

GENERAL ARTICLE

Singing Symbionts: The Fascinating Alliance Between Caterpillars and Ants

Jyoti Antil* and Amita Kanaujia

Department of Zoology, University of Lucknow, Lucknow-226007, India

*jyotiantil5794gmail.com

Abstract

The different ways of survival among different species vary based on their size and vulnerability. Insects adopt remarkably striking mechanisms such as camouflage, mimicry, or symbiosis. Symbiosis involves complex associations of insects with one another as well as with other groups, and helps in understanding the ecological dynamics of these groups. The “ant love” of caterpillars, also called myrmecophily, is one such intriguing and complex association between butterfly caterpillars, especially Lycaenidae, and different species of ants. These caterpillars maintain associations with ants in different ways, such as through the release of chemical rewards, production of substrate-borne vibrations, and influencing ant behaviour. The different adaptations of caterpillars help shape associations ranging from facultative to obligate, and from largely mutualistic to subtly manipulative interactions. An extreme form of obligate myrmecophily occurs in the Lilac Silverline, *Cigaritis lilacinus*, whose caterpillars are associated with the cocktail ant *Crematogaster hodgsoni*. The larvae are maintained within ant colonies and receive food from the ants in addition to protection. Several specialized organs have developed in these caterpillars, including the dorsal nectary organ (DNO), or Newcomer’s gland, tentacle nectary organs (TOs), and stridulatory structures, muscular contractions, or specialized sclerotized surfaces for producing vibroacoustics, aptly describing them as “singing caterpillars.” The association between vulnerable caterpillars and the dominance of ants is remarkably widespread, with nearly 41% of ant genera known to engage in associations with other organisms. Such protection of caterpillars from predators and parasitoids, together with the ecological dominance of ants, may have played an important role in shaping the evolution and persistence of lycaenid-ant associations.

Keywords: Myrmecophily, Vibroacoustic, Caterpillar, Ants, Lycaenidae

Introduction

Survival is the central challenge for every species on Earth, but the ways organisms meet it are remarkably diverse. In insects, despite their small size and apparent vulnerability, these strategies can be especially striking. Butterflies, for instance, evade predators through a range of adaptations: blending into their surroundings (camouflage or crypsis), storing toxins and advertising them with

warning colours (aposematism), imitating toxic species (mimicry), or even resembling inedible plant parts (masquerade) (Prabhulinga et al., 2022).

Some butterflies take their interactions with other organisms a step further by forming remarkable alliances with ants. Lycaenidae is particularly well known for these associations, with approximately 75% of its ~5,200 species estimated

to be myrmecophilous, while ant associations have also been reported in roughly 20% of the ~1,500 species of Riodinidae (Pierce & Dankowicz, 2022). In these relationships, caterpillars-and, in some species, pupae-interact closely with ants through a range of chemical, tactile and vibrational signals. This association, known as myrmecophily (“ant love”), can range from loose and facultative interactions to highly specialized obligate partnerships. Many myrmecophilous caterpillars possess specialized organs that help them communicate with, attract and reward ants, often through nutrient-rich secretions (DeVries, 1992). In return, ants may provide protection from predators and parasitoids. Thus, what begins as a simple association can become a finely tuned ecological partnership in which vulnerable butterfly larvae effectively turn their vulnerability into an evolutionary advantage (Basu & Kunte, 2020).

At the heart of this relationship are sugary, energy-rich secretions produced by specialized organs in the caterpillars. Interestingly, similar secretions are produced by plant extrafloral nectaries, which ants also exploit (DeVries, 1992). In both cases, ants are effectively “paid” for their services, protecting the caterpillars, as well as such plants and other associated insects. The protective

role of ants in these associations is well documented across many lycaenid butterflies (Leimar & Axén, 1992; Pierce & Dankowicz, 2022).

The family Lycaenidae, often called the gossamer-winged butterflies, accounts for nearly 40% of all butterfly species globally, making it one of the largest and most diverse groups (Khyade et al., 2018). Many species are characterized by delicate, thread-like tails on their hindwings, ranging from short tufts to long, flowing extensions. Compared to other butterfly families, Lycaenidae is considered a tough and complex group, owing to its remarkable variation in form, colouration, and wing patterns. The complexity is clearly visible in the myrmecophilous nature of their caterpillar, which has adapted quite complex modifications to attract ants (Pierce et al., 2002).

Myrmecophilous Butterfly Caterpillar Adaptations

Lycaenid caterpillars associated with ants possess a remarkable suite of myrmecophilous organs that release chemical rewards, produce substrate-borne vibrations, and influence ant behaviour. These adaptations help shape associations ranging from facultative to obligate (Pierce & Dankowicz, 2022; DeVries, 1992), and from largely mutualistic to subtly manipulative interactions. In India, such associations have been reported in the Scarce Shot Silverline (*Cigaritis elima*), Common Shot Silverline (*C. ictis*), Long-banded Silverline (*C. lohita*), Plumbeous Silverline (*C. schistacea*), Common Silverline (*C. vulcanus*) and Sahyadri Common Tinsel (*Catapaecilma major callone*), particularly in association with *Crematogaster* ants. Other examples include Redspot (*Zesius chrysomallus*), Pointed Ciliate Blue (*Anthene lycaenina*), Large Oakblue (*Arhopala amantes*) and Centaur Oakblue (*Arhopala centaurus*), which are associated with *Oecophylla*



Fig.1 An ant individual tending a caterpillar of lime blue butterfly (a lycaenid butterfly), Photo: Raghavendra Rajadhyaksha

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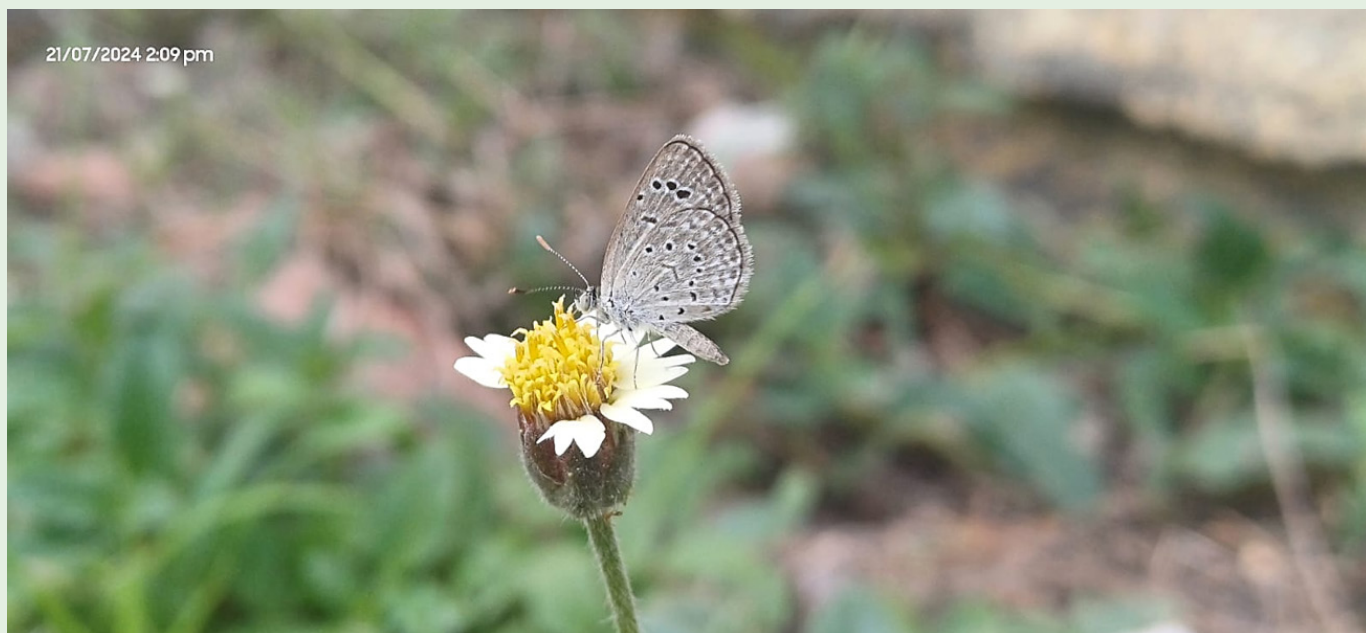


Fig.2 Dark grass blue is one of many butterflies that, as a caterpillar, enters into a symbiosis with ants and is called myrmecophily or love for ants, which has evolved in Lycaenidae and Riodinidae butterflies (Photo: Jyoti Antil)

and other ant genera (Sujitha et al., 2023; Kalesh & Prakash, 2005).

An extreme form of obligate myrmecophily occurs in the Lilac Silverline, *Cigaritis lilacinus*, whose caterpillars are associated with the cocktail ant *Crematogaster hodgsoni*. The larvae are maintained within ant colonies and receive food from the ants in addition to protection, illustrating how deeply some lycaenids can integrate into ant societies (Basu & Kunte, 2020).

These relationships are mediated by several specialized organs. Pore cupola organs (PCOs) release cuticular chemicals that facilitate recognition and acceptance by ants, helping to suppress aggressive responses (Casacci et al., 2019).

The dorsal nectary organ (DNO), or Newcomer's gland, located around the seventh abdominal segment in many lycaenids, produces carbohydrate-rich secretions that reward attending ants and encourage continued tending (Pierce & Dankowicz, 2022; Fiedler 1991). Ants

may stimulate secretion through antennal contact, creating a dynamic exchange in which increased attendance can trigger additional rewards. In some species, however, caterpillars can manipulate this exchange by producing droplets and subsequently reabsorbing them before ants consume them (Basu & Kunte, 2020).

Caterpillars can further regulate ant attendance through eversible tentacle nectary organs (TOs). These organs can be rapidly extended and retracted and are involved in signalling during interactions with ants, helping regulate the intensity and persistence of attendance (Pierce & Dankowicz, 2022). Together, chemical recognition, nutritional rewards, tactile signalling and vibrational communication create a sophisticated multimodal communication system, allowing caterpillars not merely to coexist with ants but to actively recruit, reward and manipulate their defensive partners" (Casacci et al., 2019).

Apart from chemical secretions and specialized tentacular or nectary organs, many

myrmecophilous lycaenid caterpillars also communicate with attending ants through substrate-borne vibrational signals-making them, in a sense, “singing caterpillars” (Casacci et al., 2019). These vibroacoustic signals may be produced through stridulatory structures, muscular contractions, or specialized sclerotized surfaces and can help recruit and maintain ant attendance (Travassos, & Pierce, 2000).

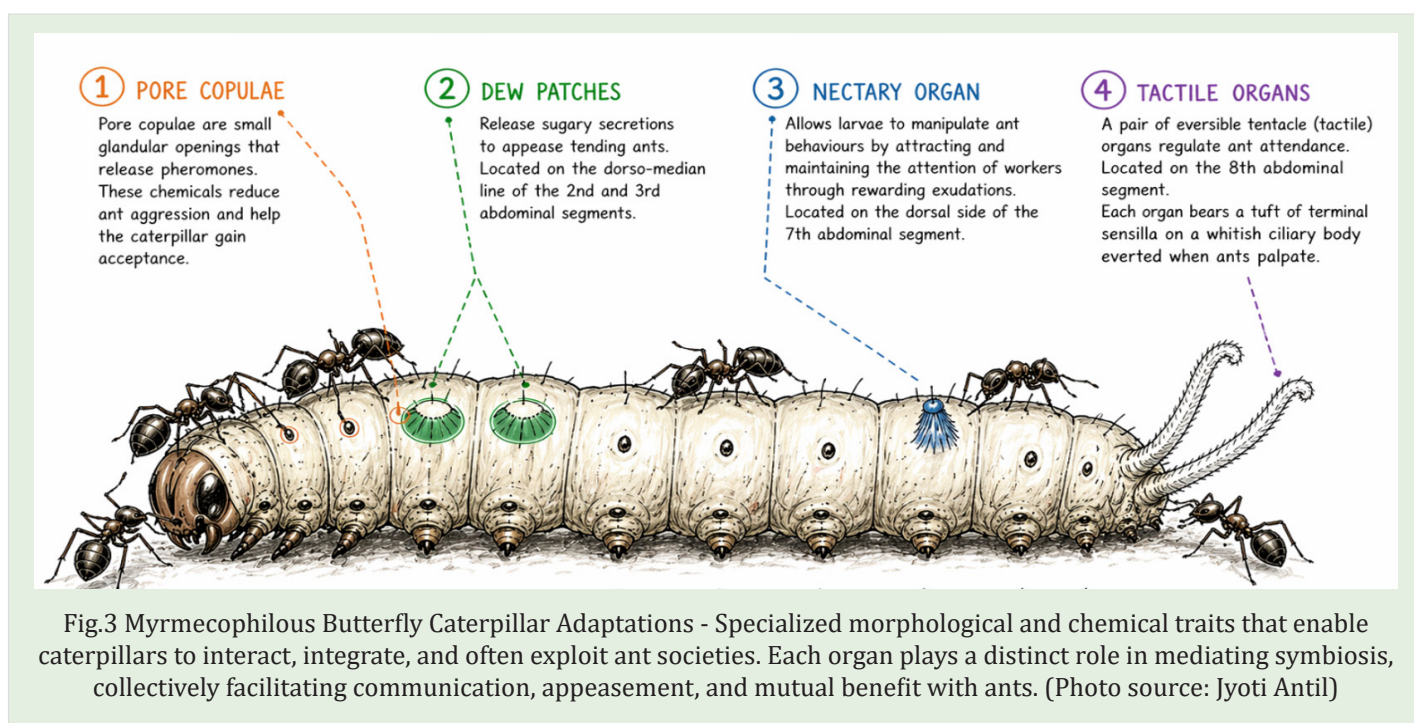
In the Imperial Hairstreak, *Jalmenus evagoras*, larvae produce grunts, hisses and drumming sounds, while experiments showed that pupal vibrational calls increase ant attraction and help maintain an attendant ant guard. Larvae also produced more sounds when attended by the tyrant ant *Iridomyrmex anceps*, suggesting that vibrations contribute to maintaining the butterfly–ant association. Thus, chemical secretions may provide ants with information about the caterpillar and its rewards, whereas vibrational signals provide an additional, spatially localized cue that helps draw ants towards and maintain their attention on the caterpillar (Casacci et al., 2019; Travassos, & Pierce, 2000). Rather than functioning as an

isolated “sound signal,” caterpillar stridulation is therefore better understood as part of a multimodal communication system, in which vibrational cues complement chemical signals to recruit, retain and influence attendant ants (Pierce & Dankowicz, 2022; DeVries, 1990).

A specialized larval stridulatory organ has also been described in the Bright Oak-blue, *Arhopala madytus* (Pierce & Dankowicz, 2022). Similarly, in the riodinid Irênea Metalmark, *Thisbe irenea*, experimentally silenced larvae received fewer attending ants, providing direct evidence that vibrational signalling can influence ant attendance (Pierce & Dankowicz, 2022; DeVries, 1992).

Myrmecophilous Association: Ants as Bodyguards

Interlocking symbioses are a defining feature of many terrestrial ecosystems, with ants often maintaining relationships with multiple organisms on the same plant. Such interactions are remarkably widespread, with nearly 41% of ant genera known to engage in associations with other organisms (Oliver et al., 2008). In myrmecophilous



associations, ants provide protection to butterfly caterpillars from predators and parasitoid, while receiving nutrient-rich secretions in return. The dependence of this relationship is well illustrated by the Reakirt's Blue, *Hemiargus isola*. Its larvae are principally parasitized by the braconid wasp *Cotesia cyaniridis*, which accounted for more than 99% of recorded parasitism, while the tachinid fly *Aplomya theclarum* was also recorded (Weeks, 2003). Experimental exclusion of ants resulted in 78% larval mortality due to parasitism, nearly twice that observed among ant-attended larvae, demonstrating the protective value of ant attendance (Weeks, 2003; Casacci et al., 2019). Moreover, when exposed to simulated attacks, larvae increased their nectar secretion and received greater ant attendance, indicating that caterpillars can actively enhance their rewards when protection is most needed. Thus, the interaction represents more than a simple exchange of food for protection: caterpillars can modulate their rewards to recruit defensive partners, while ants reduce enemy pressure on the caterpillar (Leimar & Axén, 1992). Such protection from predators and parasitoids, together with the ecological dominance of ants, may have played an important role in shaping the evolution and persistence of lycaenid-ant associations (Casacci et al., 2019; DeVries, 1992).

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