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Phoresy in Insects: Evolutionary Pathways, Hitching Strategies and Departure Dynamics

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Abstract

Phoresy, a non-parasitic dispersal strategy, enables less mobile organisms to hitch rides on others, aiding survival in fragmented habitats. This review examines the evolutionary pathways, hitching strategies and departure dynamics of phoresy in insects. Key factors for successful phoresy include size differences, life history synchronization and specialized attachment mechanisms. Case studies of nematodes, beetles, cockroaches, flies, hymenoptera and thrips illustrate diverse ecological interactions and evolutionary adaptations. Understanding phoresy enhances knowledge of species evolution and ecosystem dynamics.

Understanding Phoresy

Dispersal is a fundamental ecological and evolutionary process essential for species survival, particularly in patchy and degrading habitats. While many organisms disperse autonomously some, particularly those with limited mobility or in specific developmental stages utilize phoresy. Phoresy involves the transport of organisms on the bodies of others for non-parasitic purposes, a strategy often observed in species facing environmental challenges or limited mobility. Scientists define it as transportation without direct parasitism of the vehicle's developmental stage, highlighting its role in evolutionary transitions toward parasitism.

Embarkation and Disembarkation

- **Criteria for successful phoresy:** Successful phoresy requires an appropriate size differential between rider and vehicle, reliable transfer to suitable habitats and often life history synchronization between the rider and the vehicle. This ensures safe passage, reproductive opportunities and environmental resilience during transit.
- **Attachment mechanisms:** Riders often have specialized attachment devices or adhesive secretions ensuring stability during travel. This includes morphological adaptations like hooks or suckers and chemical secretions that enhance adherence.

- **Chemical communication**: Chemical cues play a significant role in phoresy, aiding in the identification of suitable vehicles and optimal disembarkation sites. For instance, phoretic nematodes use chemical signals to synchronize their life cycles with their insect hosts.

Life history and evolutionary context

- **Immature stages in Phoresy:** Immature stages resistant to environmental stress, such as dauer larvae in nematodes or triungulins in beetles, are often the phoretic stages. This strategy maximizes survival and ensures arrival at suitable habitats.
- **Mutualistic and density-dependent relationships:** Some phoretic relationships are mutualistic with both rider and vehicle benefiting from the association. Density-dependent selection may limit the number of riders, optimizing the survival and reproductive success of both parties.
- **Sexual selection**: Phoresy can also facilitate sexual selection among riders, as seen in species where multiple conspecifics embark on a single vehicle, ensuring mating opportunities at the destination.
- **Avoidance strategies by vehicles:** While less understood, some vehicles exhibit avoidance strategies to minimize the burden of phoretic riders, indicating a complex interplay of selection pressures within these associations.

Case studies

Insects as Rides

Nematode species	Insect host	Mutualistic role	Transmission method
Diplogastrellus monhysteroides	Dung beetle *Onthophagus taurus*	Maintains microbiome in dung brood chambers which aids in plant material breakdown and provides nutrients for larvae	Horizontal (between beetles during mating) and Vertical (across generations)
Fergusobia nematodes	Flies *Fergusonina*	Forms galls on plant tissues, completes life cycle within galls,	Vertical (nematodes carried and deposited with eggs)

		fertilized nematodes enter fly larvae	
Bursaphelenchus xylophilus	*Monochamus* beetles	Enters beetles *via* spiracles, inhabits tracheae; dauer stages latch onto beetles for transmission	Dauer larvae attracted by terpenes emitted by beetle larvae; Ascarosides involved in life cycle synchronization
Nematodes associated with fig wasps	Pollinating and non-pollinating fig wasps	Use fig wasps to move between fig inflorescences; negatively impact fig-wasp mutualism	Attracted to CO_2 emitted by fig wasps; prefer to board wasps carrying some conspecifics.

Insects as riders

1. Phoretic Cockroaches

Attaphila cockroaches live in nests of leaf-cutting ants (*Atta* and *Acromyrmex*) and feed on the fungus cultivated by the ants. Wingless females and males with reduced wings use specialized pads on their feet (arolia) to hitch rides on winged reproductive ants into new queen nests. They mimic the ants' surface chemicals to avoid detection and use their enhanced sense of smell to follow ant trails. These cockroaches attach to ants carrying leaves to enter active colonies. Despite being small (less than 4.5 mm), they lay few eggs per clutch, which supports their lifestyle of living and thriving in ant colonies by accessing a steady supply of fungal food.

2. Phoretic beetles

Triungulins, the first larval stage of Meloidae beetles attach themselves to bees and reach their nests for further development. These larvae have three-clawed legs that enable them to latch onto flower-visiting bees, and they can also hitch rides on other insects like flies to get to flowers. Phoresy has evolved multiple times within Meloidae beetles, helping them access resource-rich bee nests and aiding in their diversification and stability. To enhance their chances of success, triungulins gather on twigs and emit pheromones that attract male bees, mimicking female *Habropoda* bees. Female Meloe beetles lay thousands of eggs at a time, potentially leading to large aggregations of triungulins. These adaptations through phoresy and mimicry illustrate the evolutionary success and specialization of triungulins within their ecological niche.

3. Phoretic Strepsiptera

Strepsiptera, such as *Xenos vesparum*, have a unique life cycle characterized by hypermetamorphosis and phoretic behavior. In their first larval stage, known as triungulins, they are equipped with suction discs and claws to attach to hosts. These viviparous triungulins are either expelled by infected bees during flower visits or ingested with nectar, eventually finding their way to bee nests. Once there, they feed on pollen and subsequently parasitize hymenopteran larvae, such as those of *Polistes dominula* wasps. Inside these host larvae, the triungulins mature and develop. Strepsipterans manipulate their wasp hosts to aggregate on flowers, which aids in the transfer of triungulins and facilitates mating. This manipulation helps to disperse the Strepsipterans to new hosts and locations. Their life cycle, involving hypermetamorphosis and phoretic behaviour, ensures their survival and reproduction within host populations.

4. Phoretic Flies

Minute Sphaerocerid flies hitch rides on dung beetles to access dung. They feed on the dung collected by the beetles and often mate on the beetles. Unmated female *Norrbomia frigipennis* Spuler flies prefer beetles with larger groups of flies to increase their chances of finding a mate. In contrast, mated females avoid large groups to reduce male harassment. Research on what influences female fly choice of beetle hosts is limited but could help understand how female flies optimize their chances for reproductive success.

5. Phoretic Hymenoptera

Phoresy in Hymenoptera involves hitching rides for survival. For example, wasps like Braconids use colors and scents to find host eggs. *Ausasaphes shiralee*, a pteromalid wasp, rides beetles for egg hunting. *Hydrophylita emporos* rides damselflies underwater to lay eggs on damselfly eggs. *Mantibaria manticida* sheds wings on dragonflies to feed on wounds. In some wasps, males fly with females to mate. Even ants use phoresy, with smaller ones hitching rides on larger workers for nest protection. These adaptations show how species evolve to survive and interact in ecosystems.

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6. Phoretic Thrips

Phoretic thrips, such as *Frankliniella* species, primarily disperse by riding on wind currents due to their limited flying abilities and delicate, feathery wings. Their flight mechanism, known as 'clap and fling', restricts their ability to travel long distances independently. Recent studies have uncovered an additional dispersal strategy among florivorous thrips, including *Frankliniella* species, which involves hitching rides on honeybees (*Apis mellifera*). Thrips take advantage of honeybees visiting flowers for feeding or collecting nectar, clinging onto them to access new flower patches and potentially discover new host plants for feeding and reproduction. This behaviour not only provides thrips with an alternative means of dispersal beyond wind currents but also highlights the intricate ecological interactions and adaptive strategies that enable survival in diverse habitats.

Conclusion

Phoresy represents a fascinating aspect of dispersal with significant ecological and evolutionary implications. The adaptations facilitating phoresy, from chemical communication to morphological traits, underscore the intricate relationships between riders and their vehicles. Further research is essential to fully understand the dynamics of phoretic associations and their broader impacts on species evolution and ecosystem function.

References

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