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Brood Stimulation Hypothesis

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Synonyms

Brood stimulation theory

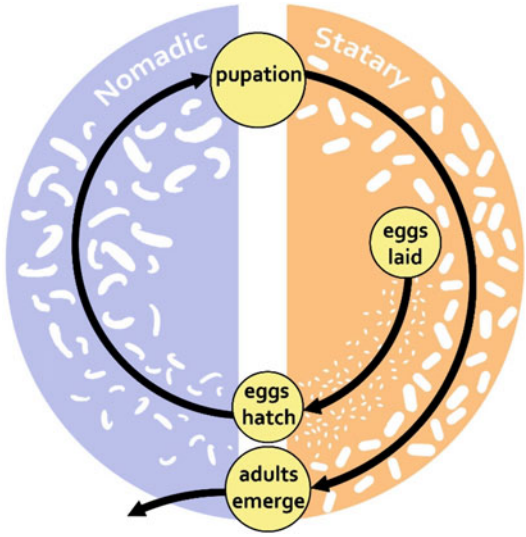
A distinctive feature of the colony cycle in some army ants is an alternation between a nomadic phase in which the colony emigrates frequently and a statary phase in which the colony remains in place for longer periods. During an emigration the workers carry brood to a new temporary nesting site known as a "bivouac" (Fig. 1). The transition from the statary to the nomadic phase was previously supposed to be a simple, direct result of exhaustion of the local food supply. Against this, it was originally proposed by Theodore C. Schneirla that transitions between phases are triggered by developmental changes in the colony's synchronous brood, rather than environmental circumstances or an endogenous rhythm of the adult ants (the brood stimulation hypothesis; [8, 9]). Schneirla suggested that hungry, simultaneously hatching larvae abruptly increase the colony's demand for food, signaling adult workers to forage and emigrate frequently in order to avoid local resource depletion. This energizing force was hypothesized to continue until dampened by collective pupation, at which time brood are believed to cease excitatory signaling. Due to the overlapping nonfeeding egg and pupal stages common in army ant colony cycles during the statary phase (Fig. 2), synchronous army ant colonies should, by this hypothesis, engage in nomadic and statary phases driven by and catering to brood demands.

Because the hypothesis concerns the proximate causes of army ant phase transitions, it was originally thought to apply only to phasic army ant species. Phasic army ants have regular and partially overlapping synchronous brood cycles corresponding to either the nomadic or statary phases of colony movement (Fig. 2). These species include all studied New World species of the genera *Eciton* and *Neivamyrmex*, as well as some Old World species of *Aenictus* [7, 9] and possibly some New World *Labidus* [2], but no known Old World *Dorylus* [6].

Early tests of the brood stimulation hypothesis came in the form of field observations and manipulations using synchronous army ants in the genera *Neivamyrmex* and *Eciton* [8, 11]. Because adult emergence and larval hatching occur almost simultaneously in synchronous army ant

C. Starr (ed.), *Encyclopedia of Social Insects*,
https://doi.org/10.1007/978-3-319-90306-4_16-1

Brood Stimulation Hypothesis, Fig. 1 *Eciton burchellii parvispinum* colony emigrating during the nomadic phase. (**a**) A section of the emigration column. (**b**) Detail of the same. Note workers transporting larval brood



Brood Stimulation Hypothesis, Fig. 2 Colony cycle in a phasic army ant with synchronous brood stages. The brood stimulation hypothesis suggests that synchronous brood life stage transitions (yellow circles) drive changes between the colony's nomadic high-feeding and statary low-feeding phase

phase cycles, there was debate about relative contributions of each in starting and maintaining the nomadic phase [11]. Because true army ants are notoriously difficult to rear in the lab, the only highly controlled lab experiments to date have used the distant army ant relative *Ooceraea biroi*, the clonal raider ant, as a model. As predicted by the brood stimulation hypothesis, foraging phases in *O. biroi* are stimulated by larval emergence alone, rather than an increase in new adults, and may be inhibited by the presence of eggs and pupae [12]. This is also consistent with less-controlled studies conducted in *Eciton* and some studies of *Neivamyrmex*, showing wide taxonomic support for the brood stimulation hypothesis as it applies not just to true army ants but also to some of their legionary kin.

Modern Interpretations and Mechanisms

Although the basic principle of the brood stimulation hypothesis – that army ant phase changes are driven by transitions in brood development – has been generally well supported, there has been notable criticism of Schneirla's original assertion that strictly timed brood development alone controls phase transitions [15]. Critics have drawn attention to the fact that food availability, colony satiation, predation, and ambient temperature variation also modify the length of and transitions between phases [4, 6].

Despite support for the brood stimulation hypothesis, the exact mechanism by which larvae stimulate nomadic behaviors has also long remained unclear. Early studies of *Neivamyrmex* suggested that secretions produced by larval exocrine glands play a role [14], but it

was not until recently that insulin-like peptide 2 signaling was proposed as a possible mechanism of communication between brood and adult workers in clonal raider ants [3]. Such pathways may similarly control foraging and emigration patterns in true army ants; however, the level of conservation of this mechanism remains to be investigated. Insulin signaling pathways are, however, heavily related to caste differentiation and behavioral regulation in a wide variety of other social insects.

The seemingly opposing evidence for internal and external influences on army ant colony movement patterns can be at least partially reconciled by considering both ultimate and proximate causes in due measure. While it is adaptive for a well-fed colony to cease foraging, the mechanism by which this is accomplished may be a change in signaling from satiated larvae to adults within the colony. Similarly, when ambient temperatures are low, bivouacs (temporary army ant nests) often allow larvae to cool [1]. If this cooling increases development time and decreases metabolic demand, as it does in most insects, then this too could affect brood to adult signaling, resulting in alterations of colony movement cycles. Adult worker response to larval conditions as a mechanism for colony response to climatic conditions was not considered a possibility at the time the brood stimulation hypothesis was originally conceived, due in part to the long-held assumption that brood are narrowly thermoregulated within the bivouac [5, 10]. However, it has more recently come to light that brood, particularly larvae, within army ant bivouacs do indeed experience partially buffered drops in internal bivouac temperature in response to periods of ambient low temperatures, particularly in colder, high elevation environments [1, 2].

Applications Outside of Army Ants

In addition to explaining proximal control of army ant movement cycles, the brood stimulation hypothesis has been useful in considering factors associated with emigration and foraging in other species. Obligate inquiline rove beetles (*Vatesus* spp.) have evolved a similar phasic life cycle coinciding with host army ant phase transitions [13]. It has also been widely supported across many social insects that increases in larval brood load stimulate episodes of more avid foraging.

Cross-References

- Army Ants
- Brood
- Caste Differentiation
- Colony Cycle

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