Beyond Nector: Unravelling Puddling in Butterflies

Rekha R Biradar[1]*, P. S. Pavani[1] and Shweta[1]

[1]*Department of Entomology, College of Agriculture, University of Agricultural Sciences, Raichur, Karnataka-584104, India*

Corresponding Author
Rekha R Biradar
Email: biradarrekha21@gmail.com

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ABSTRACT

Puddling is a specialized nutrient-acquisition behaviour in butterflies and several other insect groups, where individuals visit mineral-rich substrates such as moist soil, dung, carrion and animal secretions. Since nectar and plant sap are poor in essential minerals particularly sodium puddling enables insects to supplement their diet with sodium, nitrogen and amino acids necessary for physiological and reproductive functions. Male butterflies puddle more frequently than females, as the sodium obtained is incorporated into spermatophores, enhancing female fecundity and offspring fitness. Puddling behaviour varies across species and families, with Lycaenidae exhibiting the highest frequency, followed by Papilionidae and Nymphalidae. Aggregation patterns range from solitary individuals to mixed-species groups, influenced by substrate quality, chemical cues and social stimuli. Environmental factors such as sunlight, moisture, humidity and mineral concentration strongly shape site selection. Puddling is also documented in non-lepidopteran insects, including Orthoptera, Hymenoptera, Diptera and Blattodea, indicating its broader ecological significance. Overall, puddling represents a multifaceted behaviour integrating nutritional demand, reproductive strategies and environmental interactions and remains an important subject for understanding insect ecology and evolutionary adaptation.

INTRODUCTION

Puddling is a behaviour observed in butterflies and other insects where they gather on mineral rich substrates such as mud, animal excrement, carrion and even human perspiration. This activity allows them to acquire important nutrients particularly sodium and other micro nutrients that Gare often missing from their primary diet of nectar (Arms *et al.,* 1974). These nutrients are absorbed through the proboscis and assimilated into their tissues. Puddling can take the form of mud-puddling or salt-licking and is considered a form of supplementary feeding rather than energy intake. The behaviour is often accompanied by head butting, especially among males competing for optimal puddling spots (Lamie *et al*., 2025). Butterflies are typically active in puddling between 08:00 AM and 01:00 PM, with peak activity around 11:30 AM and the behaviour is most commonly observed during the summer and rainy seasons. The duration of puddling varies widely, ranging from just a few seconds to over an hour (Patwardhan, 2019).

1. GROUPISM DURING PUDDLING (Patwardhan, 2019)

1. **Individual puddling:** Angled Sunbeam (*Curetis dentata*) male. A single butterfly puddling alone, sipping moisture from a wet rock. Represents solitary behaviour, where the butterfly does not interact or form a group. This may reduce competition or reflect territorial habits.

2. **Single species group or closed group:** Plains Cupid (*Chilades pandava*). Multiple individuals of the same species puddling closely together. Indicates a species-specific group, where all individuals belong to one species, possibly for safety, signaling or due to shared preferences for particular minerals.

3. **Two distinct closed groups:** Papilionids and Pierids, each represented by a single species, may puddle near each other but do not intermix. This behaviour reflects species integrity, as butterflies tend to group with their own kind even in shared habitats, possibly due to species-specific chemical signals or behavioural cues.

4. **Multiple species group or open or mixed group:** A group of five species puddling together. Butterflies from different species form a mixed group at the same puddling site. This shows resource sharing across species, possibly due to high nutrient availability or common ecological needs (e.g., sodium).

1.2 PUDDLING IN INSECTS

Although puddling is most common in butterflies (Lepidoptera), a few insects belonging to the orders Orthoptera, Hemiptera, Hymenoptera, Diptera and Blattodea also exhibit this behaviour (Molleman, 2010).

1. **Lepidoptera:** Among butterflies, skippers, blues and coppers, Yellows and swallow tails are the predominant puddlers. The puddling sites of butterflies include mud, rotting fruit, bird dropping, dung and carrion.

2. **Orthoptera:** This is the first published record of puddling in an insect with chewing mouthpart. locusts are known to regulate sodium intake and crickets can cannibalize the salt.

3. **Hemiptera:** Sap feeders with nutrient-poor diets, some are known to supplement their intake through puddling behaviours.

4. **Hymenoptera:** Among the Hymenoptera there are some records of honey bees puddling and feeding on sweat or tears is common among sweat bees (Halictidae) and stingless bees. Ants may also puddle as they readily visited salt baits.

5. **Diptera:** Flies are among the most common groups found on excrements, carrion, sweat and mammalian eyes, but this is rarely considered puddling, even though such substrates may only be primary resources for a subset of fly species. For example, tephritid fruit-flies feed on bird droppings, but fruits, yeasts, honey dew and substances grazed from the surface of leaves.

6. **Blattodea:** Probably their main resources puddling for nitrogenous compounds can directly enhance fecundity. This has convincingly been shown in the cockroach *Xestoblatta hamata* where males forage for urates in bird and reptilian droppings prior to mating. Females then acquire these urates by actively feeding on male uricose gland secretions following copulation.

1.3 PUDDLING IN LEPIDOPTERA

Family wise distribution of butterflies observed engaging in puddling behaviour, based on field data. It visually highlights that Lycaenidae dominate the puddling community, making up approximately 76.63 per cent of all individuals recorded. This is a significant proportion, indicating that Lycaenids have the strongest puddling response among butterfly families, following Lycaenidae, the Papilionidae (9.34%) and Nymphalidae (7.47%) show moderate levels of puddling activity, while Hesperiidae (3.73%) and Pieridae (2.80%) are much less frequently observed. The variation among families reflects differences in ecological requirements, physiological needs and behavioural adaptations (Beck *et al*., 1999). Lycaenids high activity is likely due to their greater demand for sodium and proteins, their sensitive chemoreception (especially olfaction) and their gregarious nature, often forming large puddling groups. In contrast, other families may rely more on dietary sources or have less physiological pressure to supplement sodium externally.

1.4 PUDDLING – FEMALES OR MALES??

Male butterflies are generally more active than females, particularly during the mating season, as they expend significant energy flying around in search of receptive mates. To support this high level of activity, males engage in puddling a behaviour in which they seek out nutrient rich moist substrates such as mud, dung or sweat to absorb essential minerals, especially sodium (Na^+), which enhances neuromuscular function and stamina required for sustained flight. In contrast, female butterflies puddle far less frequently due to their different energetic and reproductive demands. Females tend to prioritize egg production, survival and long-term reproductive output over risky or energy-intensive behaviours. When they do puddle, it typically occurs later in life, when their reproductive prospects are reduced. Moreover, females often puddle alone (as observed in species like *Papilio canadensis*) and avoid male dominated sites. This avoidance is not random but a well-adapted strategy to escape male harassment, which can be energetically

costly, cause frequent interruptions and lead to physical exhaustion. By steering clear of these sites, females also conserve valuable energy during non-reproductive periods and minimize stress, which is crucial for maintaining hormonal balance, immune health and reproductive success. Altogether, this sexual difference in puddling reflects a divergence in behavioural priorities, males puddle to enhance mating competitiveness, while females do so selectively, only when the nutritional benefits outweigh the ecological and physiological costs.

2. WHY DO INSECTS PUDDLE?

2.1 Intake of water

Puddling behaviour in butterflies is believed to have evolved from the basic need to drink water, especially in species inhabiting dry or arid regions. In such environments, access to moisture is limited and puddling plays a crucial role in helping butterflies meet their water requirements. For instance, the species *Euphydryas editha bayensis* has been observed to puddle only during periods of extreme drought, emphasizing the role of puddling as a survival response to dehydration. In contrast, butterflies in humid climates exhibit reduced puddling behaviour because ambient moisture levels are generally sufficient for hydration through nectar, dew or rainfall. This suggests that water is not the primary driver of puddling in such habitats.

2.2 Intake of scarce nutrients

Butterflies primarily seek sodium during puddling, as it is a vital mineral often lacking in their natural nectar or plant-based diet. Since most plants are naturally low in sodium, adult butterflies supplement their intake by puddling on sources like mud, dung and animal remains. Studies show that butterflies prefer sodium concentrations ranging from 0.001 to 0.01M, with species like *Pieris napi* exhibiting strong attraction to these levels. Beyond sodium, other puddling substrates offer additional nutrients. Carrion and bird droppings provide proteins, nitrogen, amino acids and oligopeptides, which are essential for body maintenance and reproductive processes. Species like skippers (*Matapa aria*) and *Charaxes etesipe* utilize bird urates, rich in nitrogen to support egg yolk formation and muscle maintenance. Similarly, dung feeders absorb ammonium (NH_4^+) ions, another important nitrogen source. Additionally, rotting fruits offer simple sugars and alcohols, which serve as metabolic fuels, aiding in ATP production for energy-intensive activities like flight and mating. Altogether, puddling is a crucial behaviour not just for hydration or sodium intake, but also for acquiring a broad range of nutrients essential for adult butterfly survival and reproduction.

2.2 Nuptial gifts

In many butterfly species, males transfer a complex spermatophore to the female during mating. This spermatophore is not just a packet of sperm but also contains a variety of beneficial substances, including sodium, calcium phosphate and secondary plant metabolites known as allelochemicals. These nutrients and chemicals contribute to the females reproductive success by improving egg development and overall health. Additionally, male accessory glands secrete chemical compounds that are passed to the female during copulation. These substances serve several important functions. Allelochemicals, for example, are often derived from host plants and retained in the males body, when passed to the female, they can help deter predators, offering chemical protection to both the female and her eggs. Another important component is the release of anti-aphrodisiacs chemicals that make the female less attractive to other males after mating. This helps reduce further male harassment, allowing the female to conserve energy and focus on oviposition (egg-laying),

rather than wasting energy fending off unwanted attention. Overall, the males spermatophore acts as both a nutritional gift and a protective package, enhancing the females chances of survival and reproductive success.

2.4 Excretion of excess nutrients

When butterflies engage in puddling, especially males, they exhibit a remarkable physiological process that enables them to extract vital minerals, primarily sodium, from dilute sources like mud, dung, carrion or urine-soaked ground. During this behaviour, males actively suck up water containing dissolved salts. As they imbibe the fluid, it is rapidly pumped through their digestive system, enabling efficient absorption of essential ions such as sodium. An extraordinary aspect of this process is the sheer volume of fluid that circulates through their bodies. Studies have shown that male butterflies can process fluids up to 600 times their own body mass during a single puddling session. This is necessary because the concentrations of sodium and other minerals in natural puddling sites are typically very low. To acquire a sufficient mineral load, they must filter vast amounts of liquid. To handle this volume, butterflies have evolved a mechanism for quickly eliminating the excess water. This is done by expelling fluid through the anus, which can appear as drops or strong jets. In some species, like male notodontid moths, this fluid expulsion happens rhythmically every three seconds while they are puddling. This allows continuous mineral uptake while preventing internal flooding and maintaining osmotic and ionic balance. Males excrete excessive potassium during puddling, helping them rid the body of this ion to maintain balance. In contrast, females tend not to excrete potassium, as their bodies retain more of it due to its importance in egg production and reproductive physiology (Inoue *et al*., 2015).

2.5 Protection against predation

Butterflies that puddle in groups often benefit from a strategy known as "safety in numbers". By gathering in large clusters, individual butterflies reduce their chances of being singled out and attacked by predators. This collective behaviour lowers the risk for each individual, especially in open areas where puddling sites are exposed. Additionally, while puddling, butterflies may ingest foul-smelling or distasteful compounds from the soil or organic matter. These substances can make them unpalatable to predators, offering a chemical defense. Their small size and camouflaged coloration further enhance their ability to blend into surroundings and avoid detection. Despite these adaptations, butterflies do face threats from common predators such as birds, lizards and frogs, especially while they are vulnerable on the ground during puddling.

3. FEATURES OF PUDDLING SITES

- Butterflies are selective in choosing puddling sites and several environmental factors influence their preferences. They tend to avoid deep, narrow ravines under heavy shade, likely because such areas offer low light, poor visibility and limited ability to detect predators or locate other butterflies (Patwardhan, 2019).
- On the other hand, open, flat, sunlit areas promote evaporation, which concentrates dissolved minerals and makes them more accessible.
- However, excessively open areas with strong winds are also avoided, as butterflies cannot settle or feed comfortably.
- The most preferred puddling sites are typically along rivers or streams that are 3 to 5 meters wide, with moderate forest cover along the banks. These sites offer the

right balance of sunlight, shelter and mineral-rich moisture.

- Additionally, butterflies rarely visit puddling spots that are far away from forested areas, likely due to the increased risk of predation, lower humidity and fewer nearby resources. Thus, ideal puddling sites are semi-open, mineral-rich and close to forest habitats.

Mud

Decaying fruit

Dung

Bird dropping

Carcass

4. STIMULANTS OF PUDDLING IN BUTTERFLIES

4.1 Species or genotype

Different species may show varying levels of puddling behaviour based on their ecological needs and evolutionary traits. Even within the same species, different genotypes may cause some individuals to puddle more actively than others due to genetic differences affecting mineral needs or sensory response (Lamie *et al.,* 2025).

4.2Age and mating status of the individual

The age and mating strategy of butterflies influence how much they engage in puddling, especially in relation to their reproductive roles. Young, mature males are typically the most active puddling participants. Their high activity levels and reproductive goals drive them to collect sodium, which enhances spermatophore quality and increases chances of reproductive success. In species where multiple matings occur, males puddle more frequently. They need continuous sodium replenishment to produce spermatophores for several females. In contrast, in single-mating systems, females may puddle more, particularly after mating, to gather essential minerals for egg development and improve offspring viability.

4.3Visual cues from the substrate

Visual cues play a major role in attracting butterflies, especially species like papilionids (swallowtails) and pierids (whites and sulphurs). These butterflies may be drawn to the colour, texture, and reflectance of moist soil, dung, other organic material that suggests mineral. The presence of other butterflies at a site also acts as a social cue. Butterflies are often more likely to land and puddle in areas where others are already feeding, signaling that the site is safe and mineral rich. Some puddling sites are revisited regularly, especially those known to contain NaCl (sodium chloride) solutions or other essential salts.

4.4Olfactory cues from the substrate

Butterflies do not depend solely on their vision to locate puddling sites, their sense of smell plays a crucial role, especially when visual cues are minimal or absent. Through specialized olfactory receptors, butterflies can detect chemical signals rising from substances like dung, urine, carrion, decaying vegetation or moist soil. These odours often signal the presence of essential nutrients such as sodium, nitrogenous compounds and amino acids. The strong scent of these organic materials helps butterflies identify nutrient rich spots that may

not be visually obvious. Olfactory cues work synergistically with visual and social cues, allowing butterflies to optimize their selection of puddling sites to meet their physiological needs.

5. FACTORS AFFECTING PUDDLING IN BUTTERFLIES

Puddling is a nutrient seeking behaviour crucial for butterfly survival and reproduction, especially in males. However, this behaviour is not uniform across individuals or species. It is influenced by a variety of biological, ecological and environmental factors, each playing a key role in determining when, where and who puddles (Lamie *et al.,* 2025).

5.1 Sex of the individual

Male butterflies engage in puddling far more frequently than females. This is because males require large amounts of sodium and other minerals to produce nutrient-rich spermatophores packages of sperm and nutrients transferred to females during mating. These nutrients boost female fecundity and egg viability, indirectly increasing the males reproductive success.

5.2 Mating status of the species

In polyandrous species where females mate multiple times males must replenish mineral reserves repeatedly to sustain frequent spermatophore production. This drives higher puddling activity. In contrast, monogamous species experience lower reproductive turnover, so the mineral replenishment requirement is reduced and puddling events are correspondingly less frequent.

5.3 Age and nutrient status of the individual

Young males that have recently reached sexual maturity show intense puddling behaviour to quickly build up sodium and amino acid reserves needed for early reproductive success. Similarly, butterflies in poor nutritional condition, whether due to depleted reserves or lack of access to mineral-rich nectar are more motivated to puddle to correct deficiencies in sodium, nitrogen and amino acids that are essential for metabolism, muscle function and reproductive fitness.

5.4 Competitive ability

Prime puddling sites those richest in dissolved minerals are often limited in space. In group puddling events, stronger, more dominant butterflies secure central, mineral-rich positions. Weaker individuals are usually pushed to the periphery, where mineral concentrations may be lower. This social hierarchy in puddling sites leads to more efficient nutrient uptake for dominant individuals, potentially translating into higher reproductive success and survival rates.

5.5 Habitat

Puddling frequency is shaped by the habitats mineral availability. Moist tropical environments such as riverbanks, forest clearings and muddy trails offer abundant puddling opportunities. In contrast, arid zones, high-altitude grasslands or heavily urbanised regions often lack suitable substrates, restricting both the occurrence and intensity of puddling behaviour.

5.6 Pollution

Chemical contamination can significantly alter puddling behaviour. While certain pollutants might temporarily attract butterflies due to high sodium content, toxic substances like pesticides or heavy metals can deter them or cause mortality. Chronic exposure to contaminated sites can also reduce reproductive success and population health over time.

5.7 Environmental factors

Weather and climate directly influence puddling activity. Warm, humid conditions,

especially after rainfall soften soil and increase the solubility of minerals, creating ideal puddling conditions. Seasonal patterns also play a role, activity peaks during wetter or warmer months when mineral-rich mud is most available, whereas dry seasons limit puddling opportunities.

6. COST AND RISK OF PUDDLING

Though puddling offers important nutritional benefits, it also comes with ecological and physiological trade-offs (Lamie *et al*., 2025).

a. Predation risk

Butterflies feeding on dung or mud are exposed and less alert, making them easy targets for predators. Papilionids and pierids are frequently observed puddling in exposed areas. Larger and colorful species may stand out more, increasing predation risk. Interestingly, predators may prefer butterflies with higher sodium levels, as they are nutritionally richer.

b. Pathogen exposure

Puddling increases the chance of coming into contact with harmful pathogens. Sites like dung, carrion and urine harbor bacteria and viruses. Human dispersed pathogens and environmental microbes may be ingested. Frequent grooming and behavioural defenses are essential to reduce this risk.

c. Gut defenses needed

The ingestion of impure substances requires a robust gut immune response. Digestive enzymes and protective gut microbiota are important for breaking down harmful substances. Not all species may be equally capable of handling such microbial loads.

d. Utilization of extra energy

Searching for puddling sites demands additional energy. Butterflies may travel long distances, requiring prolonged flight and time investment. Energy spent here could otherwise be used for mating or foraging.

7. APPLICATIONS OF KNOWLEDGE ON PUDDLING

a. Palynological studies

Palynology is the study of pollen and spores. Butterflies may inadvertently carry pollen while puddling on damp soil that contains plant residues. Studying the pollen content in puddling areas can help reconstruct past vegetation and plant-butterfly interactions. This provides insight into both historical ecology and pollination networks (Basumatary *et al*., 2017).

b. Migration patterns of butterflies

Some butterflies puddle intensely before or during migrations to build mineral reserves (especially sodium). Understanding where and when puddling occurs helps track migration timing, routes and stopover points. It aids in mapping butterfly corridors, especially for migratory species like the Plain Tiger or Monarch.

c. Past climatic interpretation in the region

Puddling behaviour can be climate-sensitive, influenced by temperature, humidity and rainfall. Patterns of puddling activity over time (especially in fossil records or through citizen science) can indicate past climatic conditions. Puddling site composition (minerals, soil chemistry) also reflects historical environmental changes.

d. Conservation of endangered species

Some endangered butterflies rely on specific puddling habitats (e.g., wet streambeds, mineral-rich mud). Understanding their puddling needs helps in habitat protection, restoration and policy decisions. Can guide

butterfly sanctuary design or selection of release sites in reintroduction efforts.

e. Mass rearing of butterflies

In butterfly farming or breeding for conservation, knowing puddling needs ensures better health and reproductive success. Supplementing sodium and essential minerals in rearing cages mimics natural behaviour, leading to higher survival and mating rates. Essential for butterfly parks, research labs and commercial butterfly houses.

CONCLUSION:

Although puddling may appear to be an unhygienic or "dirty" activity, since butterflies gather on mud, animal dung, carrion or other unclean surfaces, it serves an important biological function. Many essential nutrients, particularly sodium and other minerals are often lacking in nectar, the primary food source for adult butterflies. Through puddling, butterflies supplement their diet with these scarce minerals, which play crucial roles in reproduction (such as enhancing male fertility and the quality of nuptial gifts), flight endurance and overall health. Studying this behaviour provides scientists with valuable insights into butterfly ecology revealing how they interact with their environment, select foraging sites and adapt to nutrient limitations while also shedding light on their behavioural strategies for survival and reproductive success. Puddling in butterflies, performed primarily by males, is a vital strategy for obtaining critical nutrients, especially sodium and nitrogen, which are often deficient in their natural diet. This behaviour not only enhances reproductive success but may also assist in predator avoidance and varies across species, sexes, climates and diets. While sodium acquisition has long been considered the main driver, recent evidence also suggests the potential importance of potassium excretion, along with other factors such as mating strategies and environmental conditions.

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