Protective devices of the carnivorous butterfly, *Spalgis epius* (Westwood) (Lepidoptera: Lycaenidae)

The apefly, *Spalgis epius* is a rare butterfly and an inhabitant of wooded areas. Usually most observers miss it due to its retiring nature, small size and rather drab colour. The species is known to occur in Sikkim, Kolkata, Malda, South India, Burma and Sri Lanka[1–3]. Lycaenids are unique in their larval stage as they eat unrelated food, including flowering plants, fungi, lichens, cycads, ferns, conifers, ant larvae and homopterans[4,5]. The larva of *S. epius* has been recorded as a predator on various species of pseudococcids (mealybugs)[2,6–16] and coccids (scale insects)[8,17,18]. Recently, the larvae of this butterfly were found on different species of croton plants, *Codiaeum* spp. infested with mealybug, *Planococcus citri* (Risso) (Homoptera: Pseudococcidae) at the Jnanabharathi campus, Bangalore University. Though the butterfly is known to be a potential predator of different species of mealybugs[19–23], its activity is rarely noticed these days in the field wherever insecticides are used indiscriminately for the control of various insect pests, particularly homopterans.

Except for being reported as a predator, not much information is available on the biology and behaviour of *S. epius*. Adult of *S. epius* is a small butterfly with dark brown wings above, and grey underside with dark striations. Forewing has a small quadrate spot at the cell end in male (Figure 1 *a*), and larger and somewhat diffuse in female[1,2]. Dorsal side of the thorax is dark and glossy, encircled by tufts of white hair. Dorso-lateral region of abdomen is dark brown, whereas ventral side is covered with layers of white hair. The body length and wingspan of the adult are 9.95–11.50 mm (10.63 ± 0.48) and 18.0–22.5 mm (20.83 ± 1.44) respectively. The butterfly flies rapidly and erratically in the vicinity of bushes infested with mealybugs and it swiftly deposits eggs in the mass of the mealybugs. Occasionally, it has the habit of landing to rest persistently on its preferred perch. Owing to the dull colour, rapid and erratic flight, and swift egg deposition habits of adult *S. epius* females, it is difficult for the predators (birds, lizards, etc.) to attack them in the field.

The larva of the butterfly has a peculiar appearance and it is morphologically different from that of other species of butterflies in general, being short, slug-like and covered with white wax coating (Figure 1 *b*). Legs of the larva are short and hidden. Aitken[6] described the larva and pupa of *S. epius*. The larvae were found feeding voraciously on the egg masses, nymphs and adults of mealybugs. As the young larvae of *S. epius* simulate mealybugs, it is difficult to recognize them amidst the host population. Similarly, the young larvae of *S. lemolea* (Holl.) in Africa[24] and *S. substrigata* (Snell) in Philippines[25] are camouflaged with the mealybug population. The mature larva of *S. epius* measures 14.5–19.0 mm (16.48 ± 1.66) in length and 5.08–6.50 mm (5.72 ± 0.38) in width.

The red ant, *Oecophylla smaragdina* (F.) or the black ant, *Crematogaster* sp. attends the mealybugs since they secrete honeydew, as reported earlier[26–29] (Figure 2 *a*). These ants, particularly *O. smaragdina* were found attacking the mature larvae of *S. epius* whenever they encountered them. These larvae are much bigger than the mealybugs and do not secrete honeydew sought by the ants; thus ants interfere with the predatory activity of the larvae. *Crematogaster* sp. was found to be less hostile to *S. epius* caterpillars. However, both the ants did not attack young larvae of *S. epius* that look like mealybugs. Though most of the honey-secreting lycaenids are myrmecophilous (associated with ants), either to protect themselves against larval and pupal enemies, especially parasitoids, or to feed on the larvae of ants[4,8,24,27,29,30–33], a few lycaenid homopterophagous aberrant genera such as *Aslauga* of subfamily Leptininae, and *Spalgis*, *Fenisca* and *Megalopalpus* of subfamily Lycaeninae are amyrmecophilous (not associated with ants). They defend themselves from the homopteran-associated ants by means other than honey secretion and ants derive no benefit from the presence of the lycaenin larvae[8,28,32]. Unlike other lycaenids, the larvae and pupae of these genera lack any sort of organ that yields an ant confection, and ants that visit honey-secreting homopterans are hostile to the caterpillars[8,32]. However, these are protected against ants either by their obscure position among or beneath their host prey, by the thick cuticle on the dorsal body wall, or by their bristly vestiture[8]. The mature larvae of *S. epius* seem to protect themselves against the mealybug-attending ants by maintaining an adequate distance from them and by having hard, thick dorsal cuticle. *S. epius* larva headed for pupation, crawls to the lower surface of the leaf and pupates after firmly attaching on its ventral side to the leaf.

The length, width and height of the pupa are 5.0–6.1 mm (5.6 ± 0.44), 3.5–4.2 mm (3.90 ± 0.19) and 3.2–4.1 mm (3.55 ± 0.32) respectively. The bold pattern on the hard dorsal side of the pupa of *S. epius* resembles the face of a rhesus monkey (Figure 2 *b*). The pupa shows clear spots of eyes, nose, mouth, cheeks and forehead on the dorsal side. *S. epius* pupa is light brown on the dorso-lateral side and whitish-grey on the ventral side. It is known that many edible, unrelated species avoid predation by mimicking the appearance of a dangerous or offensive species. Many lycaenid adults display patterns of colour, structure and behaviour that are consistent with deflecting predator attacks towards a false pattern[34]. There is always a chance of predation of quiescent pupae of *S. epius* by predatory birds or by other natural enemies that visit mealybugs. Though the insect-predatory bird, dull green leaf warbler, *Phylloscopus trochiloides* (Sundevall) seldom visited the mealybug-infested bushes and devoured the crawling mature *S. epius* larvae on the leaves, it

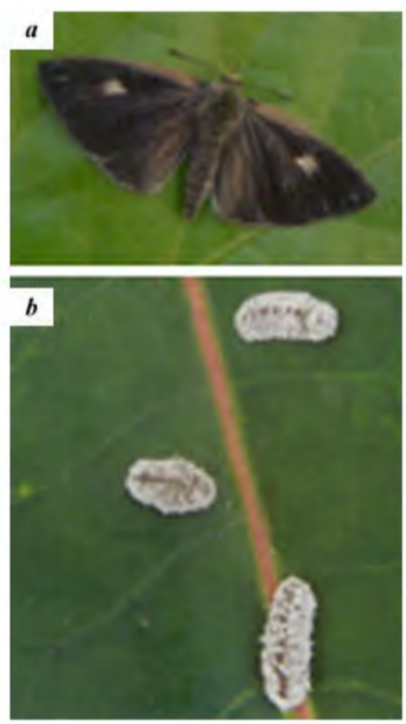

Figure 1. ***a***, Male *Spalgis epius* butterfly. ***b***, Fully grown larvae of *S. epius*.

avoided attacking the monkey-faced pupae that existed in the same bushes. However, the birds were never found to attack the stationary larvae, probably since they resemble bird-droppings at a distance. Similarly, various lycaenid caterpillars are known to escape from bird predation[35]. Moreover, the ants *O. smaragdina* and *Crematogaster* sp. attending the mealybugs are common predators of insects that do not secrete honeydew[8,27–29,36,37]. Even the pupae of lycaenid, *Iolaus* spp. are devoured by *Crematogaster* ants, which conversely protect them as larvae[35]. However, these ants never attacked amyrmecophilous *S. epius* pupae. Even though the pupa is small, it might scare away enemies because of its appearance (monkey-faced). Balduf[8] considers the monkey-faced appearance of some lycaenid pupae as a means of protection, but does not clearly state its significance. Generally, lycaenid pupae are protected from natural enemies either by ants, which are attracted to pupal ant-gland, by camouflage, or by making a creaking noise[8,38]. As these features are not found in *S. epius* pupae, the aposematic sign of the pupae to predators perhaps has a great adaptive value in protecting them in the sedentary stage under vulnerable habitat.

It is generally agreed that the primitive members of lycaenids were plant-feeders, and that homopterophagous (carnivorous) habit is a secondary specialization arising from association with ants[39,40], which live in the vicinity of honeydew-secreting homopterans. Thus many species of Lycaenidae counter attack from natural enemies by associating with protective ants. When many phytophagous–myrmecophilous/homopterophagous–myrmecophilous lycaenid genera get protection by associating themselves with ants, why a few homopterophagous lycaenids, including *S. epius* evolved as amyrmecophilous type is not clearly understood.

Figure 2. ***a***, The black ant, *Crematogaster* sp. attending mealybugs. *S. epius* larva seen nearby. ***b***, Monkey-faced pupae of *S. epius*.

1. Bingham, C. T., In *The Fauna of British India Including Ceylon and Burma, Butterflies*, Taylor and Francis, London, 1907, vol. II.
2. De Niceville, L., In *Butterflies of India, Burma and Ceylon*, The Calcutta Central Press Co Ltd, 1890.
3. Kunte, K., In *Butterflies of Peninsular India* (ed. Gadgil, M.), Universities Press, 2000.
4. Atsatt, P. R., *Am. Nat.*, 1981, **118**, 638–654.
5. Richards, O. W. and Davies, R. G., In *Imm's General Textbook of Entomology*, B.I. Publ Pvt Ltd, New Delhi, 1993.
6. Aitken, E. H., J. *Bombay Nat. Hist. Soc.*, 1894, **8**, 485–489.
7. Ayyar, T. V. R., *J. Bombay Nat. Hist. Soc.*, 1929, **33**, 668–675.
8. Balduf, W. V., In *The Bionomics of Entomophagous Insects. Part II*, Swift, St. Louis, 1939.
9. Chacko, M. J. and Bhat, P. K., *J. Coffee Res.*, 1976, **6**, 56–57.
10. Green, E. E., *Entomologist*, 1905, **35**, 202.
11. Jalil, A. F. M. A. and Kabir, A. K. M. F., *Agric. Pak.*, 1972, **22**, 237–240.
12. Mani, M., *J. Entomol. Res.*, 1995, **19**, 61–70.
13. Mani, M. and Krishnamoorthy, A., *J. Biol. Control*, 1990, **4**, 61–62.
14. Mani, M., Thontadarya, T. S. and Singh, S. P., *Curr. Sci.*, 1987, **56**, 624–625.
15. Pushpaveni, G., Rao, P. R. M. and Rao, P. A., *Indian J. Entomol.*, 1974, **35**, 71.
16. Rao, P. R. M., Kanakaraju, A., Apparao, R. V. and Azam, K. M., In Quarterly Newsletter of FAO Asia Pacific Plant Protection Commission, 1984, vol. 27, p. 12.
17. Ali, M., *Bangladesh J. Zool.*, 1980, **6**, 69–70.
18. Mani, M. and Krishnamoorthy, A., *Pest Manage. Hortic. Ecosyst.*, 1996, **2**, 49–50.
19. Chacko, M. J., Bhat, P. K. and Ramanarayan, E. P., *J. Coffee Res.*, 1978, **7**, 69–71.
20. Gowda, D. K. S., Manjunath, D., Pradip Kumar, Datta, R. K. and Kumar, P., *Insect Environ.*, 1996, **2**, 87–88.
21. Mani, M. and Krishnamoorthy, A., *Entomon.*, 1998, **23**, 105–110.
22. Prakasan, C. B., *J. Coffee Res.*, 1987, **17**, 114–117.
23. Reddy, K. B., Bhat, P. K. and Naidu, R., *Pest Manage. Econ. Zool.*, 1999, **5**, 119–121.
24. Lamborn, W. A., *Trans. Entomol. Soc. London*, 1914, **61**, 438–524.
25. Smith, H. S., *Bull. St. Comm. Hort. Calif.*, 1914, **3**, 26–29.
26. Anon., In *Coffee Guide*, Central Coffee Research Institute, 1998.
27. Holldobler, B. and Wilson, E. O., In *The Ants*, The Belknap Press of Harvard University Press, Cambridge, 1990.
28. Wheeler, W. M., In *Ants*, Columbia University Press, New York, 1960.
29. Wilson, E. O., In *The Insect Societies*, The Belknap Press of Harvard University Press, Cambridge, 1976.
30. Clark, G. C. and Dickson, C. G. C., In *Life Histories of South African Lycaenid Butterflies*, Purnell, Capetown, 1971.
31. DeVries, P. J., *Science*, 1990, **248**, 1104–1106.
32. Hinton, H. E., *Proc. Trans. Soc. London Entomol. Nat. Hist. Soc.*, 1949–50, 111–175.
33. Pierce, N. E. and Mead, P. S., *Science*, 1981, **211**, 1185–1187.
34. Robbins, R. K., *Am. Nat.*, 1981, **118**, 770–775.
35. Farquharson, C. O., *Trans. Entomol. Soc. London*, 1922, **69**, 319–448.
36. Dennis, H., In *Agricultural Insect Pest of the Tropics and their Control*, Cambridge University Press, 1993.
37. Le Pelley, R. H., In *Pests of Coffee*, Longman, Green and Co Ltd, 1968.
38. De Niceville, L., *J. Asiat. Soc. Bengal*, 1900, **69**, 187–278.
39. Eliot, J. N., *Bull. Br. Mus. Nat. Hist. Entomol.*, 1973, **28**, 373–505.
40. Vane-Wright, R. E., In *Diversity of Insect Faunas* (eds Mound, L. A. and Waloff, N.), Blackwell Scientific, Oxford, 1978.

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Current Science received correspondence by D. S. Ramesh on the efficacy of recent crustal images of the Indian shield from receiver functions. It was reviewed by four reviewers, including three from overseas and was subsequently revised. Since it critiques a few published papers, including one in Current Science, we approached the authors of these papers for a response. We are publishing a response, alongside of this correspondence. As a highly technical problem, we recognize that a unique solution may not exist and the debate can go on. However, we believe that a paper outlining the limitations and inherent biases in using receiver function as a tool in estimating the crustal thickness will help in recognizing the sources and nature of uncertainties.

—Editor

On the efficacy of recent crustal images of the Indian shield from receiver functions

The availability of broadband digital data has significantly improved our ability to 'see' the crust–mantle domains with more precision than hitherto possible[1–8]. Modern seismological tools such as the receiver functions (RFs) are used to generate crust–mantle images that permit finer interpretations of their evolution and structure. Recent efforts to obtain crustal images of the Indian shield using RF analysis are one of the latest additions in this direction[9–13]. While admitting the efficacy of these new tools, it is important to recognize the limitations starting with data quality to interpretations. Clearly, this topic deserves a much more rigorous treatment than what can be done in a short correspondence. Here we wish to restrict our discussion to two recent papers by Gupta *et al.*[9,10], hereafter referred to as GA and GB respectively, that have presented new images of the crust beneath the southern Indian shield comprising mainly the western Dharwar Craton (WDC) and the eastern Dharwar craton (EDC) using the RF approach. Major conclusions by GA and GB, based on crustal multiple phases (*Pps* and *Pss*) and direct *P*-to-*S* converted phases at the Moho (*Ps*; see Figure 1) can be summarized as follows: (a) the Mid-Archaean segment (3.4–3.0 Ga) of the WDC is underlain by an anomalously thick crust (43–52 km) with felsic-intermediate average composition; (b) EDC, the adjoining late Archaean (2.7–2.5 Ga), is much thinner (33–40 km) and Poisson's ratio varying between 0.23 and 0.26; (c) GB concludes that the southern Granulite Terrain (SGT) is characterized by a thick crust (42–60 km) and the Poisson ratio varies from 0.25 to 0.28. Studies on the thickness of the lithosphere using teleseismic residual data presented by GA suggest that the velocity in WDC is higher and its thickness is about 60–80 km more than the 200-km-thick EDC.

Obviously, these observations have important implications on the evolution and dynamics of the Indian crust and it is necessary to understand the limitations of the techniques used. In particular, we must pay attention to the quality of the basic data and processing strategies adopted. Here, we provide a brief review of the techniques followed by these authors in developing these crustal images, paying attention to the potential sources of errors.

What is a receiver function

A seismic signal (time series or seismogram) that essentially contains the effects of local structure (primarily crust) beneath a station devoid of effects due to source complexities and path effects is termed as RF (Figure 1). Owing to the large velocity contrast across a discontinuity (e.g. Moho, Lehmann, etc.), part of the steeply incident teleseismic *P*-wave energy becomes converted to an *SV* wave (e.g. *P*-to-*S*-converted wave from the Moho) and forms part of the *P*-wave coda. Besides the direct/primary *P*-to-*S* conversion, there are also many multiple reflections and conversions that occur between the surface and the interface. The *P*-wave and its multiples dominate the vertical component (*Z*), while the *P*-to-*S* conversion and its multiples are registered prominently on the horizontal radial (*SV*) component. Therefore, to isolate *P*-to-*S* energy (that contains information about Moho, in our case here) from that of *P*, we need to indulge in appropriate component rotation to arrive at the *SV* component time series or seismogram (Figure 2). The effects related to source, mantle propagation and instrument response are

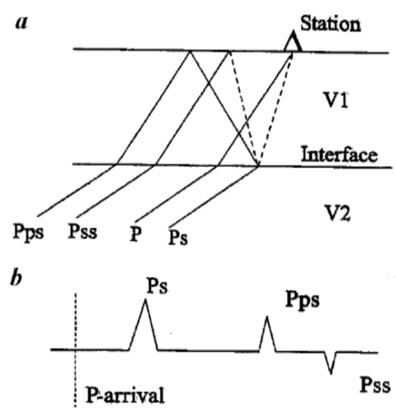

Figure 1. ***a***, Schematic sketch showing the propagation (travel paths) of various types of seismic waves recorded at a seismic station (triangle) that are used in receiver function (RF) studies. Besides the first arrival designated as *P*, of importance are the *P*-to-*S* converted wave (*Ps*), and the reverberations between the surface and the interface (e.g. Moho), named as *Pps* and *Pss*. The *Pps* wave is a multiple that is converted at the interface, while *Pss* is a conversion at the free surface and reflected by the interface. The *S*-paths are stippled lines and *P*-paths are solid lines. Note that both *Pps* and *Pss* have three legs of travel, while the *Ps* has only one leg between the interface and the station. Also, the *Pps* wave travels only one leg as *S*-wave (after conversion from a *P*-wave) and *Pss* has only one leg as a *P*-wave and two as *S*-wave. Naturally, after the first arrival *P*, *Ps* arrives followed by *Pps* and then *Pss*. ***b***, Typical RF sketch showing the *Ps*, *Pps* and *Pps* arrivals. Note the size and polarities of the amplitudes of these waves and their corresponding delayed arrivals after the *P*-arrival. Vertical stippled line marks the first arrival *P*-wave.