Resource Specialization in Puddling Lepidoptera

CAROL L. BOGGS[1] AND BIRGITT DAU[2]

Rocky Mountain Biological Laboratory, Crested Butte, CO 81224 and Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020

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ABSTRACT Lepidoptera feed at mud puddles, dung, and carrion in a behavior known as puddling. Sodium and sometimes protein are feeding cues, are actively collected, and play a potentially important role in lepidopteran nutritional and mating ecology. We showed that montane butterfly species have feeding preferences among mud, herbivore dung, and carnivore dung, and that these preferences differed among butterfly species. The puddling substrates varied in soluble sodium content, with mud having the lowest concentrations and carnivore dung having the highest. Within one species, *Pieris napi* L., visit frequencies to mud versus dung matched visit frequencies to sand trays filled with sodium solutions matching the concentrations seen in mud or dung. This suggests that the preference hierarchy of this species is driven by soluble sodium concentration. Overall, the results indicate that lepidopteran species specialize on different puddling substrates, likely obtaining different arrays of nutrients. This suggests that there are species- or family-specific roles for puddling nutrients in the overall nutrient budget of the insects.

KEY WORDS foraging, mud puddling, *Pieris napi*, sodium

"PUDDLING" IS A BEHAVIOR IN which adult Lepidoptera feed from mud, dung, carrion, or sweat (Norris 1936, Downes 1973, Adler 1982). Such feeding is stimulated by sodium (Arms et al. 1974, Adler and Pearson 1982, Beck et al. 1999), or in some species, by proteins (Beck et al. 1999). Additionally, puddling intensity differs within species among sex and age classes (Collenette 1934, Adler 1982, Adler and Pearson 1982, Berger and Lederhouse 1985, Boggs and Jackson 1991, Launer et al. 1993, Sculley and Boggs 1996).

In at least some species, puddling is an important dietary source of sodium, a scarce nutrient in the diet of herbivores and nectivores (Smedley and Eisner 1995). Young males that have fed on sodium-containing substrates can transfer substantial amounts of sodium to females at mating (Adler and Pearson 1982, Pivnick and McNeil 1987, Smedley and Eisner 1996). The extent of this sexual division of foraging effort varies with the mating structure of the species (Sculley and Boggs 1996). Females of species that mate several times were rarely seen puddling themselves, whereas females of species that mate only once were more often seen puddling when old, presumably because their male-derived sodium reserves had been depleted. Hall and Willmott (2000) further speculate that, within the Riodinidae, feeding at carrion (presumably a richer substrate) may also supplement nutrients from larval feeding for use by the males themselves.

[1] E-mail: cboggs@stanford.edu.
[2] Present address: Department of Internal Medicine, University of Washington, Seattle, WA 98195.

Experimental studies of the nutritional function of puddling have not evaluated the role of potential specialization by Lepidoptera on different substrates (but see Beck et al. 1999), although species in this group are known to specialize in other aspects of their adult foraging ecology (reviewed in Boggs 1987). Certainly carrion and mud, for example, are likely to differ not only in sodium content, but also in availability of other nutrients that may be used by the puddling insect. The first step in understanding the role of puddling in the overall nutrition of Lepidoptera is to examine whether feeding preferences exist and the extent of their variation among species.

Because sodium stimulates feeding, it could also be the cue by which Lepidoptera distinguish among different puddling substrates, if preferences exist. The second step in understanding the role of puddling in lepidopteran nutrition is therefore to examine the concentrations of sodium in puddling substrates and the relation between sodium concentration and species' preferences for natural substrates.

To explore these issues, we asked five questions, working with a montane butterfly assemblage in Colorado. Do species within a butterfly community exhibit preferences for feeding at mud versus herbivore dung versus carnivore dung? Are there differences among butterfly species in those preferences? Is there variation among substrates (mud, herbivore, and carnivore dung) in soluble sodium content? Within a focal species, *Pieris napi* L., does preference for sodium concentration tested in isolation mirror the species' preference for mud versus dung, given the sodium concentrations of those substrates? Finally, do other compounds that may be found in dung (ammonium, urea, and uric acid) also stimulate feeding by *P. napi*, or is sodium likely to be the major feeding cue?

Materials and Methods

This study was carried out near the Rocky Mountain Biological Laboratory (RMBL), Colorado (38°58′ N, 107°0′ W), in July and August of 1995 and 1996. Areas used for the natural puddle observations were the same as those used by Sculley and Boggs (1996). Experimental manipulations of sodium were performed at a 5 by 3.2-m seep from a bank dominated by spruce along Copper Creek, ≈0.3 km northwest of RMBL along Forest Service Trail 983. The seep itself is also a well-used puddling site.

Natural Substrate Puddling Observations. We compared butterfly visitation to mud, herbivore dung, and carnivore dung. Herbivore dung included marmot dung and bear dung without hair, indicating that the digested meal did not include small mammals. Carnivore dung included coyote and bear dung with hair, determined by visual inspection. All samples had attracted puddling butterflies before being collected and moved. A sample of each dung type was placed adjacent to an area of a natural mud puddle that was also known to attract butterflies. Thus, butterflies were known to puddle at all substrates used. Dung surface area for each sample was approximately equal. It was difficult to determine the surface area for the natural mud puddles, given the uncertainty as to how much of the puddle margin was attractive, but the puddles likely had greater exposed surface than did dung.

Observations were carried out between 1000 and 1700 MDT on 16, 19–21, 24–28, 30–31 July and 4, 10–11, and 22 August in 1995 and on 13–14, 19, and 24 July 1996. An observer recorded the number and species of Lepidoptera puddling at each of the three possible substrates. If two substrates were sampled, a preference for the second was scored if the butterfly sampled one briefly ($< \approx 2$ s), but fed ($> \approx 2$ s) from the second. If feeding ($> \approx 2$ s) was observed at both, each of the two substrates was scored as if one-half a butterfly had visited it. Such indecision involving all three substrates was never observed. All individuals were caught as they left the area after puddling, marked with an individual number, and released. The individual number and sex were recorded. The few multiple visits by the same individuals were not included in the pattern analysis below.

Sand Tray Experiments. Preferences of *P. napi* for different concentrations of sodium were tested with sand trays similar to those used by Arms et al. (1974). Playground sand was washed with >10 times its volume of demineralized water (<2 ppm Na^+) and dried at 120°C. Aluminum pans (22 by 12 cm) were lined with plastic wrap and filled with 375 g of cleaned sand. For tests involving sodium, 75 g of solutions of 0.001, 0.01, 0.1, 1, or 5 M sodium chloride in demineralized water were added to the sand. (Whereas demineralized water alone was not included, preliminary trials indicated that trays with demineralized water attracted no butterflies over 1 h, while trays with 0.01 M sodium chloride attracted six feeding butterflies.) Trays were weighed every 1–2 h in the field, and demineralized water was added as necessary to compensate for evaporation. Each tray also contained a pinned, dead *P. napi*, with its wings open to about a 45° angle, to serve as an attractant to conspecifics. Preliminary trials using demineralized water, sodium chloride, and ammonium chloride indicated that the presence of conspecifics helped to attract butterflies (unpublished data; see also Arms et al. 1974, Beck et al. 1999).

Each salt concentration was duplicated for a total of 10 trays. The trays were placed on the ground at a mud puddle site currently used by *P. napi*. Trays were arranged in two adjacent rows of five trays each, with each concentration represented once per row. The first row was arranged arbitrarily with respect to neighboring concentration; the second row was arranged so that no two trays with the same salt concentration were next to or diagonally across from each other.

Observations were conducted continuously in 1- to 2.5-h blocks at midday (between 1030 and 1400 MDT) on 11 and 15 August 1995 for a total of 4.5 h, and on 6, 7, 10, 14, and 20 July 1996 for a total of 9.3 h. The number of butterflies feeding from each tray was recorded. Time spent feeding at each salt concentration was recorded in 1995 as the cumulative time across all butterfly visits per each salt concentration, and in 1996 as time by individual butterflies at each salt concentration. Data from 1996 were therefore used in analyses of time spent at each salt concentration. Butterflies were not captured and marked in this experiment because this would have disrupted feeding by other butterflies on the sand trays. Repeat visitors were thus not distinguished, but the numbers are likely to be small, given that trials at natural substrates with marked butterflies yielded a return visit rate of 3 of 74 individuals.

The experimental design was repeated, using 0.1 M ammonium chloride, 0.1 M urea, 0.1 M uric acid (all "sodium free"), and demineralized water as a control. Observations were made in 2-h blocks at mid-day on 8–9 August 1995, for a total of 4 h. The number of butterflies feeding, the time feeding (recorded to the nearest 0.5 min), and the number of times that a butterfly landed on a tray and left immediately after an initial probe were noted.

Sodium Analysis. In 1995, samples from each of the sand trays were collected for analysis of actual sodium content. Samples were also collected from dung and mud in 1995 and 1996 for sodium content analysis. Samples from 1995 consisted of one sample each from mud, cow, and marmot dung and two samples of coyote dung. Although cow dung was not used in the preference trials, it was included here because it is another herbivore dung that butterflies will visit (unpublished data). Samples from 1996 included duplicate samples from each of one piece of marmot dung, two pieces of herbivorous bear dung, and three pieces of coyote dung, with additional single samples from pieces of marmot and coyote dung. The mud sample came from a chronically well-used mud puddling site

Table 1. Lepidopteran species visiting mud, herbivore dung, and carnivore dung

Species	No. of individuals feeding at			
	Carnivore dung	Herbivore dung	Mud	Total
Pieridae				
Pieris napi[a]	24	0	50	74
Papilionidae				
Papilio gothica	1	0	1	2
Nymphalidae				
Nymphalis milberti	0	0	1	1
Vanessa carduii[b]	10	0	2	12
Speyeria atlantis	1	0	1	2
Speyeria mormonia	27	3.5	28.5	59
Microtia palla	1	0	1	2
Erebia epipsodea	0	0	1	1
Lycaenidae				
Everes amyntula	17.5	2.5	8	28
Glaucopsyche lygdamus	16	0	4	20
Plebejus icarioides	2	0	6	8
Plebejus saepiolus	0	0	2	2
Lycaena dorcas	0	0	6	6
Agriades rustica	0	0	4	4
Hesperiidae				
Thorybes mexicana[b]	6	0	0	6
Erynnis icelus[b]	0	1	0	1

Individuals seen visiting two sources and not showing a preference between them are counted as 0.5 at each source. All individuals were males, except for[a] 67.7 males:females total; 21.5:2.5 males:females on dung; 45.5:4.5 males females on mud; [b] all individuals were female.

Table 2. *G*-tests for heterogeneity of preference for three puddle sources among species pairs

	E. amyntula	*S. mormonia*	*P. napi*
G. lygdamus	3.6 NS	8.4 $P < 0.025$	14.9 $P < 0.005$[a]
E. amyntula		3.1 NS	16.8 $P < 0.001$[a]
S. mormonia			9.3 $P < 0.025$

All tests, 2 df. Significance indicates that the species differ from each other in their preferences.

[a] Significant at $P < 0.05$ after Bonferroni correction for sequential tests.

NS, not significant.

(the seep on the bank of Copper Creek), and feeding was observed on all dung samples before collection except the two herbivorous bear and one of the two marmot samples.

Each sample was dried to constant mass and mixed with a measured amount of demineralized water. The sample sat for several hours and was centrifuged. Decanted liquid was frozen for transport to Stanford University, where sodium was analyzed using atomic absorption spectroscopy. Exposure to borosilicate glass was avoided during storage to avoid possible sodium exchange. The resulting sodium concentration (μg/ml) was multiplied by the volume (ml) of water added to the dried sample to obtain the microgram sodium per gram dry mass of the original sample. While wetness of the substrate, either naturally or through addition of fluid by the insect, will affect the concentration of sodium in the liquid actually imbibed, these numbers give a first approximation to concentrations experienced by the insect.

Results

Species' Feeding Habits at Natural Puddle Sources. Butterflies exhibited species-specific preferences for feeding from different substrates. Fifteen species visited the experimental set-up with choices of carnivore dung, herbivore dung, or mud (Table 1). We analyzed data from the four species with ≥20 individuals observed: *Pieris napi* (Pieridae), *Speyeria mormonia* (Boisduval) (Nymphalidae), *Everes amyntula* (Boisduval), and *Glaucopsyche lygdamus* (Doubleday) (Lycaenidae). The number of individuals feeding at the three sources was significantly different from a 1:1:1 distribution of carnivore dung: herbivore dung: mud, which is the null hypothesis expected if no preferences were exhibited (*P. napi*, $G = 69.7$, 2 df, $P < 0.001$; *S. mormonia*, $G = 26.0$, 2 df, $P < 0.001$; *E. amyntula*, $G = 13.6$, 2 df, $P = 0.001$; *G. lygdamus*, $G = 24.3$, 2 df, $P < 0.001$; Table 1). The four species also differed from each other in their preferences when examined as a group for heterogeneity ($G = 29.8$, 6 df, $P < 0.001$). *P. napi* was found significantly more often at mud than were the two lycaenids, based on *G*-tests with Bonferroni correction for sequential tests (Table 2).

Only in *P. napi* were both sexes caught puddling in this study. The sex ratio did not differ between those puddling at mud and those puddling at carnivore dung ($G = 0.04$, 1 df, not significant).

Sodium Content of Natural Puddling Sources. Year, or year by dung type interaction, had no significant effect on sodium content of dung. (Sodium content of mud was only measured in 1995.) Data for 1995 and 1996 were therefore combined in subsequent analyses.

The mud sample contained less sodium than did any of the dung samples (Table 3). Herbivore dung contained significantly less sodium than did carnivore dung (analysis of variance [ANOVA]: $F_{1,16} = 57.6$, $P < 0.001$; Table 3). Furthermore, an analysis of only those 1996 samples that were duplicated and incorporating duplicate groupings as a category effect in the ANOVA yielded the same result ($F_{1,6} = 12.4$, $P = 0.01$). Finally, within herbivore dung, bear dung contained significantly more sodium than did marmot dung (770 ± 345 and 220 ± 88 μg/g dry mass of dung for bear and marmot, respectively; $F_{1,6} = 9.6$, $P = 0.02$).

***Pieris napi* Sodium Concentration Preference and Comparison to Response to Natural Sources.** The number of *P. napi* visiting five concentrations of sodium solution in a sand substrate was significantly

Table 3. Sodium concentrations, in micrograms per gram dry mass of substrate, for mud, herbivore dung, and carnivore dung

	Sodium	
	mean ± SD (n)	Range
Mud	55 (1)	
Herbivore dung	456 ± 370 (9)	106–1,211
Carnivore dung	6,281 ± 2,273 (9)	3,916–11,675

Table 4. ***Pieris napi*** **response to sodium-containing sand tray baits**

	Concentration				
	0.001 M	0.01 M	0.1 M	1 M	5 M
Number of butterflies					
1995 + 1996	28	13	8	8	9
Visit duration (minutes/butterfly)					
1995 + 1996	10.0	12.7	6.8	0.6	4.8
1996 mean (*n*)	13.9 (6)	14.5 (4)	4.2 (4)		0.8 (5)
SD	11.8	2.2	2.7		0.8
μg Na/g dry mass sand[a]	9	60	336	3419	18895
	9	60	677	802	9870

[a] μg Na/g dry mass and sand are replicate values.

different from an even distribution ($G = 18.8$, 4 df, $P < 0.001$). More butterflies visited the weaker solutions (Table 4). Amount of time feeding at the solutions in 1996 also decreased with increasing sodium concentration (square-root time = 1.40–0.76 $\log_{10}$ molarity, $F_{1,17} = 15.62$, $P = 0.001$).

The sodium content of mud as determined above corresponds roughly to the sodium content of the sand trays with 0.001 and 0.01 M sodium solutions. The sodium content of dung corresponds roughly to the sodium content of the sand trays with 0.1, 1, and 5 M sodium solutions (Tables 3 and 4). A total of 41 *P. napi* visited the 0.001 + 0.01 M solutions, whereas 25 *P. napi* visited the 0.1 + 1 + 5 M solutions. These proportions (41:25) were not significantly different from the proportion of *P. napi* visiting mud (50) versus dung (24; $\chi^2 = 0.9$, 1 df, not significant.

Response of *P. napi* to Ammonium, Urea, and Uric Acid. The proportion of observed butterflies classed as feeding on (as opposed to sampling) sand trays with demineralized water, ammonium, urea, or uric acid (4 of 36) was significantly lower than the proportion feeding on salt trays (66 of 79; $\chi^2 = 138.1$, 1 df, $P < 0.005$). The proportions of butterflies sampling the water, ammonium, urea, or uric acid trays for <2 s did not differ significantly from a 1:1:1:1 ratio ($G = 0.8$, 3 df, not significant; Table 5).

Discussion

The butterfly species studied here showed species-specific preferences for feeding from mud versus dung. Additionally, these substrates differed in their sodium content, with mud lower than herbivore lower than carnivore dung. Our focal species, *P. napi*, preferred sodium concentrations equivalent to that of its preferred natural puddling substrate, mud. *P. napi* did not respond to other potential puddling cues likely associated with dung, including ammonium, urea, or uric acid, indicating that sodium could be the primary puddling cue for this species.

Table 5. ***Pieris napi*** **response to non–sodium-containing sand tray baits**

	Substance			
	Demineralized water	0.1 M NH_4Cl	0.1 M urea	0.01 M uric acid
Number of butterflies sampling	7	6	8	11
Number of butterflies feeding	0	2	2	0
Mean visit duration (min)	—	4.25	1.25	—

Sampling is defined as landing followed by immediate departure. Mean visit duration is for feeding butterflies only.

Preference Variation Among Species. The among-species preferences seen here are consistent with observations by Downes (1973) in a nonexperimental setting. He reported only lycaenids, nymphalids, and hesperiids visiting dung, whereas he included pierids and pyralids in the list of species seen at puddles. Our findings in a temperate montane butterfly community are also consistent with the study of Beck et al. (1999) of attraction patterns to sodium versus albumin in a tropical butterfly community. Although the amount of salt in the albumin baits was unknown and presumed low, their results nonetheless suggest differences in foraging patterns between pierids and lycaenids.

Differential use of puddling resources among species implies that puddling may play quantitatively and qualitatively different roles in the resource budgets of different species. Such variation in preference for dung versus mud is likely to be even more extreme among other species. For example, Smedley and Eisner (1995) showed that male *Gluphisia septentrionis* (Walker) (Notodontidae) imbibe and void large quantities of fluid from puddles with very low sodium content while absorbing the sodium from the fluid as it passes through the body, suggesting that this species is adapted to exploit low ionic strength substrates. Possible alternative hypotheses explaining interspecific variation in preference for puddling substrate include phylogenetic history, different species-specific requirements for micronutrients, or selection pressures associated with relative availability of different substrates in the insect's habitat. These remain to be tested. The successful hypothesis must also account for why substrates with lower amounts of sodium, requiring greater feeding time per unit sodium, are preferred by species such as *P. napi.*

The data reported here are for preferences in the simultaneous presence of several substrate types. Actual use of each substrate by a species will depend not only on preference but also on encounter rate. Likewise, substrate condition, and hence availability or concentration of nutrients in the dung or mud, will vary through time and among patches and may affect usage.

Substrate Sodium Composition. Sodium content of mud measured here was consistent with measurements in other studies, lending support to our conclusion that mud contains less sodium than does dung. The value reported here for mud was 55 μg Na/g dry mass of substrate (55 ppm dry mass) and 456 ppm for herbivore dung, which was lower than carnivore dung. Adler and Pearson (1982) found 82.5 ppm sodium in four pooled surface soil samples from an area in Pennsylvania used by puddling *Pieris rapae* L., which is similar to our mud sample and well below our herbivore dung value. Other sodium analyses have been done on a milligram per liter basis, which is not directly comparable with our dry mass basis. For example, Miller and Litvaitis (1992) found a mean of 45.9 ppm sodium (range, 19.0–74.9 ppm) in water from roadside puddles uncontaminated by road salt run-off. Mud sodium content in general is expected to be variable, depending on past mud history. This includes biotic impacts as well as mineral content of the soil itself (e.g., Abrahams 1999). Nonetheless, the similarity of our data with the data of Adler and Pearson (1982) suggests that mud puddling butterflies could be seeking out mud with a specific sodium content.

Sodium content of dung was predictable based on the diet and digestive physiology of the animal species from which the dung originated. The diet of carnivores is richer in sodium than that of herbivores, and the carnivore dung is also richer in sodium. Likewise, omnivorous animals such as bears have a higher overall intake of sodium than do stricter herbivores such as marmots. Furthermore, marmots are scatophagous; therefore, dung remaining in the environment has been reprocessed and probably contains fewer nutrients, including less sodium, which is otherwise scarce in their herbivorous diet.

Feeding Preference by the Focal Species. The close match between sodium concentration of natural substrates preferred by our focal species, *P. napi,* and their preferred sodium concentrations in the sand tray experiment, along with the lack of interest in nitrogen-containing sand trays, provides further support for the hypothesis that sodium is the crucial stimulus for puddling behavior in at least some species (Arms et al. 1974, Smedley and Eisner 1995).

The relative lack of interest by *P. napi* in sand trays containing ammonium solution contrasts with results of Erhardt and Rusterholz (1998), who found that both sexes of the nymphalid butterfly *Inachis io* L. detected and preferred ammonium ions in test solutions. This suggests that butterflies (such as nymphalids) that feed to a greater extent on dung as opposed to mud may have differing preferences or detection abilities for ammonium than do pierids.

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