank (Figs. 1 and 2), those that did so infrequently (less than 10% of the individuals of a given species), or those that did not (Table 1). Species that habitually discharged invariably drank from puddles or soil with a thin film of water. Non-discharging and infrequently discharging species preferred damp soil without standing water and sometimes

FIG. 1. Male *Dyspteris abortivaria* Herrich-Schaeffer, a typical discharging species, at wet soil. Arrow indicates formation of a droplet of liquid at the tip of the abdomen.

drank from the cracked bottoms of drying puddles. I observed no female of any species discharge while at soil.

The position in which moths held their wings while at soil or puddles was characteristic for each species. Among geometrids, approximately 80% including all discharging species held their wings toward the perpendicular (Fig. 3). Other geometrids such as *Hydria prunivorata* (Ferguson), *Lobophora nivigerata* Walker, both *Metanema* spp., and *Scopula limboundata* (Haworth) held their wings against the substrate.

Individuals that settled at soil or puddles generally remained stationary for several hours. The formation of liquid droplets at the tip of the abdomen and/or antennal palpation was often the only visible activity. All individuals were seemingly unaffected by light or close proximity of the observer. When moths completed their drinking or were touched they were capable of immediate flight except *Gluphisia septentrionis* Walker and *Clostera albosigma* Fitch, which vigorously vibrated their wings before actual flight.

G. septentrionis and *C. albosigma* restricted their drinking to areas of soil associated with a puddle or pond. *C. albosigma* often drank from scum and algal mats that floated on the surface, as well as from the edges of the water. This moth occasionally floated on shallow water while drinking. *G. septentrionis* frequented pond and puddle edges, where I observed individuals drink for more than an hour on

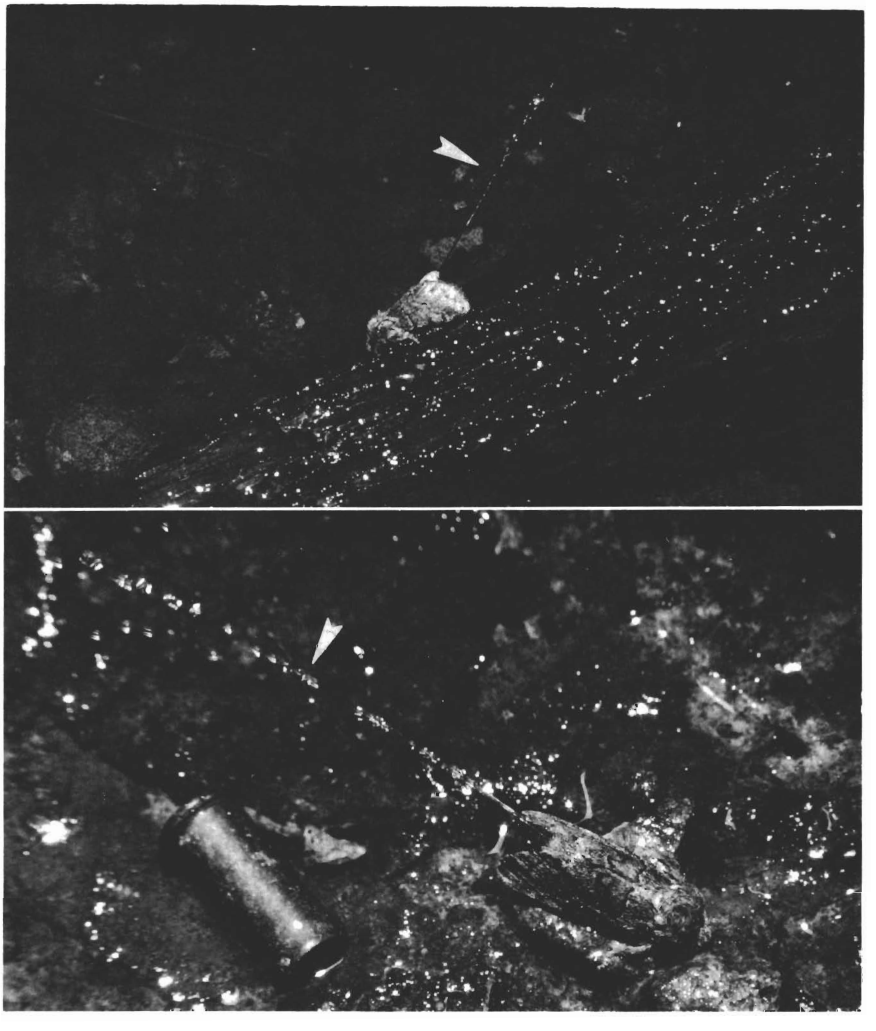

FIG. 2. Male *Gluphisia septentrionis* Walker discharging a jet of water (indicated by arrow). **Above,** substrate is a wet board. **Below,** rifle (.22 caliber) shell case indicates size.

wet boards, stones, moss, or head-down on the stems of emergent vegetation. All observations indicated that these species discharged water from the tip of the abdomen at a very rapid rate. *G. septentrionis* forcibly expelled rhythmic jets that traveled distances up to 30 cm (Fig. 2) whereas *C. albosigma* discharged large drops that diffused into the surrounding water. Among the geometrids that discharged liquid,

FIG. 3. Male *Dyspteris abortivaria* Herrich-Schaeffer showing usual position of the wings while visiting soil. Only the apical portion of the proboscis is applied to the water film.

drop size was generally proportional to body size, and when water was freely available, drops were produced at the rate of one or two per second. Suspended soil particles were also passed with the water.

No other species at this site passed water through its system as rapidly and in such quantities as *G. septentrionis*. A typical individual on a wet cinder road discharged 5.7 ml in 40 minutes (15 jets/min) along with 10.0 mg (dry weight) of particulate. An individual brought into the lab and offered a 10 μM solution of NaCl passed 22.7 ml in 78 minutes (35 jets/min or 510 times its wet weight in liquid). Bromophenol red placed in the drinking water of three moths in the field was passed with the first ejection, i.e., within three to five seconds.

DISCUSSION AND CONCLUSIONS

The preceding results emphasize the highly developed habit of soil and puddle visitation in the ditrysian Lepidoptera, while a synopsis of the literature (Norris, 1936) reveals the widespread geographical nature of the habit. This attraction to soil and puddles probably evolved from water-drinking, a behavior necessary for maximum fitness in most Lepidoptera (Norris, 1934, 1936). The drinking behavior may have acquired further significance as individuals that satisfied their water requirements at soil or puddles accrued additional benefits, despite predation risks (Morris, 1953; pers. obs. of Chipping, Song and Whitecrowned Sparrows and Eastern Towhees on *Lomographa semiclarata* (Walker) and *Erynnis juvenalis* and Common Grackles on *Pieris rapae*).

Common (1975) believes that the simple haustellate mouthparts of Lepidoptera prefaced the appearance of Angiosperms and further notes that the evolution of a functional proboscis would have allowed the early Lepidoptera with mandibles to move into drier places if they imbibed moisture droplets. If, in fact, the soil-visiting habits evolved from the habit of water-drinking, one would expect the more primitive Lepidoptera with a functional proboscis to visit soil.

Until the previously unrecorded observations of the Gracillariidae and Lyonetiidae (Table 1), soil visitation was believed generally restricted to the higher families of Lepidoptera. With the addition of these records, the habit assumes significance as a more widespread behavioral and physiological character. As in the higher Lepidoptera, a paucity of female soil visitors is evident among the Gracillariidae and Lyonetiidae, and may be considered characteristic of the soil-visiting Ditrysia.

The results of this survey increase the numbers of Geometridae that are known to characteristically discharge droplets of liquid while drinking from soil and puddles and provide the first records of this behavior for the Notodontidae. Drinking at dry or damp soil and drinking at open puddles appear to be variants of the same behavior. Whether or not a discharge occurs is related to the choice of microhabitat (often species-specific), which is, in turn, a function of water availability. This behavior is quite similar to that of aphids which pass copious amounts of plant juices in order to extract nutrients present in trace quantities (Mittler, 1958). I have also seen scores of *Halysidota tessellaris* (Smith) imbibe superfluous volumes of dilute *Asclepias* nectar just after a rain and discharge large droplets of liquid but have not observed this situation on nights without rain.

An anatomical and histological study of the alimentary tract of *G. septentrionis*, including a comparative study of the sexes, with respect to the rapid and forceful passage of large quantities of liquid would be informative. My preliminary dissections suggest that, superficially, the gut of the male does not differ markedly from that of an actively feeding noctuid, *Plusia gamma* Linnaeus (Mortimer, 1965).

All feeding habits associated with animal excreta probably evolved from the habit of visiting soil, and Downes (1973) is probably correct in assuming that animal excreta provide higher levels of attraction than soil and puddles. Sodium represents one common factor linking soil and puddles with animal excreta as nutrient substrates and has been suggested (Poulton, 1917) and implicated (Arms et al., 1974;

Adler & Pearson, 1982) as the feeding stimulus. However, the exclusively lachryphagous noctuid, *Lobocraspis griseifusa* Hampson, serves as a caveat that not all lepidopteran feeding habits associated with animal excreta involve uptake of similar nutrients. The fact that both sexes are commonly involved (Bänziger, 1975), and the species is unique among Lepidoptera thus far studied in producing proteinases (Bänziger, 1972), sets it apart from typical soil and animal associated Lepidoptera.

Viewed as a whole, there seems little question that soil and puddle visitation represent an integral part of the biology of many taxonomically diverse Lepidoptera. Species such as *G. septentrionis* that discharge large volumes of liquid as they drink afford excellent subjects for quantifying the dietary aspects of soil and puddle visitation through determination of substances in the imbibed medium versus the discharge.

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