

SHORT COMMUNICATION

## Mud puddling by butterflies is not a simple matter

CAROL L. BOGGS<sup>1,2</sup> and LEE ANN JACKSON<sup>1,3\*</sup> <sup>1</sup>Rocky Mountain Biological Laboratory, Crested Butte, Colorado, <sup>2</sup>Department of Biological Sciences, Stanford University, and <sup>3</sup>Department of Biology, Princeton University

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### Introduction

Adult Lepidoptera of many families feed from puddles, carrion and excreta (Norris, 1936; Downes, 1973; Adler, 1982). Such behaviour is termed 'puddling', and may involve aggregations of individuals feeding at a location which is used repeatedly. The participants are usually male, and often young (e.g. Collenette, 1934; Adler, 1982; Adler & Pearson, 1982). However, there are reports in the literature of females puddling singly (Berger & Lederhouse, 1985), and of a few noctuid species in which only females are found at perspiration or wet sand (Collenette, 1934). Those females puddling are reported to be old and worn, if any indication of age is given (Adler & Pearson, 1982; Berger & Lederhouse, 1985).

Sodium, which may be an otherwise scarce nutrient in the adult diet, triggers puddling behaviour, at least in *Papilio* (Arms *et al.*, 1974). Two sets of hypotheses based on sodium limitation have been proposed to explain the sexual dimorphism in puddling behaviour. First, Arms *et al.* (1974) suggested that males may have a greater need for sodium in neuromuscular activity because they spend a larger time in flight than do females. Second, males may be

collecting sodium at puddles and transferring it to females at mating, as demonstrated in *Thymelicus lineola* Ochseneimer (Pivnick & McNeil, 1987). Further, sodium is important for egg production in *Pieris rapae* Linn. (Adler & Pearson, 1982) and *T. lineola* (Pivnick & McNeil, 1987), with the total egg sodium content greater than can be provided by the female alone.

Puddles, dung and carrion contain substances other than sodium which could be nutritionally important to puddling insects. However, no studies even qualitatively assess the major classes of compounds available through puddling.

Hypotheses to account for puddling in Lepidoptera are not mutually exclusive. They fall into two categories: (1) some otherwise scarce nutrient (e.g. sodium) is obtained from puddling; (2) puddling is the result of competitive exclusion of males or young individuals from a richer resource (e.g. flowers) by females or older individuals. The first class of hypotheses argues that puddling behaviour is an integral part of the foraging repertoire. As nutritional requirements vary with sex and age, the foraging pattern should follow these requirements, as occurs in some cockroaches (Schal & Bell, 1982). The second class of hypotheses postulates that puddling is an alternative foraging strategy. Some classes of individuals may be less able to successfully compete for nectar, and hence may be forced into feeding from a less rewarding but also less easily depleted resource – puddles. Tendency to puddle may depend on age and sex, due to competitive ability, but should vary

\* Present address: School of Forestry and Environmental Sciences, Yale University, New Haven, CT 06511, U.S.A.

Correspondence: Dr Carol L. Boggs, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, U.S.A.

both through the flight season and among generations as the relative abundance of nectar changes.

In the present study, we examine the proportion of individuals of each sex and age class caught puddling versus feeding from flowers, using the butterfly *Speyeria mormonia* Edwards (Lepidoptera: Nymphalidae). The data provide the first extensive study of the effects of age and sex on these foraging behaviours in Lepidoptera, are pertinent to specialization by individuals on nectar or puddles in the short term, and address the two sets of hypotheses concerning factors driving puddling behaviour.

## Methods

*Speyeria mormonia* is a univoltine, temperate zone, montane butterfly of North America. Females usually mate once, shortly after adult emergence (Boggs, 1986).

The study was done near Gothic, Gunnison County, Colorado, from 13 July to 26 August 1987, and 8 July to 23 August 1989. The flight season of *S. mormonia* at this site lasted from 1 July to 26 August in 1987 and about 28 June to 23 August in 1989. The study began in both years before females were numerous. This species exhibits extreme protandry, with the peak of female emergence 2 weeks or more after the peak of male emergence (Boggs, 1987).

*S. mormonia* were sampled from all puddle locations and flowers in the surrounding grassland within the 1 ha site. The 'puddle' sites were located along a stream. The primary area used by the butterflies was a 4 m<sup>2</sup> strip where the stream crossed a dirt road after flowing through a seasonal horse corral. This area dried up by 13 August 1987, but remained moist throughout 1989. Observations after 13 August 1987 were taken upstream above the corral in an area which remained moist.

Mark-release techniques were used both at flowers and the mud puddle. After capture, individuals were numbered on their left hindwing with a permanent pen. We recorded the activity, date, sex and wing wear for each captured individual. Length of the right forewing was measured with calipers in 1989. Wing wear was rated on a scale of 1.5–5.0 (Boggs, 1987), where 1.5 = damp wings, and 2.0 = dry

but undamaged wings. Wear rating increases up to 5.0 in increments of 0.5, as scale erosion and cuticle tears increase. Each wing wear change of 0.5 (after 2.0) equals about 7 days, depending on weather and activity patterns (Boggs, 1987, and unpubl.).

Neither the ratio of hours collecting data in the field:hours at the puddle nor of hours in the morning:hours in the afternoon differed significantly from 50%. 154 and 317 butterflies were caught in 1987 and 1989 respectively, including recaptures. The larger sample size in 1989 was due to increased sampling effort and population size (Boggs, unpubl.).

## Results

The two sexes differed in puddling activity, with males exhibiting a higher ratio of captures at puddles versus flowers. The number caught puddling to number caught at flowers in 1987 and 1989 respectively was 54:63 and 54:177 for males, and 6:31 and 4:82 for females (three-way contingency table log likelihood ratio test, with sex, age and activity as variables: sex × activity interaction: 1987:  $G=11.62$ , 1 d.f.,  $P<0.001$ ; 1989:  $G=18.11$ , 1 d.f.,  $P<0.001$ ).

Age (as measured by wing wear) interacted with sex to affect activity patterns (Table 1). Butterflies of each wing wear class of 2.5 or greater lumped over the entire season did not differ in proportion puddling with age (1987:  $G=0.75$ , 3 d.f., n.s.; 1989:  $G=2.19$ , 3 d.f., n.s.), or between the sexes (1987:  $G=0.06$ , 1 d.f., n.s.; 1989:  $G=0.22$ , 1 d.f., n.s.). However, males with wing wear 1.5–2.0 spent a greater proportion of time puddling than older butterflies of either sex, and females with wing wear 1.5–2.0 spent less time puddling than older individuals of either sex (sex × age × activity: 1987:  $G=14.68$ , 1 d.f.,  $P<0.001$ ; 1989:  $G=6.63$ , 1 d.f.,  $P=0.01$ ).

Size of butterflies caught puddling versus feeding from flowers in 1989 did not differ significantly. The mean and standard deviation of forewing lengths of males nectaring and puddling were  $2.52\pm 0.11$  cm ( $n=161$ ) and  $2.53\pm 0.12$  cm ( $n=50$ ), respectively ( $F_{1,209}=0.07$ , n.s.). The values for nectaring and puddling females were  $2.64\pm 0.11$  cm ( $n=78$ ) and  $2.62\pm 0.11$  cm ( $n=4$ ), respectively ( $F_{1,80}=0.13$ , n.s.).

**Table 1.** Proportion of individuals puddling by sex and age throughout the flight season in 1987 and 1989. Age is recorded as wing wear rating. Time spent by observers at the puddle and field sites differed only during 29 July to 1 August 1987. The original data and the data adjusted for proportion of sampling time are both given for these dates.

Date	No. puddling/total			
	Males		Females	
<b>A. Individuals with wing wear of 1.5–2.0 in 1987</b>				
13–24 July	16/29	(55%)	0/2	(0%)
25–28 July	8/10	(80%)	0/1	(0%)
29 July to 1 August				
Original	2/6	(33%)	0/9	(0%)
Adjusted	0.6/4.6	(13%)	0/9	(0%)
6–26 August	1/2	(50%)	0/8	(0%)
<b>Total</b>	<b>27/47</b>	<b>(57%)</b>	<b>0/20</b>	<b>(0%)</b>
date × activity: $G = 18.96$ , 3 d.f., $P < 0.005$				
sex × date × activity: $G = -13.65$ , 3 d.f., $P < 0.005$				
<b>B. Individuals with wing wear 1.5–2.0 in 1989</b>				
8–11 July	16/46	(35%)	0/3	(0%)
14 July	6/27	(22%)	0/6	(0%)
17 July	12/24	(50%)	1/10	(10%)
20 July	5/11	(45%)	0/8	(0%)
28 July	1/9	(11%)	0/6	(0%)
31 July	1/12	(8%)	0/11	(0%)
7 August	0/6	(0%)	1/10	(10%)
10–23 August	0/2	(0%)	0/12	(0%)
<b>Total</b>	<b>41/137</b>	<b>(30%)</b>	<b>2/66</b>	<b>(3%)</b>
date × activity: $G = 26.25$ , 7 d.f., $P < 0.005$				
sex × date × activity: $G = -3.76$ , 7 d.f., n.s.				
<b>C. Individuals with wing wear <math>\geq 2.5</math> in 1987</b>				
13–24 July	10/21	(48%)	1/3	(33%)
25–28 July	4/16	(25%)	0/2	(0%)
29 July to 1 August				
Original	9/21	(43%)	3/5	(60%)
Adjusted	3/15.3	(20%)	1/3.5	(28%)
6 August	4/5	(80%)	0/1	(0%)
12–13 August	0/4	(0%)	2/5	(40%)
18–19 August	0/3	(0%)	1/1	(0%)
<b>Total</b>	<b>27/70</b>	<b>(38%)</b>	<b>6/17</b>	<b>(35%)</b>
date × activity: $G = 10.20$ , 5 d.f., $0.10 > P > 0.05$				
sex × date × activity: $G = -6.75$ , 5 d.f., n.s.				
<b>D. Individuals with wing wear <math>\geq 2.5</math> in 1989</b>				
8–17 July	4/32	(12%)	0/5	(0%)
20 July	4/10	(40%)	2/3	(67%)
28 July	1/10	(10%)	0/4	(0%)
31 July	2/18	(11%)	0/2	(0%)
7–10 August	1/20	(5%)	0/2	(0%)
23 August	1/4	(25%)	0/4	(0%)
<b>Total</b>	<b>13/94</b>	<b>(14%)</b>	<b>2/20</b>	<b>(10%)</b>
date × activity: $G = 11.11$ , 5 d.f., $P > 0.05$				
sex × date × activity: $G = -4.55$ , 5 d.f., n.s.				

The proportion of butterflies caught puddling differed between years (Table 1). A higher proportion of both young and older butterflies were caught puddling in 1987 as compared to 1989, based on significant year  $\times$  activity interactions in three-way contingency table log likelihood ratio tests with sex, year and activity as variables (for young butterflies, wing wear 1.5–2.0,  $G=9.05$ , 1 d.f.,  $P<0.005$ ; for old butterflies, wing wear 2.5+,  $G=16.71$ , 1 d.f.,  $P<0.005$ ). The sex  $\times$  year  $\times$  activity terms were not significant, indicating that the patterns seen within years did not change between years.

Activity patterns varied through the season within each year (Table 1). Changes were more dramatic for young animals than for older animals. Except for young animals in 1987, when no females were caught at puddles, the age  $\times$  date  $\times$  activity interaction was not significant. This indicates that there was no consistent heterogeneity between the sexes in trends through the season.

Twenty-five butterflies were recaptured during the 2 years, one of which was recaptured twice. Activity on capture and recapture was the same for each individual in both years. Of the twenty-one individuals initially caught nectaring and subsequently recaptured, the ratio of puddling:nectaring expected on recapture was 6:15, based on year, sex and age class of the individuals involved. This is significantly different from the observed ratio of 0:21 ( $G=14.1$ , 1 d.f.,  $P<0.005$ ). Of the four individuals originally caught puddling and later recaptured, the expected ratio of puddling:nectaring on recapture was 1:3, significantly different from the observed 4:0 ( $G=11.1$ , 1 d.f.,  $P<0.005$ ). The second recapture event for one individual is excluded from this analysis.

## Discussion

The preservation of sex- and age-specific patterns of puddling behaviour between generations is consistent with both hypotheses: that puddling is determined by age- and sex-specific nutritional needs for an otherwise scarce resource, and by age- and sex-specific competitive abilities. However, the lack of constancy through the season or between years of proportion of butterflies puddling suggests that age- and sex-specific nutritional needs are not

the sole determinant of puddling. Mating activity and weather conditions are unexplored, and may affect nutrient requirements. Variation in *per capita* nectar availability was not assessed, and may affect intensity of competition.

The proportion of female *S.mormonia* observed puddling is greater than that reported for other well studied species. Only two of 983 animals caught puddling were female during a 4-year study of *P.rapae* (Adler & Pearson, 1982). Similarly, Pivnick & McNeil (1987) recorded no female *T.lineola* puddling, of 143 individuals, when the surrounding population was 20–25% female.

Older individuals of both sexes show similar puddling frequency. This suggests similar need for sodium, although the causes may be different in each sex. Females do not remate, and so may have to replenish sodium reserves as they age; males may need to replenish reserves after a mating.

The constancy of behaviour for recaptured animals suggests that specific individuals specialize on either puddles or nectar in the short term. Such constancy has been demonstrated for butterflies for choice of flower species (e.g. Murphy, 1984), but never for use of such diverse resources as nectar and puddles.

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## References

- Adler, P.H. (1982) Soil- and puddle-visiting habits of moths. *Journal of the Lepidopterists Society*, **36**, 161–173.
- Adler, P.H. & Pearson, D.L. (1982) Why do male butterflies visit mud puddles? *Canadian Journal of Zoology*, **60**, 322–325.
- Arms, K., Feeny, P. & Lederhouse, R.C. (1974) Sodium: stimulus for puddling behaviour by tiger swallowtail butterflies. *Science*, **185**, 372–374.
- Berger, T.A. & Lederhouse, R.C. (1985) Puddling by single male and female tiger swallowtails, *Papilio*

- glaucus* L. (Papilionidae). *Journal of the Lepidopterists Society*, **39**, 339–340.
- Boggs, C.L. (1986) Reproductive strategies of female butterflies: variation and constraints on fecundity. *Ecological Entomology*, **11**, 7–15.
- Boggs, C.L. (1987) Within population variation in the demography of *Speyeria mormonia* (Lepidoptera: Nymphalidae). *Holarctic Ecology*, **10**, 175–184.
- Colenette, C.L. (1934) On the sexes of some South American moths attracted to light, human perspiration and damp sand. *Entomologist*, **67**, 81–84.
- Downes, J.A. (1973) Lepidoptera feeding at puddle-margins, dung and carrion. *Journal of the Lepidopterists Society*, **27**, 89–99.
- Murphy, D.D. (1984) Butterflies and their nectar plants: the role of the checkerspot butterfly *Euphydryas editha* as a pollen vector. *Oikos*, **43**, 113–117.
- Norris, M.J. (1936) The feeding habits of the adult Lepidoptera Heteroneura. *Transactions of the Royal Entomological Society of London*, **85**, 61–90.
- Pivnick, K.A. & McNeil, J.N. (1987) Puddling in butterflies: sodium affects reproductive success in *Thymelicus lineola*. *Physiological Entomology*, **12**, 461–472.
- Schal, C. & Bell, W.J. (1982) Ecological correlates of urates in a tropical cockroach (*Xestoblatta hamata*). *Science*, **218**, 170–173.

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