Contents lists available at ScienceDirect

Food Webs

journal homepage: www.elsevier.com/locate/fooweb

Short communication

Butterflies with a taste for elephant dung: Puddling of adult butterflies on elephant dung in India's Western Ghats

N.R. Anoop^{a,b,*}, Ezhuthupallickal Benny Femi^{a,b}, M.A. Yathumon^c, Aswaj Punnath^d

^a Ashoka Trust for Research in Ecology and the Environment, Royal Enclave, Srirampura, Bengaluru 560 064, India

^b Manipal Academy of Higher Education, Manipal 576 504, India

^c Wildlife Institute of India, Dehradun, India

^d Entomology and Nematology Department, University of Florida, 1881 Natural Area Drive, Gainesville, FL 32611, USA

ARTICLE INFO	A B S T R A C T
<i>Keywords:</i> Asian elephants Butterflies Elephant dung Mud-puddling Western Ghats	Elephants ingest a large quantity of plant material across the landscape and concentrate it at specific locations through dung and urine excretion, greatly enhancing local nutrient availability for various organisms. During our two-year study in India's Western Ghats, we documented 26 butterfly species from five families puddling on elephant dung. This observation suggests that elephant dung may offer mineral supplementation, which could contribute to the fitness and reproductive physiology of butterflies in elephant habitats.

1. Introduction

Nutrient availability and its acquisition are crucial for organisms' survival, reproduction, and for shaping their distribution and density (Milewski, 2000; Geister et al., 2008). Puddling (See Fig. 1) is one such typical behaviour seen in adult Lepidoptera (butterflies and moths), where they procure water and essential dissolved nutrients such as sodium, albumin, amino acids, and secondary plant metabolites from moist ground, decaying plant matter, animal corpses, and animal excrement (Beck et al., 1999; Inoue et al., 2015, 2019). Puddling behaviour is a supplementary feeding strategy that enhances survival, reproductive fitness, and temperature regulation (Sculley and Boggs, 1996; Beck et al., 1999). Additionally, it is an alternative foraging strategy for butterflies in situations when they are unable to compete for resources like nectar (Boggs and Jackson, 1991). Studies reported that, male butterflies transfer spermatophores to females during mating, containing various minerals such as sodium, calcium phosphate, or amino acids (multiple types of nuptial gifts), which are crucial for successful breeding(Sculley and Boggs, 1996; Molleman et al., 2009). Butterflies commonly utilize herbivore excrement as a puddling site since most mammals only digest a fraction of the nutrients they consume (Williams and Haynes, 1990; Stanbrook, 2018). Research has shown that butterflies typically exhibit a preference for fresh excrement for puddling (Fernando et al., 2017; Bodri, 2018). However, there is limited knowledge regarding the utilization of non-plant sources to fulfil the nutrient requirements of butterflies.

The globally endangered Asian elephant (Elephas maximus) is the largest land animal in Asian ecosystems, contributing significantly to ecosystem functions by facilitating seed dispersal, modifications of structure and composition of vegetation community through selective feeding, and transfer of nutrients (Campos-Arceiz and Blake, 2011; Williams et al., 2020; de Silva et al., 2023). Elephants are often recognized as umbrella species, influencing not only the vegetation structure but also the richness and abundance of several other species, from arthropods to large mammals (Sukumar, 2003; Williams et al., 2020). Elephants spend about 60% of their daylight hours feeding and consuming plant matter equivalent to 5% of their body mass (160-300 kg) and up to 225 l of water daily (Sukumar, 2003; Baskaran et al., 2010). Nutrients such as crude protein, sodium, magnesium, iron, potassium, copper, and zinc are known to influence their diet selection (Sukumar, 1990). The elephant is a hind-gut fermenter, and plant cellulose is digested through symbiotic microbes, with only about 40-50% of the forage being digested. Also, they consume soil (geophagy) to obtain minerals, especially Na⁺ (Holdø et al., 2002). Previous studies have found that elephant dung is rich in minerals such as nitrogen, phosphorus, and potassium (Dougall, 1963; Weir, 1972). With over 150 kg of wet manure deposited per day by an individual, an elephant's dung is frequently used as a source of mud puddling for butterflies (Coe, 1972; Stanbrook, 2018). In this study, we examined the diversity of butterfly species performing mud puddling on elephant dung in the Western

https://doi.org/10.1016/j.fooweb.2023.e00323

Received 14 February 2023; Received in revised form 28 September 2023; Accepted 28 September 2023 Available online 30 September 2023 2352-2496/© 2023 Elsevier Inc. All rights reserved.







^{*} Corresponding author at: Ashoka Trust for Research in Ecology and the Environment, Royal Enclave, Srirampura, Bengaluru 560 064, India. *E-mail address:* anoop.nr@atree.org (N.R. Anoop).

Ghats. We predict that (1) Butterflies are expected to show a preference for fresh dung due to its higher moisture content compared to older, drier dung, making it easier for them to extract water and dissolved nutrients (2) male butterflies are anticipated to predominantly engage in puddling on elephant dung.

2. Materials and method

The study was conducted in the Wayanad plateau (11⁰ 34¹ and 11⁰ 58¹N latitude, 76⁰26¹ and 75⁰ 59¹E longitude, covering an area of 520 km2) in Kerala state, India (Fig. 2). Field sampling covered the postmonsoon and summer seasons from September to May 2019-2020. This timing was chosen due to the elevated activity of butterflies and the high abundance of elephants in the study area (Sujin et al., 2019; Vinayan et al., 2023; Anoop et al., 2023). Wayanad is part of the Brahmagiri-Nilgiri Eastern Ghats elephant landscape, which supports the largest contiguous population of Asian elephants globally (Gajah, 2010). The major vegetation type in Wayanad consists of southern moist deciduous and dry deciduous forests interspersed with monoculture plantations of teak and eucalyptus (Anoop and Ganesh, 2020). The weather is monsoonal and receives southwest (June-Sep) and northeast monsoons (Nov-Dec) with heavy rains from June to September, a cool period from October to January, and a hot season from February to May. The average annual rainfall ranges between 1200 and 1700 mm, with maximum precipitation from the southwest monsoon (Anoop et al., 2023). The data presented here originates from a broader study that examined elephant habitat use in the Wayanad plateau (See Anoop et al., 2023). For this, the study area was overlaid with 2×2 km grid cells as spatial sampling units. Every alternative grid was selected to perform the elephant dung survey. While conducting the dung sampling, one observer recorded all mud-puddling butterflies on elephant dung. Photographs of mud-puddling butterflies were taken from different angles using a digital camera (Canon EOS 60D and Canon 70–300 F/ 4–5.6 II USM Lens). The freshness of the dung was recorded as 'fresh' and 'old' based on the wetness, colour, and odour. Two types of dungs were categorized as fresh *viz*. (1) the dung that are warm with fatty acid sheen glistening on exterior and strong smell, and (2) odour present (break the boli), there may be flies, but the fatty acid sheen has disappeared. The overall form still present although boli may be partly or completely broken down into an amorphous mass, no odour and tending to disappear are classified as old dung (See Hedges, 2012).

3. Results

Mud puddling was observed on 25 dungs during the study period and butterflies were found feeding heavily on these dungs. A total of 107 individuals belonging to 26 species of butterflies under five families, Pieridae, Lycaenidae, Papilionidae, Nymphalidae, and Hesperiidae, were recorded puddling on elephant dung (Fig. 3). Lycaenidae (11 species) was the most commonly observed family showing puddling, followed by three species each in Pieridae, Nymphalidae, and Hesperiidae. Eurema hecabe (Common grass yellow) and Prosotas nora (Common line blue) were the most frequently observed species on dung (Table 1). Puddling was found to occur in both fresh and old dung, but as predicted, it was most prevalent in fresh dung (70%). Butterflies were only found in old dung that was close to streams or that had retained wetness due to rain or mist. The most abundant species involved in puddling was Catopsilia pomona (32 individuals) followed by Eurema hecabe (28 individuals). We determined the sex of 32% of the puddling individuals, and as predicted, all were males. The minimum and the maximum number of butterflies observed in each dung were 1 and 21, respectively $(3.4 \pm 4.9 \text{ butterflies})$ per dung).



Fig. 1. Butterflies puddling on elephant dung in the Western Ghats: (1) Common Emigrant *Catopsilia Pomona* (2) Lesser Grass Blue *Zizina otis* (right) (3) Chocolate Pansy *Junonia iphita* (4), Common Grass Yellow *Eurema hecabe*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

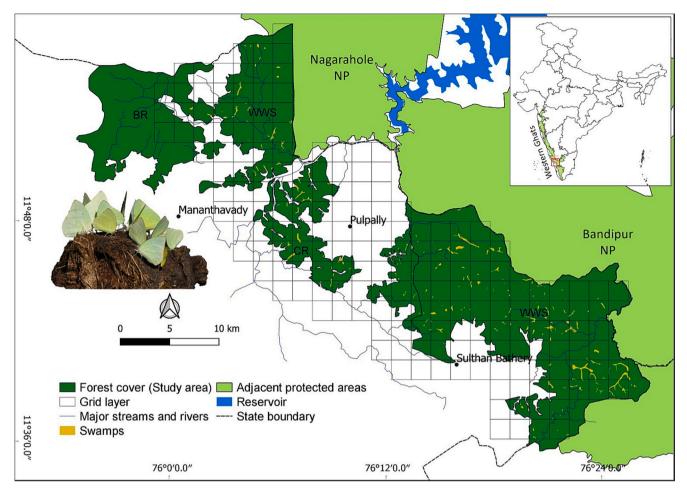


Fig. 2. Map showing the study area (Wayanad Wildlife Sanctuary [WWS], Begur Range [BR], Chethalayam Range [CR]) and adjacent farmlands overlaid with sampling grids to assess the habitat use of Asian elephants in Wayanad Plateau, Western Ghats, India. Inset is the location of the study area in India.

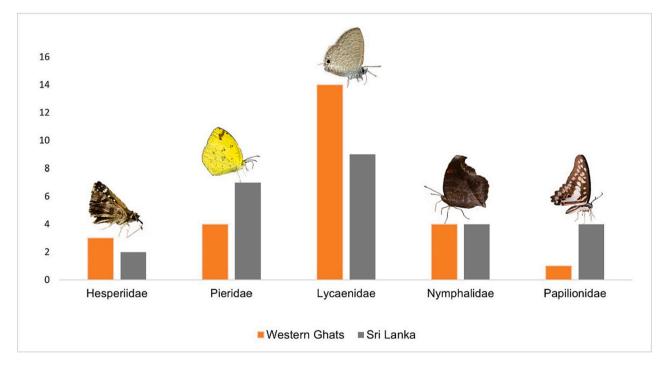


Fig. 3. Number of butterfly species puddled on elephant dung in the Western Ghats and Wasgamuwa National Park in Sri Lanka (See Fernando et al., 2017).

Table 1

Butterfly species and the number of dungs in which the species were observed puddling (frequency of occurrence) from September to May 2019–2020 in Wayanad plateau.

Sl. No.	Common Name	Scientific Name	Family	Frequency
1	Three-spot grass vellow	<i>Eurema blanda</i> (Boisduval, 1836)	Pieridae	3
2	Angled pierrot	Caleta decidia (Hewitson, 1876)	Lycaenidae	3
3	Blue bottle	Graphium sarpedon (Linnaeus, 1758)	Papilionidae	1
4	Common grass yellow	Eurema hecabe (Linnaeus, 1758)	Pieridae	8
5	Mottled emigrant	Catopsilia pyranthe (Linnaeus, 1758)	Pieridae	3
6	Chocolate pansy	Junonia iphita (Cramer, 1779)	Nymphalidae	4
7	Common line blue	Prosotas nora (C. Felder, 1860)	Lycaenidae	7
8	Common sailor	Neptis hylas (Linnaeus, 1758)	Nymphalidae	4
9	Dingy line blue	Petrelaea dana (de Nicéville, 1884)	Lycaenidae	3
10	Forget-me-not	Catochrysops strabo (Fabricius, 1793)	Lycaenidae	2
11	Great Eggfly	Hypolimnas bolina (Linnaeus, 1758)	Nymphalidae	2
12	Indian cupid/ Oriental cupid	Everes lacturnus (Godart, 1824)	Lycaenidae	5
13	Indian skipper	Spialia galba (Fabricius, 1793)	Hesperiidae	3
14	Lesser grass blue	Zizina otis (Fabricius, 1787)	Lycaenidae	5
15	Pointed ciliate blue	Anthene lycaenina (R. Felder, 1868)	Lycaenidae	2
16	Pygmy scrub hopper	Aeromachus pygmaeus (Fabricius, 1775)	Hesperiidae	2
17	Siva sunbeam	<i>Curetis siva</i> (Evans, 1954)	Lycaenidae	1
18	Tawny spotted grass dart	Taractrocera ceramas (Hewitson, 1868)	Hesperiidae	1
19	Tiny grass blue	Zizula hylax (Fabricius, 1775)	Lycaenidae	5
20	Zebra blue	Leptotes plinius (Fabricius, 1793)	Lycaenidae	2
21	Common pierrot	Castalius rosimon (Fabricius, 1775)	Lycaenidae	3
22	Common emigrant	Catopsilia Pomona (Fabricius, 1775)	Pieridae	4
23	Banded blue pierrot	Discolampa ethion (Westwood, 1851)	Lycaenidae	2
24	Dark pierrot	<i>Tarucus Ananda</i> (de Nicéville, (1884)	Lycaenidae	2
25	Commander	Moduza Procris (Cramer, 1777)	Nymphalidae	1
26	Quaker	Neopithecops zalmora (Butler, 1870)	Lycaenidae	3

4. Discussion

Butterflies in puddles are a common sight in the forests of the Western Ghats (Ramalingam, 2016). Of the 192 species of butterflies belonging to six families recorded from Wayanad Wildlife Sanctuary (Sujin et al., 2019), 13.5 % were found involved in puddling on elephant dung. Puddling of these butterflies on elephant dung despite abundant nectar plants in the study area indicates that elephant dung may have certain constituents essential for their survival and fitness. However, we observed that butterflies puddled on a small number of dung. This observation suggests that butterflies may selectively feed on dung, as the dung's contents can vary based on the elephant's diet. The copious number of nutrients like nitrogen, potassium, sodium, magnesium, and calcium in the elephant dung (Masunga et al., 2006) might act as an attractive nutrient pool because these nutrients might play a vital role in

butterflies' fitness and reproductive physiology. For instance, a study by Fernando et al. (2017) from Sri Lanka documented 26 species of butterflies across five families puddling on elephant dung. Thus, elephants might play an important role in maintaining a healthy population of butterflies in their habitat by providing essential nutrients necessary for the fitness and breeding of these butterflies. Puddling is a characteristic of male butterflies (Adler and Pearson, 1982). Our study, as well as a study conducted in Sri Lanka (Fernando et al., 2017), vielded similar findings indicating a predominance of male butterflies participating in puddling. This indicates that puddling on elephant dung might be determined by sex-specific nutritional needs and reproductive physiology in butterflies. However, puddling in butterflies is still a poorly studied behaviour (Otis et al., 2006; Molleman, 2010). Hence, further systematic studies are required to understand what substances are sought from elephant dung and how this affects the fitness of butterflies in elephant habitats.

Elephants have been part of the evolutionary history of Asian ecosystems for several millennia, with the opportunity for extensive coevolution with the biodiversity in their habitat (Sukumar, 2003). One of the crucial functions of elephants in their ecosystem is ingesting plant material across the landscape and concentrating it at specific locations through dung and urine excretion, thereby enormously increasing local nutrient availability (Wolf et al., 2013). The significance of elephant dung is not just restricted to butterflies; they directly and indirectly affect other animal species throughout the food web, including smaller herbivores, a wide array of beetles, flies, other insects, amphibians, and fungi, and hence modify the abiotic and biotic processes in complex ways (Sabu et al., 2006; Masunga et al., 2006). For instance, elephant dung is used by amphibians belonging to the genera Microhyla and Sphaerotheca as a daytime refuge, particularly in the dry season when leaf litter is scarce (Campos-Arceiz, 2009). However, recent studies suggested that elephant dung can be used as a raw material for paper production, cooking fuel, and vermicomposting (Farah et al., 2014; Sannigrahi, 2015; Stępień et al., 2019). But the removal of dung from forest ecosystems can affect the nutrient requirements of dependent animals and vegetation communities. With elephant populations continuing to decline due to loss and fragmentation of habitat, negative interactions with humans, and poaching for body parts (Leimgruber et al., 2003; de Silva et al., 2023), it is a matter of concern as it is not just about the elephants but also the important role they play as connecting links in the survival and reproductive success of countless other organisms.

Funding

This work was supported by Rufford Foundation, UK [34159–1, 34159–2, 39310-B].

Disclosure statements

The corresponding author confirms on behalf of all authors that no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

ANR collected the data; ANR, EBF, YMA, and AP analysed the data; and ANR wrote the paper with the contribution of all other authors.

Declaration of Competing Interest

The corresponding author confirms on behalf of all authors that no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Food Webs 37 (2023) e00323

Acknowledgement

Permission for the study was granted by the Kerala Forest and Wildlife Department. The work of ANR was supported by Rufford Foundation, UK, and Idea Wild, United States. We thank Dr. T Ganesh, Vikram Aditya, and Arjun Kannan for their comments that helped strengthen the manuscript. We thank Chandran and Rajan for their field assistance.

References

- Adler, P.H., Pearson, D.L., 1982. Why do male butterflies visit mud puddles? Can. J. Zool. 60, 322–325.
- Anoop, N.R., Ganesh, T., 2020. The forests and elephants of Wayanad: challenges for future conservation. Curr. Sci. (00113891) 118 (3). https://doi.org/10.18520/cs% 2Fy118%2Fi3%2F362-367.
- Anoop, N.R., Krishnaswamy, J., Kelkar, N., Bunyan, M., Ganesh, T., 2023. Factors determining the seasonal habitat use of Asian elephants in the Western Ghats of India. J. Wildl. Manag. https://doi.org/10.1002/jwmg.22477.
- Baskaran, N., Balasubramanian, M., Swaminathan, S., Desai, A.A., 2010. Feeding ecology of the Asian elephant *Elephas maximus Linnaeus* in the Nilgiri Biosphere Reserve, southern India. J. Bombay Nat. Hist. Soc. 107, 3–13.
- Beck, J., MuEhlenberg, E., Fiedler, K., 1999. Mud-puddling behavior in tropical butterflies: in search of proteins or minerals? Oecologia 119, 140–148. https://doi. org/10.1007/s004420050770.
- Bodri, M.S., 2018. Puddling behavior of temperate butterflies: preference for urine of specific mammals? J. Lepid. Soc. 72, 116–120.
- Boggs, C.L., Jackson, L.A., 1991. Mud puddling by butterflies is not a simple matter. Ecol. Entomol. 16, 123–127.
- Campos-Arceiz, A., 2009. Shit happens (to be useful)! Use of elephant dung as habitat by amphibians. Biotropica. 41, 406–407. https://doi.org/10.1111/j.1744-7429.2009.00525.x.
- Campos-Arceiz, A., Blake, S., 2011. Megagardeners of the forest-the role of elephants in seed dispersal. Acta Oecol. 37, 542–553.
- Coe, M., 1972. Defecation by African elephants (Loxodonta africana africana (Blumenbach)). Afr. J. Ecol. 10, 165–174.
- de Silva, S., Wu, T., Nyhus, P., Weaver, A., Thieme, A., Johnson, J., Leimgruber, P., 2023. Land-use change is associated with multi-century loss of elephant ecosystems in Asia. Sci. Rep. 13, 5996.
- de Silva, S., Wu, T., Nyhus, P., Weaver, A., Thieme, A., Johnson, J., Wadey, J., Mossbrucker, A., Vu, T., Neang, T., Chen, B.S., Songer, M., Leimgruber, P., 2023. Land-use change is associated with multi-century loss of elephant ecosystems in Asia. Sci. Rrep 13, 5996.
- Dougall, H.W., 1963. On the chemical composition of elephant faeces. Afr. J. Ecol. 1, 123–123.
- Farah, N., Amna, M., Naila, Y., Ishtiaq, R., 2014. Processing of elephant dung and its utilization as a raw material for making exotic paper. Res J Chem Sci. 4, 94–103.
- Fernando, C., Corea, R., Weerasinghe, C., Fernando, P., 2017. Puddling in elephant dung by lepidopterans in Wasgamuwa, Sri Lanka. Gajah 46, 14–20.
- Gajah, 2010. Securing the Future for Elephants. The Report of the Elephant Task Force. Ministry of Environment and Forest, Government of India.
- Geister, T.L., Lorenz, M.W., Hoffmann, K.H., Fischer, K., 2008. Adult nutrition and butterfly fitness: effects of diet quality on reproductive output, egg composition, and egg hatching success. Front. Zool. 5, 1–13. https://doi.org/10.1186/1742-9994-5-10.
- Hedges, S., 2012. Monitoring Elephant Populations and Assessing Threats: A Manual for Researchers, Managers, and Conservationists. Universities Press Private Limited, Hyderabad, India.

- Holdø, R.M., Dudley, J.P., McDowell, L.R., 2002. Geophagy in the African elephant in relation to availability of dietary sodium. J. Mammal. 83, 652–664. https://doi.org/ 10.1644/1545-1542(2002)083%3C0652:GITAEI%3E2.0.CO;2.
- Inoue, T.A., Ito, T., Hagiya, H., Hata, T., Asaoka, K., Yokohari, F., Niihara, K., 2015. K+ excretion: The other purpose for puddling behavior in Japanese *Papilio butterflies*. PLoS One. https://doi.org/10.1371/journal.pone.0126632 e0126632.
- Inoue, T.A., Yukuhiro, F., Hata, T., Yamagami, S.I., Yokohari, F., 2019. Ammonia as a puddling site-marshaling substance for Japanese *Papilio* butterflies. Chemoecology. 29, 143–154. https://doi.org/10.1007/s00049-019-00284-2.
- Leimgruber, P., Gagnon, J.B., Wemmer, C., Kelly, D.S., Songer, M.A., Selig, E.R., 2003. Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. Anim. Conserv. 6, 347–359.
- Masunga, G.S., Andresen, Ø., Taylor, J.E., Dhillion, S.S., 2006. Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. Mycol. Res. 110, 1214–1226. https://doi.org/10.1016/j.mycres.2006.07.004.
- Milewski, A., 2000. Iodine as a possible controlling nutrient for elephant populations. Pachyderm. 28, 78–90.
- Molleman, F., 2010. Puddling: from natural history to understanding how it affects fitness. Entomol. Exp. Appl. 134, 107–113. https://doi.org/10.1111/j.1570-7458.2009.00938.x.
- Otis, G.W., Locke, B., McKenzie, N.G., Cheung, D., MacLeod, E., Careless, P., Kwoon, A., 2006. Local enhancement in mud-puddling swallowtail butterflies (*Battus philenor* and *Papilio glaucus*). J. Insect Behav. 19, 685–698. https://doi.org/10.1007/s10905-006-9049-9.
- Ramalingam, R., 2016. Patterns of temporal variations observed in butterfly communities at puddle sites 51-60. In: Dharmarajan, P., Devy, S., Madhyastha, A., Subramanian, K.A., Seena, N.K. (Eds.), Invertebrate Diversity and Conservation in the Western Ghats. Ashoka Trust for Research in Ecology and the Environment, Bangalore, India, pp. 51-60.
- Sabu, T.K., Vinod, K.V., Vineesh, P.J., 2006. Guild structure, diversity and succession of dung beetles associated with Indian elephant dung in South Western Ghats forests. J. Insect Sci. 6 (1) https://doi.org/10.1673/2006_06_17.1.
- Sannigrahi, A.K., 2015. Beneficial utilization of elephant dung through vermicomposting. Int. J. Recent Sci. Res. 6, 4814–4817.
- Sculley, C.E., Boggs, C.L., 1996. Mating systems and sexual division of foraging effort affect puddling behaviour by butterflies. Ecol. Entomol. 21, 193–197.
- Stanbrook, R., 2018. Assessing the nutrient status of elephant dung in the Aberdare National Park, Kenya. Pachyderm 59, 86–90.
- Stepień, P., Świechowski, K., Hnat, M., Kugler, S., Stegenta-Dąbrowska, S., Koziel, J.A., Manczarski, P., Białowiec, A., 2019. Waste to carbon: biocoal from elephant dung as new cooking fuel. Energies. 12, 4344. https://doi.org/10.3390/en12224344.
- Sujin, N.S., et al., 2019. A report on butterfly survey of Wayanad Wildlife Sanctuary. In: Kerala Forest and Wildlife Department, and Ferns Nature Conservation Society. Kerala, Wayanad.
- Sukumar, R., 1990. Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. J. Trop. Ecol. 6, 33–53.
- Sukumar, R., 2003. The Living Elephants: Evolutionary Ecology, Behavior and Conservation. Oxford University Press, New York.
- Vinayan, P.A., Yathumon, M.A., Sujin, N.S., Kumar, B.N., Ajayan, P.A., Muneer, P.K., Vishnu, N.M., Anwar, C.S., Anoop, N.R., 2023. Pattern and drivers of danaine butterfly migration in southern India: implications for conservation. J. Insect Conserv. 27, 505–516.
- Weir, J.S., 1972. Mineral content of elephant dung. Afr. J. Ecol. 10, 229-230.
- Williams, P.H., Haynes, R.J., 1990. Influence of improved pastures and grazing animals on nutrient cycling within New Zealand soils. N. Z. J. Ecol. 14, 49–57.
- Williams, C., Tiwari, S.K., Goswami, V.R., de Silva, S., Kumar, A., Baskaran, N., Yoganand, K., Menon, V., 2020. Elephasmaximus. The IUCN Red List of Threatened. Species 2020 e.T7140A45818198.
- Wolf, A., Doughty, C.E., Malhi, Y., 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. PLoS One 8 (8). https://doi.org/10.1371/ journal.pone.0071352 e71352.