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FROM NECTAR TO CARRION: A REVIEW EXPLORING THE DIVERSE FEEDING ECOLOGY OF BUTTERFLIES

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Abstract

Butterflies exhibit a remarkable diversity of feeding behaviours that extend far beyond simple nectar feeding. While floral nectar remains the principal food source for most adult butterflies, numerous species also exploit alternative nutrient resources such as tree sap, rotting fruits, carrion, dung, sweat, tears, and mineral-rich mud. These feeding strategies provide essential carbohydrates, amino acids, sodium, and other minerals necessary for survival, flight, reproduction, and ecological adaptation. The present review synthesizes current knowledge on butterfly feeding behaviour, puddling ecology, and the structure and function of siphoning mouthparts. Special emphasis is placed on mud-puddling behaviour, nutrient acquisition, feeding specialization, and environmental influences on feeding frequency.

The review also examines ecological and evolutionary aspects of butterfly nutrition, including reproductive advantages associated with sodium acquisition and the adaptive significance of feeding on unconventional substrates. Understanding butterfly feeding ecology is important not only for evolutionary biology and insect physiology but also for biodiversity conservation and ecosystem management. The review highlights the complexity of butterfly nutritional ecology and underscores the need for further studies on feeding adaptations under changing environmental conditions.

Keywords- Butterflies, feeding behaviour, puddling, proboscis, nutrient ecology, Lepidoptera, sodium acquisition, carrion feeding

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Introduction:

Butterflies are among the most ecologically significant groups of insects due to their roles in pollination, nutrient cycling, and ecosystem functioning. Traditionally, butterflies have been regarded primarily as nectar feeders; however, extensive observations over the past several decades reveal that their feeding ecology is considerably more diverse and specialized. Adult butterflies feed on a wide range of liquid resources, including floral nectar, tree sap, fermenting fruits, dung, carrion, moist soil, sweat, tears, and other mineral-rich substrates. These feeding behaviours allow butterflies to obtain nutrients essential for survival, flight activity, reproductive success, and physiological maintenance.

Nectar serves as the primary carbohydrate source for most butterflies, supplying sugars necessary for energy-demanding activities such as flight and mating. Nevertheless, nectar alone often lacks sufficient quantities of sodium, amino acids, and nitrogenous compounds required for reproductive and metabolic functions. Consequently, many butterflies supplement their diet through behaviours such as mud-puddling and feeding on decomposing organic matter. These supplementary feeding strategies are especially prominent among males, which often transfer nutrients to females during mating through spermatophores.

Butterflies possess highly specialized siphoning mouthparts adapted for liquid feeding. The elongated proboscis enables efficient uptake of fluids from flowers and other substrates. Structural modifications of the proboscis in certain taxa permit exploitation of unique food sources such as rotting fruits and sap flows, reflecting evolutionary diversification in feeding strategies.

Recent studies have increasingly focused on the ecological and physiological significance of butterfly feeding behaviour. Environmental stressors such as habitat degradation, climate change, pollution, and nutritional scarcity may alter feeding frequency and substrate preference. Such changes can influence reproductive fitness, population dynamics, and butterfly diversity. This review consolidates available literature on butterfly feeding ecology, with particular emphasis on nutrient acquisition, puddling behaviour, mouthpart specialization, and environmental influences on feeding adaptations.

Feeding Behaviour of Butterflies

Butterflies primarily feed on liquids obtained through their elongated proboscis. Floral nectar constitutes the principal dietary resource for most adult butterflies because it provides sugars required for metabolic energy and sustained flight activity. In addition to sugars, nectar may contain amino acids and minerals that contribute to reproductive success and longevity (Baker & Baker, 1983).

However, many butterfly species exploit a variety of alternative food resources. These include tree sap, fermenting fruits, carrion, animal dung, bird droppings, moist soil, sweat, and tears. Such substrates provide nutrients absent or limited in nectar, particularly sodium and amino acids. Krenn (2008) observed that numerous nymphalid butterflies regularly feed on decomposing materials and mineral-rich fluids rather than relying solely on nectar.

Adult butterflies consume only liquid food because their mouthparts are specialized for siphoning rather than chewing. Water uptake from damp soil or puddles is common and contributes to hydration and mineral acquisition. Butterflies are frequently observed congregating around wet soil, dung, or carrion, a behaviour commonly known as puddling.

Certain species display highly specialized feeding habits. For example, *Morpho peleides* has been documented feeding on sap flows from exposed roots and decaying fruits in tropical forests (Young, 1975). South American butterflies of the genus *Mechanitis* often feed on bird droppings rich in nitrogenous compounds. Similarly, some butterflies are attracted to perspiration and tears due to their mineral content (Bänziger & Büttiker, 1997).

Fruit-feeding butterflies constitute a specialized ecological group, particularly in tropical forests. Fermenting fruits provide carbohydrates, amino acids, ethanol, and other fermentation products that may influence butterfly behaviour and physiology (Molleman *et al.,* 2005). Species such as *Vanessa indica* and *Argyreus hyperbius* feed not only on nectar but also on tree sap and rotting fruits (Omura *et al.,* 2008).

Feeding on carrion and dung is another important aspect of butterfly nutritional ecology. Butterflies visiting carcasses and excrement are believed to obtain amino acids, nitrogen, and minerals unavailable from floral nectar. Some species are even known to feed on human refuse and discarded sugary substances in urban environments, demonstrating remarkable ecological adaptability.

Mud-Puddling: A Unique Nutritional Strategy

One of the most fascinating feeding behaviours observed in butterflies is mud-puddling. This behaviour involves butterflies gathering on moist soil, mud, dung, carrion, or other damp surfaces to absorb dissolved nutrients and minerals (Downes, 1973).

Mud-puddling is especially common among male butterflies. Large aggregations can often be seen along riverbanks, forest trails, and wet ground after rainfall. The behaviour has attracted considerable scientific interest because it is strongly linked to reproductive physiology and nutrient acquisition.

Research indicates that sodium is the primary nutrient sought during puddling. Since floral nectar contains very low sodium concentrations, butterflies must obtain this mineral from alternative sources. Sodium is essential for neuromuscular activity, flight performance, and reproductive functions.

Mitra *et al.* (2016) proposed two major explanations for male-biased puddling behaviour. First, males may require higher sodium levels because of greater flight activity and mate-searching behaviour. Second, males transfer sodium and nutrients to females during mating through spermatophores, thereby increasing reproductive success.

Boggs and Dau (2004) demonstrated that different butterfly species specialize on different puddling substrates depending on nutrient composition. Mud generally contains less sodium than herbivore dung, while carnivore dung possesses higher sodium concentrations.

Puddling behaviour has also been observed on elephant dung in tropical forests. Fernando et al. (2017) and Anoop *et al.* (2023) reported numerous butterfly species obtaining minerals from elephant dung in South Asian ecosystems. Such observations suggest that large mammals indirectly contribute to butterfly nutrition and biodiversity.

From an ecological perspective, puddling illustrates the interconnectedness of organisms within ecosystems. Nutrients released through decomposition and animal waste become integrated into butterfly physiology, reproduction, and survival.

Unusual Feeding Sources in Butterflies

Although butterflies are commonly associated with flowers, many species utilize unusual food sources that challenge popular perceptions about their diet.

a) Feeding on Rotting Fruits

Rotting fruits provide sugars, amino acids, ethanol, and fermentation products that attract numerous tropical butterflies. Fruit-feeding butterflies form an important ecological guild, especially in rainforests. Molleman *et al.* (2005) demonstrated that different butterfly groups show distinct preferences for certain fruits and fermentation products. Species such as *Morpho peleides* and several nymphalids frequently visit overripe bananas and fermenting fruits. Fruit feeding allows butterflies to exploit nutrient-rich resources during periods when nectar is limited. Fermentation products may also function as chemical attractants guiding butterflies toward food sources.

b) Feeding on Carrion and Dung

Carrion feeding is another remarkable behaviour observed in butterflies. Species feeding on carcasses obtain amino acids, proteins, and nitrogenous compounds essential for reproduction and metabolic activity. Hall and Willmott (1999) suggested that feeding on carrion and dung supplements nutrient reserves acquired during larval stages. Butterflies feeding on decomposing materials may gain advantages in reproductive fitness and sustained flight performance. Dung feeding is widespread among several butterfly families including Nymphalidae, Pieridae, Lycaenidae, and Hesperiidae. Bird droppings, herbivore dung, and carnivore dung all serve as nutrient sources.

c) Feeding on Sweat and Tears

Some butterflies obtain sodium and minerals from perspiration and tears. Tropical species have been observed landing on humans and animals to feed on sweat, while others visit the eyes of mammals and reptiles.These unusual feeding strategies highlight the extraordinary adaptability of butterflies and their ability to exploit diverse nutritional niches.

Siphoning Mouthparts and Feeding Adaptations

The mouthparts of adult Lepidoptera are highly specialized for liquid feeding. The feeding apparatus primarily consists of the elongated galeae of the maxillae, which interlock to form a hollow tube known as the proboscis. This structure enables efficient suction of liquid food sources.

In adult butterflies, the labrum is reduced and fused with the clypeus, while mandibles are reduced or absent. The labial palps are large and scaly, consisting of three segments. The galeae are

elongated and connected through hooks and dorsal plates to form the food canal. Intrinsic muscles running along the proboscis facilitate coiling and uncoiling movements.

When not in use, the proboscis remains tightly coiled beneath the head like a watch spring. During feeding, haemolymph pressure and muscular contractions extend the proboscis toward the food source. Liquids are then sucked upward through the food canal by the cibarial and pharyngeal pumping organs located within the head (Tembhare, 2023).

Although highly efficient for siphoning liquids, the butterfly proboscis cannot pierce intact skin or plant tissues. Instead, butterflies feed from exposed fluids such as nectar, sap, fermenting fruit juices, and moist substrates. However, some groups such as Charaxinae possess stronger proboscises capable of piercing soft fruits (Molleman *et al.,* 2005).

Morphological specialization of the proboscis often reflects feeding ecology. Nectar-feeding butterflies possess slender proboscises adapted for accessing floral nectaries, while fruit-feeding and sap-feeding species exhibit broader or stronger structures suited for feeding on fermenting substrates. These adaptations illustrate the evolutionary diversification of butterfly feeding mechanisms.

Nutritional Ecology and Reproductive Significance

Butterfly feeding behaviour is closely linked to nutrient acquisition and reproductive physiology. While larval reserves contribute substantially to adult maintenance, adult-acquired nutrients significantly influence egg production, mating success, and longevity.

Nectar primarily supplies carbohydrates necessary for flight metabolism. However, amino acids present in nectar may also contribute to reproductive fitness. Studies indicate that butterflies are attracted to amino acid-rich nectar and that such nutrients can enhance fecundity under nutritionally stressful conditions (Boggs & Jervis, 2005).

Fruit-feeding butterflies derive sugars and nitrogenous compounds from fermenting fruits. Geister *et al.* (2008) demonstrated that adult dietary carbohydrates strongly influence reproductive output in the tropical butterfly *Bicyclus anynana*. Similarly, butterflies feeding on carrion and dung obtain proteins, amino acids, and minerals important for reproductive physiology.

Sodium acquired during puddling plays a particularly important reproductive role. Males may transfer sodium-rich spermatophores to females during mating, thereby enhancing egg viability and female reproductive performance. This nutrient transfer likely explains why puddling is predominantly observed among males. Different feeding substrates provide distinct nutritional benefits. Mud and dung supply minerals, carrion provides amino acids and nitrogen, while fermenting fruits offer sugars and ethanol-related compounds. The ability to exploit multiple food sources enhances ecological flexibility and adaptation to resource variability.

Environmental Influences on Feeding Behaviour

Environmental conditions strongly affect butterfly feeding patterns and substrate selection. Climate change, habitat degradation, pollution, and drought can alter the availability of nectar plants and puddling sites, thereby influencing feeding behaviour. During drought conditions or periods of

elevated temperature, butterflies may increase feeding frequency in search of moisture and nutrients (Klein et al., 2007). Reduced floral availability can drive butterflies toward unconventional food sources such as carrion, dung, or rotting fruits.

Habitat destruction caused by urbanization and agricultural expansion reduces the abundance of flowering plants and moist habitats required for puddling. Consequently, butterflies may increasingly depend on anthropogenic food sources and disturbed habitats. Pollution may further contaminate traditional feeding sites, forcing butterflies to utilize nutritionally inferior alternatives.

Nutritional deficiencies can also alter feeding preferences. When nectar lacks amino acids or minerals, butterflies may seek supplementary food sources rich in nitrogen or sodium. Such behavioural flexibility demonstrates the adaptive capacity of butterflies under environmental stress.

Table 1. Comparative Table of Butterfly Feeding Behaviours

Table showing different feeding sources, nutrient acquisition, ecological significance, and representative butterfly groups.

Feeding Source	**Substrates**	**Butterfly Groups**	**Nutrients Obtained**	**Ecological / Adaptive Significance**	**Key References**
Nectar Feeding	Flowers of herbs, shrubs, and trees	Pieridae, Nymphalidae, Lycaenidae, Hesperiidae	Sugars, amino acids	Primary energy source for flight, pollination, mating, and reproduction	Baker & Baker (1983); Krenn (2008)
Mud-Puddling	Mud, wet soil, riverbanks, sand	Papilionidae, Pieridae, Lycaenidae	Sodium, minerals, amino acids	Mineral supplementation and reproductive fitness	Arms *et al.* (1974); Boggs & Dau (2004)
Dung Feeding	Herbivore and carnivore dung	Nymphalidae, Riodinidae	Sodium, nitrogen compounds	Supports flight activity and mating success	Downes (1973); Anoop *et al.* (2023)
Carrion Feeding	Dead animals, decaying flesh	*Papilio, Danaus,* Charaxinae	Proteins, amino acids, minerals	Supplementary nutrition during stress or breeding	Hall & Willmott (1999)
Rotting Fruit Feeding	Overripe and fermenting fruits	*Morpho, Heliconius,* Charaxinae	Sugars, alcohols, amino acids	Alternative energy source when nectar is scarce	Molleman *et al.* (2005)

Tree Sap Feeding	Sap flows from trunks and branches	*Morpho, Vanessa*	Sugars, minerals	Important during dry seasons	Young (1975); Omura *et al.* (2008)
Human-associated Sources	Sweat, tears, spilled drinks, food waste	Various urban-adapted species	Salts, sugars, minerals	Opportunistic feeding in modified habitats	Plotkin & Goddard (2013)

Note: Feeding behaviour varies among butterfly species, sexes, habitats, and environmental conditions.

Conclusion:

Butterfly feeding behaviour is remarkably diverse and ecologically significant. Although nectar feeding remains the dominant strategy among adult butterflies, many species supplement their diets through puddling, sap feeding, fruit feeding, carrion feeding, and exploitation of mineral-rich substrates. These behaviours provide essential nutrients such as sodium, amino acids, and nitrogenous compounds that support survival, flight activity, and reproductive success.

Mud-puddling represents one of the most important supplementary feeding behaviours in butterflies, particularly among males. Sodium acquisition through puddling plays a vital role in reproductive physiology and mating success. Structural adaptations of the proboscis further demonstrate the evolutionary specialization of butterfly feeding mechanisms. Environmental changes including climate change, habitat loss, and pollution may significantly influence butterfly feeding ecology by altering resource availability and nutritional landscapes. Understanding these interactions is therefore essential for butterfly conservation and ecosystem management.

Future research should focus on the physiological mechanisms underlying nutrient selection, the evolutionary significance of feeding specialization, and the effects of environmental stressors on butterfly nutritional ecology. Such studies will contribute to a deeper understanding of butterfly biology and aid in conserving these ecologically valuable insects.

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