Eco-physiology of mud puddling in insects

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Puddling is basically a behavioural trait in which the insects aggregate on wet soil or dung either to obtain moisture or nutrients. Mostly in butterflies, large gatherings in hundreds assemble on the edges of puddles, on moist soil, on dung or on salts (Figure 1). Some other insects such as leafhoppers e.g. Potato leafhopper, *Empoasca fabae* (Harris), locusts and different bee species also exhibit this type of behaviour. For instance, honeybees and stingless bees are known to puddle on sweat and tears (Banziger *et al.*, 2009). It is believed that the insects puddle for sodium and nitrogen and such nutrients enhance neuromuscular activity and reproductive success. In order Lepidoptera, both butterflies and moths exhibit diverse strategies to gather liquid nutrients. Puddling generally takes place on wet soil but even reported on sweat, human skin, blood and tears. It plays a significant role in lepidopteran nutritional and mating ecology. Puddling is rare or usually absent in immature stages. Molleman (2009) remarked about the strong evidence for the widely cited hypothesis that sodium from puddles is used to enhance neuromuscular activity is still lacking. He further added that the high mobility and long life spans could be associated with puddling behavior, whereas insects such as beetles that are concealed or well defended are less likely to puddle.

The butterflies are behaviourally active only when sunlight and air temperature allow them to achieve their preferred body temperature. Butterflies keep their body temperature upto or close to 98°F by exposing themselves to warming rays of the sun as they are ectothermic (do not create their own body heat). At low temperature, the butterflies move slowly and cannot fly whereas at higher temperature they cannot survive due to heat shock. Therefore, adult Lepidopterans puddle in sunlight to maintain body temperature and get nutrients from wet soil, dung and carrion (Norris, 1936; Downes, 1973 and Adler, 1982). Puddles also contain substances other than sodium that are nutritionally important to puddling insects. Such behaviour i.e., aggregations of individuals for sunlight and feeding is termed as Puddling (Fig 2). The participants in such aggregations are usually young males (Collenette, 1934; Adler, 1982; Adler
and Pearson, 1982). The females show this behaviour singly and only females in few noctuid species are found at perspiration or wet sand. Scarcity in sodium in adult’s diet triggers puddling behaviour. The association between sex of an individual and puddling is explained by two sets of hypothesis on sodium limitation. Arms et al. (1974) suggested that males require more sodium for their neuromuscular activities because males spend larger time in flight than females.

![Image](image.jpg)

**Figure 1.** Mud puddling by butterflies on Kollar migratory path in Coimbatore. (Photo Credit: Hand out Email).

The males transfer the sodium and other nutrients collected from puddles to females at the time of mating. This transfer enhances the survival rate of eggs. Puddling is the result of competitive exclusion of males or young individuals from a richer source (e.g. flowers) by females or older individuals. This behaviour is an integral part of the foraging repertoire. The puddling phenomenon is also exhibited by butterflies in their post reproductive period and more than 75% of butterflies which do puddling in post-reproductive period are females. The older ones exhibit this behavioural aspect in order to enhance the declining concentration of sodium and calcium phosphate in their bodies (Adler and Pearson, 1982; Boggs and Dau, 2004).

Few species of butterflies attracted to dung or carrion prefer ammonium rather than sodium. The brush-footed Nymphalids such as *Charaxes bernardus* Fabricius and *Charaxes durnfordi* Distant have the ability to perceive smell and home in rotting meat over a distance of hundred meters. The attraction of yellow-spined bamboo locust, *Ceracris kiangsu* Tsai to human urine is specifically due to presence of sodium and ammonium ions in it (Shu et al., 2014). In few species where both sexes puddle for sodium, male spermatophores have been shown to
contain little sodium (Molleman et al., 2005). Feeding sodium to previously mated males increases the spermatophore size, mass of accessory gland substance and number of sperms, relative to those of virgin males (Nihira and Watanbe, 2009). It is noteworthy that the direct benefits and neuromuscular activities are not mutually exclusive. The males of many lepidopteran species perform intricate aerial courtship displays (Rutowski et al., 2010). The flight performance of males during courtship serves as an honest signal to the females about male ability to provide sodium as a nuptial gift to potential mates. The males with low body sodium are unable to produce quality flight signal due to low neuromuscular activity.

The moths are rarely recorded at puddling sites due to their nocturnal behaviour, although dead moth specimens of families Geometridae, Noctuidae and Crambidae are found in water or stuck in mud at mud puddling sites indicating their active mud puddling behaviour. Gorbunov (2015) noticed mud puddling behaviour in Clearwing moths of family Sessiidae, and observed large congregations of these moths in Laos. The individuals demonstrated aggressive behaviour often bashing other insects from puddles. Showkron et al. (2015) described and illustrated the mud puddling behaviour of clearwing moth species namely *Heterosphecia pahangenses* Showkron et al., 2015.

During puddling, the role for puddling nutrients in the overall nutrient budget of insects is species or family specific. Boggs and Dau (2004) demonstrated that butterflies referable to family Nymphalidae feed to a greater extent on dung and have different preferences or detection abilities for ammonium than pierid butterflies which prefer mud. Even marine puddling i.e., seawater puddling is known to occur among 21 species of butterflies referable to families Papilionidae, Nymphalidae, Pieridae, Lycaenidae and Hesperiidae (Pola and Garcia Paris 2005; John and Tennet 2012; John and Dennis 2019). Hewavitharana et al. (2013) recorded twenty six species belonging to five families Lycaenidae (9 species); Pieridae (7 species); Nymphalidae (4 species); Papilionidae (4 species) and Hesperiidae (2 species) puddling on bear faeces in Wasgamuwa National Park, Sri Lanka. All these species mainly feed on nectar. The most frequently observed species are Common Hedge Blue, *Acytolepis puspa* (Horsfield) and Lesser Grass Blue, *Zizina otis* (Fabricius) of family Lycaenidae. Phon et al. (2017) noticed large aggregations of males of *Trogonoptera brookiana* (Wallace) puddling on a hot spring in Malaysia. Such geothermal sources attract butterflies due to higher levels of ammonia emission.
and ammonium concentration as compared with those in surrounding waterbodies. Patwardhan (2019) recorded 128 species of butterflies puddling in and around Mumbai. The butterflies of family Riodinidae are the dominant ones, followed by Nymphalidae and Papilionidae. Kolosava et al. (2020) reported five species of butterflies namely *Papilio bianor* Cramer (Papilionidae), *P. machaon* Linnaeus (Papilionidae), *Trogonoptera brookiana* (Wallace) (Papilionidae), *Pieris napi* (Linnaeus) (Pieridae) and *Carterocephalus silvicola* (Meigen) (Hesperiidae).

**Table 1.** Recent records of mud puddling in Lepidoptera

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>SPECIES</th>
<th>SEX</th>
<th>REGION</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sesiidae</td>
<td><em>Heterosphecia pahangenses</em> Showkron et al.</td>
<td>Male</td>
<td>Laos</td>
<td>Showkron et al., 2015</td>
</tr>
<tr>
<td>Papilionidae</td>
<td><em>Trogonoptera brookiana</em> (Wallace)</td>
<td>Male</td>
<td>Ulu Geroh Perak, Malaysia</td>
<td>Phon et al., 2017</td>
</tr>
<tr>
<td>Riodinidae</td>
<td><em>Abisara echterius</em> (Moore)</td>
<td>Male</td>
<td>Sanjay Gandhi National Park, Mumbai (India)</td>
<td>Patwardhan, 2019</td>
</tr>
<tr>
<td>Nymphalidae</td>
<td><em>Danaus chryssipus</em> (Linnaeus) &amp; <em>Danaus genuitia</em> (Cramer)</td>
<td>Male</td>
<td>Tungareshwar Wildlife Sanctuary Mumbai (India)</td>
<td>Patwardhan, 2019</td>
</tr>
<tr>
<td>Papilionidae</td>
<td><em>Papillo demoleus</em> (Linnaeus) &amp; <em>Papillo polytes</em></td>
<td>Male</td>
<td>Karnala Sanctuary Mumbai (India)</td>
<td>Patwardhan, 2019</td>
</tr>
<tr>
<td>Pieridae</td>
<td><em>Appias lyncida</em> (Cramer)</td>
<td>Male</td>
<td>Indonesia</td>
<td>Suwarno et al., 2019</td>
</tr>
<tr>
<td>Papilionidae</td>
<td><em>Graphium sarpedon</em> (Linnaeus)</td>
<td>Male</td>
<td>Indonesia</td>
<td>Suwarno et al., 2019</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td><em>Carterocephalus silvicola</em> (Meigen)</td>
<td>Male</td>
<td>Kamchatka Russia</td>
<td>Kolosava et al., 2020</td>
</tr>
<tr>
<td>Papilionidae</td>
<td><em>Papilo bianor</em> Cramer</td>
<td>Male</td>
<td>Kunashir Island Russia</td>
<td>Kolosava et al., 2020</td>
</tr>
<tr>
<td>Papilionidae</td>
<td><em>Papilo machaon</em> Linnaeus</td>
<td>Male</td>
<td>Kamchatka Russia</td>
<td>Kolosava et al., 2020</td>
</tr>
</tbody>
</table>
Conclusions: Mud puddling is certainly not a simple behavioural process. The insects, particularly the Lepidopterans acquire a limited amount of minerals during the herbivorous caterpillar stage which is being sequestered in subsequent life stages. Behavioural adaptations such as puddling enable these organisms to obtain a balanced mineral uptake and overcome the shortfalls in larval nutrition. It is basically the result of competitive exclusion of males or young individuals from a richer source (e.g. flowers) by females or older individuals. The insects adopt the puddling behaviour due to the requirement of nutrients (especially sodium) and moisture for their survivals and regulated by various abiotic factors such as wind, type and texture of soil, temperature, humidity etc of the ecosystem. It further leads to uptake of other minerals as well as nitrogenous nutrients rather than simply a means of acquisition of sodium. The nutritional needs vary among different taxa (butterflies and moths). Thus, the study of puddling showered more light on nutrient enrichment in insects. Apart from the physiological factors, ecological costs of puddling are potentially important.

![Figure 2 Puddling Photo](Photo: Krista Melville CWF Photo club)

References


