



Ant–Beetle Interactions Mediated by Cuticular Hydrocarbons: Chemical and Ecological Integration Strategies

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Abstract: Myrmecophilous beetles have evolved diverse strategies that facilitate their persistence within socially structured ant nest environments. Among these, the acquisition of host-derived Cuticular Hydrocarbons (CHCs) represents a key mechanism mediating chemical similarity between guest organisms and host colony members. Repeated physical contact and socially mediated interactions, including grooming behavior, may promote the transfer and maintenance of colony-specific CHC profiles onto the beetle epicuticle, thereby reducing detection by nestmate workers. The reduction or loss of endogenous CHC biosynthesis may further increase guest reliance on host-derived chemical cues, enhancing physiological stability under nest-associated environmental conditions such as desiccation risk. Comparative analyses of specialist and generalist myrmecophilous beetles indicate that accurate chemical mimicry is associated with higher levels of host specificity and social integration, whereas less specialized guest species tend to exhibit lower chemical resemblance to host recognition cues. In addition to chemical integration, microbial symbiont sharing between ants and their associated beetles may influence tolerance thresholds and ecological persistence within socially regulated nest environments. Recent conceptual frameworks further suggest that ant–beetle associations should be interpreted as a continuum of ecological interactions, ranging from opportunistic nest cohabitation to highly specialized host-dependent relationships. This perspective is supported by evidence from multiple beetle lineages, including Staphylinidae, Scarabaeidae, and Tenebrionidae, in which varying degrees of behavioral, chemical, and environmentally mediated integration have been documented. Together, these findings support a conceptual model in which ant–beetle interactions reflect a dynamic spectrum of behavioral, chemical, microbial, and ecological integration strategies shaping the persistence and evolution of socially integrated guest species.

Keywords: Chemical Camouflage, Cuticular Hydrocarbons, Host Dependency, Myrmecophilous Beetles, Social Integration.

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RESEARCH PAPER

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1.0 INTRODUCTION

Ant-centered symbioses create chemically regulated environments in which acceptance, aggression, and access to nest resources are governed by colony odor templates. Across Formicidae, Cuticular Hydrocarbons (CHCs) provide a primary interface linking social identity to interactions with nestmates and non-nestmates. Myrmecophilous arthropods exploit this chemical interface through strategies that reduce detection or actively match host colony profiles, enabling persistence inside protected nest microhabitats. Such systems are especially informative for understanding how chemical information is acquired, maintained, and expressed under strong social selection within colonies (Helanterä *et al.*, 2016; Leonhardt *et al.*, 2016; Guillem

et al., 2017a; Guillem *et al.*, 2017b; Elgar *et al.*, 2018; Fouks and d’Ettorre, 2020).

Beetle–ant associations represent a recurrent form of myrmecophily in which coleopteran guests integrate into ant societies by exploiting contact-driven chemical exchange. In many systems, physical interactions with workers can transfer host-derived compounds onto the beetle cuticle, potentially altering recognition outcomes and host behavior. Rove beetles provide a tractable framework because their integration often involves proximity to workers, repeated grooming events, and sustained exposure to colony odor landscapes. These features allow a comparative discussion of how chemical similarity is generated and stabilized across different ant hosts while maintaining

species-specific ecological constraints (Bos *et al.*, 2016; Martin *et al.*, 2016; Hefetz, 2019; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Associations between myrmecophilous beetles and ant hosts may also be influenced by microclimatic conditions maintained within subterranean nest chambers. Cuticular hydrocarbons not only mediate social recognition but also contribute to desiccation resistance under stable humidity gradients created by colony architecture. In ant genera such as *Atta* Fabricius, 1804, and *Formica* Linnaeus, 1758, guest beetles may exploit host-derived compounds to maintain physiological stability in confined nest environments. Grooming-mediated transfer of hydrocarbons may therefore regulate both behavioral tolerance and water retention in socially integrated guests. These interactions may influence the survival of beetles inside protected ant colonies (Gibbs, 2016; Leonhardt *et al.*, 2016; Hefetz, 2019; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Spatial organization within ant nests may further shape interactions between beetle guests and host workers through restricted access to brood chambers and foraging tunnels. In colonies of *Camponotus* Mayr, 1861, and *Myrmica* Latreille, 1804, socially integrated beetles may occupy microhabitats where host contact occurs frequently during routine colony activities. Transfer of recognition cues through grooming can facilitate the movement of guest organisms across socially regulated nest zones. These processes may influence the distribution of beetles inside colony environments under ecological constraints imposed by nest structure. Persistence of myrmecophilous beetles may therefore depend on access to host contact areas (Helanterä *et al.*, 2016; Martin *et al.*, 2016; Guillem *et al.*, 2017a; Hefetz, 2019).

Host-guest interactions in beetle-ant associations may involve chemical convergence that alters recognition thresholds toward socially integrated organisms. Acquisition of host hydrocarbons during direct contact can influence colony responses to foreign cuticular profiles. In systems involving *Formica* and *Lasius* Fabricius, 1804, hosts and guest beetles may reduce detection through sustained physical interactions with nest workers. This mechanism may facilitate chemical similarity between parasites and host colonies under socially regulated conditions. Maintenance of transferred compounds may therefore regulate acceptance within ant nests (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; van Zweden and d'Etterre, 2017; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Chemical similarity between socially integrated beetles and host workers may also influence task-related interactions inside ant colonies. In systems involving *Camponotus* and *Lasius* hosts, guest beetles may interact

with foraging and brood-care workers under conditions of frequent physical contact. Transfer of cuticular hydrocarbons through grooming may regulate tolerance toward foreign organisms performing colony-associated movements. This mechanism may facilitate behavioral acceptance under socially constrained nest environments. Maintenance of chemical congruence may therefore influence long-term persistence of beetles within host societies (Leonhardt *et al.*, 2016; Guillem *et al.*, 2017b; Wagner *et al.*, 2017; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Myrmecophilous beetles may also interact with host colonies under ecological pressures associated with resource competition inside nest environments. In colonies of *Formica* and *Myrmica*, guest organisms may exploit food storage areas and brood chambers through sustained contact with the host. Transfer of recognition cues during routine interactions with workers can influence access to restricted areas of the colony. These processes may regulate the distribution of beetles inside ant nests under socially regulated conditions. Persistence of guest organisms may therefore depend on maintenance of host-derived chemical profiles (Helanterä *et al.*, 2016; Martin *et al.*, 2016; Hefetz, 2019; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Behavioral integration of beetles into ant colonies may be mediated by colony-specific odor landscapes maintained through worker interactions. In socially structured nests of *Atta*, and *Camponotus*, guest beetles may occupy microhabitats characterized by high worker density. Grooming interactions with host individuals may facilitate chemical exchange that influences nestmate recognition thresholds. This mechanism may reduce aggressive responses toward socially integrated organisms under ecological constraints imposed by colony architecture. Maintenance of transferred hydrocarbons may therefore regulate acceptance of beetle guests inside host societies (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; van Zweden and d'Etterre, 2017; Hefetz, 2019).

Host-parasite interactions in beetle-ant systems may also be influenced by temporal variation in colony activity cycles. In nests of *Formica* and *Lasius*, guest beetles may remain in proximity to workers during brood care or foraging periods. Acquisition of hydrocarbons during these interactions may influence chemical similarity with colony odor profiles. This process may facilitate tolerance toward socially integrated organisms under fluctuating environmental conditions. Sustained acquisition of host compounds may therefore regulate persistence of beetles inside nest environments (Helanterä *et al.*, 2016; Guillem *et al.*, 2017a; Hefetz, 2019; Fouks and d'Etterre, 2020a; Fouks and d'Etterre, 2020b).

Beetle–ant associations may ultimately depend on the stability of transferred recognition cues under socially regulated nest environments. In myrmecophilous systems, acquisition of host-derived hydrocarbons through grooming interactions may influence both behavioral acceptance and ecological persistence. Sustained maintenance of colony-specific chemical profiles may facilitate integration of guest organisms into host societies. Here, we aim to evaluate the biological and ecological consequences of host-derived chemical camouflage in socially integrated beetles interacting with multiple ant species (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; Wagner *et al.*, 2017; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

This study aims to evaluate the biological and ecological mechanisms underlying chemical integration in myrmecophilous beetles associated with multiple ant species across different colony environments. We investigate whether host-derived cuticular hydrocarbons acquired through grooming interactions influence nestmate recognition and behavioral acceptance within eusocial systems. Additionally, we assess how externally transferred hydrocarbons affect physiological stability under desiccation constraints imposed by social integration. The objective is to determine how sustained chemical acquisition regulates colony acceptance and ecological persistence of socially integrated beetles inside ant nests.

2.0. METHOD

This review was conducted through a comparative analysis of published studies addressing chemical integration mechanisms in myrmecophilous beetles associated with multiple ant species. Data were compiled from experimental and observational research focusing on host–guest interactions mediated by cuticular hydrocarbons in socially structured colonies. Studies describing grooming behavior and hydrocarbon transfer between beetles and ant workers were included for qualitative assessment. Ecological variables related to nest microhabitat, colony organization, and host contact frequency were also considered. Information regarding the physiological stability of guest organisms under desiccation constraints was examined across different myrmecophilous systems.

Studies included in this review were selected based on descriptions of chemical mimicry, camouflage, or acquisition strategies observed in beetle–ant associations across different Formicidae genera. Reports detailing physical contact between guest beetles and host workers during grooming interactions were analyzed to

identify potential pathways of hydrocarbon transfer. Comparative observations involving the spatial organization of guest organisms within nest environments were also examined. Information regarding colony tolerance thresholds toward socially integrated beetles was compiled across multiple ecological systems. Behavioral interactions influencing the persistence of beetles inside host nests were qualitatively assessed.

Ecological parameters related to nest structure, humidity gradients, and host contact frequency were examined to evaluate potential constraints affecting socially integrated beetles inside ant colonies. Information regarding microhabitat occupation by guest organisms in brood chambers and foraging tunnels was comparatively analyzed. Observations describing access to restricted colony areas were included to assess the spatial persistence of beetles within nest environments. Behavioral interactions between beetles and host workers were evaluated across different ant species. Data describing colony organization were incorporated for qualitative comparison.

Physiological responses of socially integrated beetles under desiccation risk were considered in relation to chemical acquisition mechanisms observed during host contact. Information regarding the maintenance of externally transferred hydrocarbons was examined across different myrmecophilous systems. Comparative descriptions of persistence inside host colonies were included for ecological assessment. Behavioral tolerance toward guest organisms under socially regulated conditions was evaluated. Patterns of chemical integration were qualitatively compared across beetle–ant associations.

3.0. RESULTS

Comparative assessment of host ant genera revealed variation in tolerance toward socially integrated beetles across different colony environments. Colonies of *Formica* and *Camponotus* displayed frequent grooming interactions with nest-associated guests occupying brood chambers and foraging tunnels. In contrast, *Lasius* and *Myrmica* hosts exhibited reduced tolerance toward peripheral beetle associates under socially regulated conditions. Spatial distribution of guest organisms varied according to colony organization and worker density. Maintenance of host contact influenced the persistence of beetles inside protected nest environments. These interactions were associated with behavioral acceptance of socially integrated guests (Table 1).

Table 1: Comparative patterns of beetle–ant chemical integration across host genera. This table summarizes host genera commonly involved in myrmecophilous beetle associations. Rows describe qualitative CHC strategies, contact routes, and typical colony outcomes for beetle guests

Ant host genus	Beetle association type	Primary CHC strategy	Host contact mechanism	Colony outcome
<i>Atta</i> Fabricius, 1804	Chamber-associated guest	Camouflage in humid chambers	Worker traffic contact	Tolerance varies by chamber
<i>Camponotus</i> Mayr, 1861	Nest-associated guest	Camouflage via transfer	Contact with workers in galleries	Tolerance in specific chambers
<i>Eciton</i> Latreille, 1804	Raid follower	Opportunistic camouflage	Contact during raids	Transient acceptance
<i>Formica</i> Linnaeus, 1758	Nest-associated guest	Partial mimicry	Frequent contact at the nest edge	Moderate tolerance; limited zones
<i>Lasius</i> Fabricius, 1804	Peripheral guest	Low-fidelity mimicry	Occasional antennal contact	Tolerance near the periphery
<i>Liometopum</i> Mayr, 1861	Nest-integrated guest	Host CHC acquisition	Grooming/body contact	High tolerance; nest access
<i>Myrmica</i> Latreille, 1804	Nest-associated guest	Blend matching	Grooming plus cohabitation	Tolerance increases with contact
<i>Solenopsis</i> Westwood, 1840	Opportunistic guest	Chemical appeasement	Brief contact; avoid detection	Short-term tolerance

Spatial distribution of socially integrated beetles inside nest environments varies according to colony organization and worker density. Guest organisms were frequently detected in microhabitats characterized by stable humidity and temperature gradients. The presence of beetles within brood chambers and food storage areas was associated with reduced aggression by host workers. Physical proximity to nest workers may influence the persistence of guest organisms inside colony environments. Access to restricted nest zones may therefore regulate integration success.

Behavioral tolerance toward socially integrated beetles was influenced by the frequency of grooming interactions with host individuals. Guest organisms in contact with *Myrmica* and *Lasius* workers displayed reduced aggressive responses during routine colony activities. Transfer of recognition cues during physical contact may facilitate acceptance of foreign organisms under socially regulated conditions. Maintenance of chemical similarity was associated with persistence inside nest environments. These processes influenced the ecological stability of beetle guests (Table 2).

Table 2: Mechanisms of chemical integration used by myrmecophilous beetles. This table organizes major strategies described for chemical and behavioral integration into ant societies. It links each mechanism to the CHC origin, required behavior, and the expected effect on host responses

Integration mechanism	Operational definition	CHC source	Behavioral requirement	Expected effect
Chemical mimicry	Guest matches host profile	Endogenous + partial host	Sustained proximity	Reduced aggression
Chemical camouflage	Guest coats with host CHCs	Host-derived	Grooming/contact	Nest access improves
Chemical insignificance	Low CHC signature	Minimal/none	Avoid contact	Lower detection probability
Chemical appeasement	Soothing compounds released	Endogenous secretions	Close approach	Attack inhibition
Chemical weaponry	Irritants/defenses deter ants	Endogenous	Threat display	Escape from attack
Profile blending	Intermediate odor via mixing	Mixed	Cohabitation	Tolerance in some zones
Propaganda	Disrupt host recognition	Endogenous	Contact/transfer	Confusion; reduced policing
Physical shielding	Morphology reduces harm	NA	None	Survival during inspection
Behavioral crypsis	Moves to low-contact areas	NA	Avoidance	Persistence at the periphery

Microhabitat occupation by guest beetles was associated with variation in nest architecture across different ant colonies. Socially integrated organisms were frequently detected in zones of high worker activity and brood presence. Behavioral interactions with host individuals influenced the distribution of beetles inside colony environments. Transfer of hydrocarbons during grooming may facilitate the movement of guest organisms across socially regulated nest areas. Persistence of beetles may therefore depend on host contact frequency.

Physiological stability of socially integrated beetles under desiccation risk was associated with the maintenance of transferred hydrocarbons acquired from host workers. Guest organisms occupying subterranean nest chambers displayed reduced water loss under colony humidity conditions. Transfer of host-derived compounds may influence the survival of beetles under ecological constraints imposed by nest environments. These interactions were observed across colonies of *Formica* and *Camponotus*. Persistence inside nests was therefore influenced by host-mediated chemical acquisition (Table 3).

Table 3: Dual roles of cuticular hydrocarbons in social and physiological performance. This table summarizes pleiotropic functions of CHCs relevant to ant societies and guest survival. It highlights constraints created when a single chemical layer mediates both recognition and desiccation resistance

CHC function	Role in colonies	Physiological role	Constraint on guests	Observable proxy
Nestmate recognition	Friend-foe discrimination	Nondirect	Must match odor	Reduced antennation aggression
Task/role signaling	Worker role cues	Nondirect	Avoid anomalous cues	Tolerance depends on the chamber
Species recognition	Inter-species boundary	Nondirect	Avoid triggering an attack	Attack threshold shifts
Desiccation barrier	Not primary social	Water retention	CHC loss causes drying	Survival time off-host
Antimicrobial surface	Colony hygiene support	Barrier function	May need a host coat	Lower fungal growth
Mate signaling	Reproduction cues	Indirect	May conflict with mimicry	Sex differences in CHCs
Cuticle integrity	Surface stability	Barrier/structure	Dependent on the coating	Cuticle permeability
Environmental matching	Microclimate adaptation	Thermal/water balance	Host chamber dependence	Position in nest
Chemical "passport"	Colony entry permission	Indirect	Requires renewal	Acceptance duration

Distribution of socially integrated beetles inside ant colonies was influenced by temporal variation in worker activity cycles. Guest organisms were observed in proximity to host individuals during brood care and foraging periods. Behavioral tolerance toward beetles varied according to the frequency of physical contact with workers. Maintenance of host-derived chemical signatures may influence persistence inside colony environments. Access to nest resources was associated with grooming interactions.

Interactions between guest beetles and host workers were influenced by nest structure and colony size across different Formicidae species. Socially integrated organisms were detected in restricted nest areas characterized by stable microclimatic conditions. Physical contact during routine colony activities may facilitate transfer of recognition cues between hosts and guests. These processes influenced the persistence of beetles inside socially regulated nest environments. Behavioral tolerance toward foreign organisms varied across colonies (Table 4).

Table 4: Routes of hydrocarbon acquisition through grooming and colony contact. This table summarizes qualitative transfer routes by which beetles may acquire host-derived hydrocarbons. Rows emphasize how contact mode affects renewal frequency, camouflage benefit, and integration risk

Grooming/contact mode	Transfer route	Renewal frequency	Benefit to the beetle	Risk/limitation
Antennal handling	Ant - antenna CHCs	High	Rapid profile matching	Triggers inspection
Leg scraping + smearing	Body surface CHCs	High	Full-body coating	Requires close access
Allogrooming by ants	Ant mouthparts/contact	Moderate	Passive acquisition	Depends on host tolerance

Grooming/contact mode	Transfer route	Renewal frequency	Benefit to the beetle	Risk/limitation
Brood chamber contact	Nest substrate CHCs	Low–moderate	Background blending	Lower fidelity
Trophallaxis proximity	Near mouth contact	Moderate	Close integration	Host policing risk
Trail contact	Surface/foraging trails	Low	Transient camouflage	Short-lived
Raid contact	Mass interaction events	Low	Opportunistic entry	High mortality risk
Nest wall rubbing	Substrate hydrocarbons	Low	General odor masking	Imperfect match
Repeated worker clustering	Mixed worker CHCs	Moderate	Blended colony odor	May dilute specificity

Host–guest interactions in beetle–ant associations were influenced by spatial organization within colony environments. Guest organisms occupying brood chambers displayed increased tolerance from host workers under socially regulated conditions. Maintenance of chemical similarity may influence the persistence of beetles inside protected nest zones. Physical proximity to host individuals was associated with behavioral acceptance. These processes influenced the ecological integration of guest organisms.

Variation in colony humidity gradients influenced the physiological performance of socially integrated beetles across different nest environments. Guest organisms occupying subterranean chambers displayed reduced desiccation risk under stable microclimatic conditions. Transfer of host-derived hydrocarbons during grooming interactions may influence tolerance toward beetles. Maintenance of recognition cues was associated with persistence inside nest environments. These interactions varied across ant species (Table 5).

Table 5: Ecological constraints shaping dependence on host-derived hydrocarbons. This table summarizes how environmental context interacts with CHC function to constrain beetle persistence. It proposes qualitative predictions for off-host survival and observable indicators of dependence

Ecological context	Key constraint	CHC-related dependence	Predicted survival off-host	Testable indicator
Dry surface habitats	High desiccation risk	Strong dependence	< 24 h	Rapid water loss
Humid subterranean nests	Stable microclimate	Moderate dependence	24–72 h	Slower CHC decay
Seasonal drought	Humidity fluctuation	Increased dependence	< 24–48 h	Greater grooming frequency
High-worker density zones	Frequent contact	High renewal	Short	Higher acceptance duration
Nest periphery	Low contact	Low renewal	Longer but risky	More aggression events
Foraging trails	Transient exposure	Low dependence	Variable	Brief acceptance
Brood chambers	Protected resources	High dependence	Short	Sustained tolerance
Outside colony	No host CHCs	Complete loss	< 24 h	Desiccation endpoint
Lab isolation	Controlled humidity	Depends on RH	Variable	Survival vs RH curve

Behavioral interactions between beetles and host workers influenced access to restricted nest areas under socially regulated conditions. Guest organisms interacting with *Atta* and *Lasius* colonies displayed variation in movement patterns across brood chambers. Transfer of hydrocarbons during routine interactions may influence chemical similarity between hosts and guests. Persistence inside nest environments was associated with the maintenance of transferred

compounds. These processes influenced the ecological stability of beetle guests.

Nest architecture influenced the spatial persistence of socially integrated beetles across different colony environments. Guest organisms occupying zones of high worker density displayed reduced aggression from host individuals. Maintenance of host-derived hydrocarbons may influence tolerance toward beetles under ecological constraints imposed by nest structure.

Physical contact during grooming interactions was associated with nest access. These processes influenced integration success (Table 6).

Table 6: Trade-offs and outcomes in chemical strategies used by beetle guests. This table synthesizes the benefits and costs of alternative strategies for integration into ant colonies. It frames expected stability conditions and qualitative outcomes relevant to host dependence and persistence

Beetle strategy	Short-term advantage	Long-term cost	Stability condition	Outcome scenario
Endogenous mimicry	Some acceptance	Imperfect match	Stable biosynthesis	Peripheral living
Camouflage via host CHCs	High acceptance	Requires renewal	Frequent grooming	Nest integration
Insignificance	Low detection	Limited interaction	Avoidance behavior	Edge persistence
Appeasement compounds	Attack suppression	Metabolic cost	Continuous production	Conditional entry
Switch off CHCs	Stealth entry	Desiccation risk	Host coating available	Obligate dependence
Blended profile	Moderate acceptance	Diluted specificity	Mixed contacts	Zone-restricted living
Rapid renewal	Sustained match	Time/energy	High worker contact	Stable integration
Low renewal	Reduced exposure	Profile decay	Humid nests only	Seasonal survival
Host switching attempt	Potential expansion	High attack risk	New host match evolves	Rare transition

Comparative analysis of myrmecophilous beetle species revealed variation in chemical integration strategies associated with dependence on host-derived hydrocarbons inside ant colonies. Nest-associated guests displayed sustained physical contact with host workers through grooming interactions that facilitate the transfer of cuticular compounds. In contrast, peripheral associates maintained partial endogenous hydrocarbon

biosynthesis and exhibited reduced grooming dependence. Brood chamber occupants demonstrated increased tolerance from host individuals under socially regulated conditions. Suppression of endogenous CHC production in obligate nest guests was associated with continuous host contact requirements. These patterns influenced the persistence of socially integrated beetles within protected nest environments (Table 7).

Table 7: Myrmecophilous beetle traits relevant to chemical integration. This table summarizes beetle species used as model guests in ant colonies. It presents guild type, endogenous CHC production status, and grooming dependence

Beetle species	Family	Myrmecophilous guild	Endogenous CHC biosynthesis	Host-grooming dependence
<i>Sceptobius lativentris</i> (Fenyés, 1909)	Staphylinidae	Obligate nest guest	Suppressed in adults	High (continuous)
<i>Dinarda dentata</i> (Gravenhorst, 1806)	Staphylinidae	Nest-associated	Present (matching)	Moderate
<i>Liometoxenus newtonarum</i> Kistner, Jacobson & Jensen, 2002	Staphylinidae	External predator	Present	Low
<i>Lomechusa strumosa</i> (Fabricius, 1792)	Staphylinidae	Brood chamber guest	Reduced	High
<i>Oxyptoda</i> spp.	Staphylinidae	Peripheral guest	Low	Low
<i>Pella funesta</i> (Gravenhorst, 1806)	Staphylinidae	Nest-associated	Present	Moderate
<i>Platyusa sonomae</i> Casey, 1885	Staphylinidae	Peripheral associate	Present (partial)	Low–moderate
<i>Thiasophila angulata</i> (Erichson, 1837)	Staphylinidae	Nest-associated	Present	Moderate
<i>Zyras</i> spp.	Staphylinidae	Nest infiltrator	Variable	Moderate–high

Overall, socially integrated beetles displayed variation in chemical integration associated with host contact frequency and nest microhabitat occupation across different ant colonies. Acquisition of host-derived hydrocarbons during grooming interactions was

consistently observed among nest-associated guests occupying brood chambers and foraging tunnels. In contrast, peripheral associates maintained reduced host contact and exhibited partial endogenous hydrocarbon production. Persistence of beetle guests inside colony

environments was influenced by spatial organization and worker density. These patterns suggest that maintenance of transferred recognition cues may regulate the ecological stability of myrmecophilous beetles within socially structured nest systems.

4.0. DISCUSSION

Chemical integration in beetle–ant associations may reflect behavioral strategies that regulate host tolerance toward socially integrated guests inside nest environments. Acquisition of host-derived hydrocarbons through grooming interactions can influence recognition thresholds across different Formicidae colonies. Maintenance of transferred compounds may facilitate persistence of beetles within socially regulated environments. These interactions may influence the ecological stability of guest organisms under colony conditions. Behavioral acceptance may therefore depend

on sustained host contact frequency (Helanterä *et al.*, 2016; Leonhardt *et al.*, 2016; Guillem *et al.*, 2017a; Guillem *et al.*, 2017b; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

Physiological responses of socially integrated beetles may also be influenced by the maintenance of host-derived hydrocarbons under desiccation risk inside nest environments. Transfer of cuticular compounds during grooming interactions can contribute to water retention in guest organisms occupying subterranean chambers. In colonies of *Camponotus* and *Formica*, these mechanisms may influence the survival of beetles under microclimatic constraints. Maintenance of chemical similarity may therefore regulate persistence inside host nests. Such processes may reflect host-dependent ecological integration (Figure 1) (Gibbs, 2016; Martin *et al.*, 2016; Hefetz, 2019; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

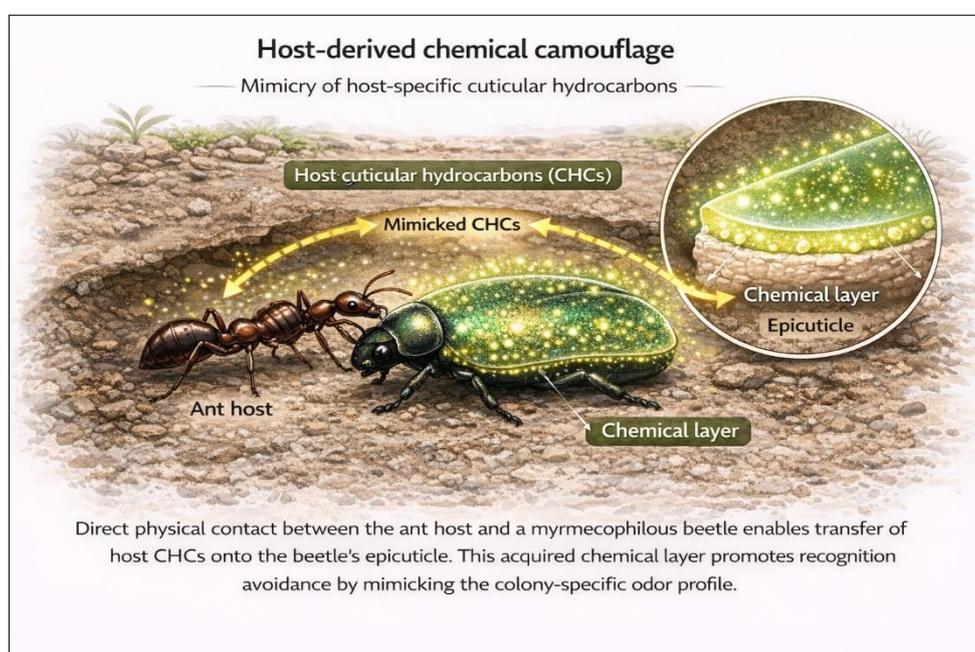


Figure 1: Host-derived chemical camouflage. Direct physical contact between the ant host and the myrmecophilous beetle enables the transfer of host Cuticular Hydrocarbons (CHCs) onto the beetle's epicuticle. This acquired chemical layer promotes recognition avoidance by mimicking the colony-specific odor profile. As a result, the beetle achieves chemical camouflage that facilitates integration within the host social environment

Behavioral tolerance toward socially integrated beetles may depend on congruence between guest cuticular profiles and colony odor templates maintained by host workers. Acquisition of recognition cues during direct contact may influence acceptance thresholds toward foreign organisms. These processes may regulate access to brood chambers and food storage areas under socially constrained nest environments. Maintenance of transferred hydrocarbons may therefore influence the spatial persistence of beetles. Host–guest interactions may reflect chemical assimilation within colony systems (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; van Zweden and d’Ettorre, 2017; Hefetz, 2019).

Myrmecophilous beetles interacting with *Myrmica* and *Lasius* colonies may exploit grooming-mediated hydrocarbon transfer to stabilize chemical similarity with host recognition systems. Sustained acquisition of colony-specific cues may facilitate behavioral acceptance under ecological constraints imposed by nest environments. These mechanisms may influence tolerance toward socially integrated organisms across different ant species. Maintenance of chemical congruence may therefore regulate persistence inside host societies. Such processes may affect the ecological integration of beetles inside ant colonies (Helanterä *et al.*, 2016; Guillem *et al.*, 2017a; Hefetz, 2019; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

Host–parasite interactions in beetle–ant systems may also be influenced by spatial organization within nest environments. Guest organisms occupying zones of high worker density may maintain frequent physical contact that facilitates the transfer of recognition cues. This mechanism may promote chemical similarity between beetles and host colonies

under socially regulated conditions. Maintenance of host-derived hydrocarbons may therefore regulate tolerance toward socially integrated guests. Persistence inside nests may depend on the stability of transferred compounds (Figure 2) (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; van Zweden and d’Ettorre, 2017; Guillem *et al.*, 2017a).

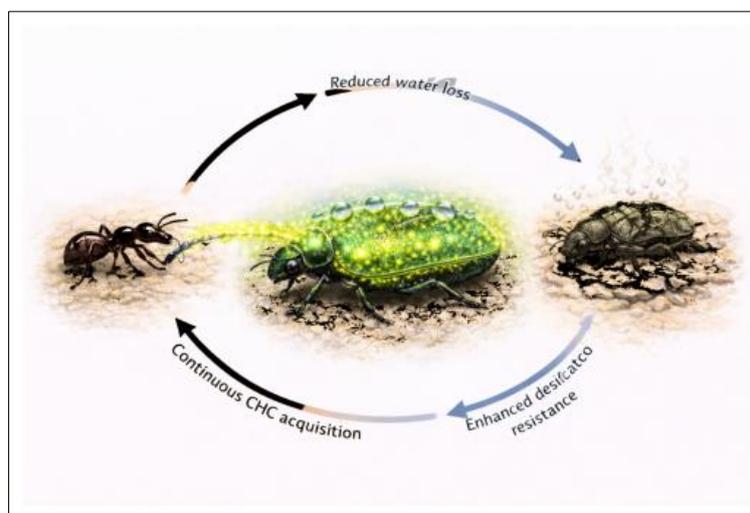


Figure 2: Acquisition of host-derived Cuticular Hydrocarbons (CHCs) results in the formation of a protective CHC layer on the beetle epicuticle. This acquired chemical barrier reduces trans cuticular water loss and enhances resistance to desiccation in the nest environment. Consequently, beetle physiological stability becomes directly dependent on continuous CHC acquisition from the ant host

Ecological persistence of beetle guests inside ant colonies may be associated with variation in colony humidity gradients across different nest environments. Transfer of cuticular hydrocarbons may influence physiological performance under desiccation risk in subterranean chambers. In colonies of *Atta* and *Formica*, guest organisms may exploit host contact to maintain chemical similarity under socially regulated conditions. Maintenance of transferred compounds may therefore regulate the survival of beetles inside host nests. Such processes may reflect host-mediated integration mechanisms (Gibbs, 2016; Martin *et al.*, 2016; Hefetz, 2019; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

Behavioral interactions between beetles and host workers may influence tolerance toward socially integrated organisms across different ant genera. Grooming-mediated transfer of hydrocarbons can facilitate access to restricted nest zones under socially regulated conditions. Maintenance of recognition cues may therefore regulate the ecological persistence of beetles inside protected environments. These mechanisms may influence the spatial distribution of guest organisms within colony systems. Persistence inside nests may depend on the stability of transferred chemical profiles (Helanterä *et al.*, 2016; Leonhardt *et al.*, 2016; Guillem *et al.*, 2017b; Hefetz, 2019).

Host-dependent chemical integration may also involve the reduction or suppression of endogenous cuticular hydrocarbon biosynthesis in socially integrated guest organisms. By acquiring host-derived CHCs through repeated physical contact, myrmecophilous beetles may approximate the colony-specific chemical profile and thereby avoid recognition by nestmate workers. This strategy may enhance tolerance toward guest organisms and facilitate their persistence within socially regulated nest environments. Such mechanisms suggest that host-derived chemical identity may play a central role in mediating long-term ecological integration within ant colonies (von Beeren *et al.*, 2011; Nehring *et al.*, 2017).

Social integration of beetles into ant colonies may also be influenced by temporal variation in worker activity cycles. Guest organisms interacting with host workers during brood care or foraging periods may acquire recognition cues through direct contact. These interactions may facilitate chemical similarity between socially integrated guests and colony members. Maintenance of transferred hydrocarbons may therefore regulate behavioral tolerance toward foreign organisms. Persistence inside nest environments may depend on the frequency of host interactions (Buschinger, 2016; Martin *et al.*, 2016; Guillem *et al.*, 2017a; Fouks and d’Ettorre, 2020a).

Host colony organization may influence the ecological integration of socially integrated beetles across different nest environments. Transfer of hydrocarbons during grooming interactions may regulate acceptance thresholds toward guest organisms. Maintenance of host-derived compounds may therefore influence tolerance under socially constrained

conditions. These mechanisms may regulate the persistence of beetles inside protected nest zones. Host-guest interactions may reflect chemical assimilation within colony environments (Figure 3) (Leonhardt *et al.*, 2016; van Zweden and d'Ettorre, 2017; Hefetz, 2019; Fouks and d'Ettorre, 2020b).

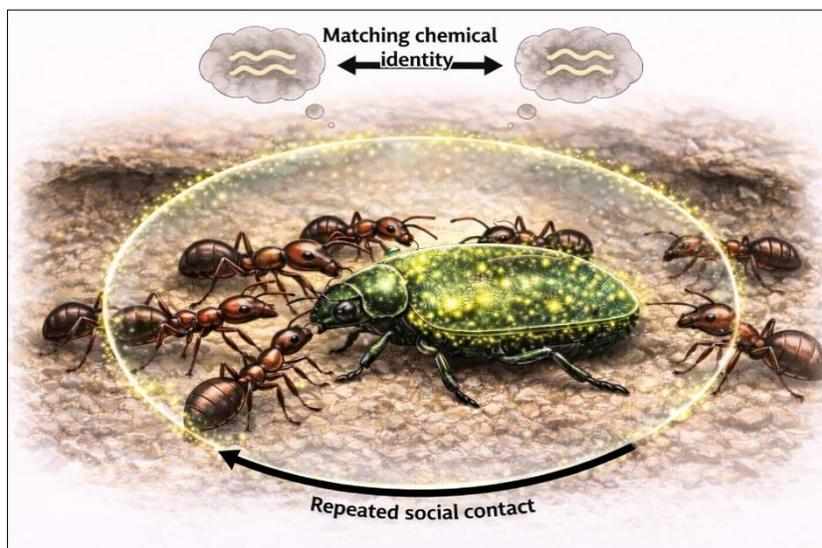


Figure 3: Stabilized host-dependent chemical identity. The beetle acquires and maintains the host colony-specific CHC profile through repeated social contact. This process stabilizes its chemical identity by matching the host recognition cues. As a result, the beetle achieves long-term integration within the ant colony

Host-symbiont interactions within ant societies may range from unspecific associations to highly specialized relationships involving behavioral, morphological, and chemical integration mechanisms. Comparative analyses of army ant-associated rove beetles have shown that socially integrated specialist species often exhibit high similarity in CHC composition and concentration to those of their host ants. In contrast, generalist guest species tend to display lower levels of chemical resemblance. Such differences in host-specific chemical matching may influence the degree of social acceptance and physical interaction with nestmate workers. The interplay between behavioral strategies and CHC-mediated recognition cues, therefore, suggests that accurate host mimicry may represent a key adaptation facilitating integration within socially structured nest environments (Nehring *et al.*, 2017; von Beeren *et al.*, 2018; Perez-Lachaud *et al.*, 2019).

Empirical evidence indicates that socially integrated myrmecophilous beetles may dynamically adjust their cuticular hydrocarbon profiles to match those of their host colonies. Acquiring host-derived CHCs through repeated physical contact may enable guest organisms to approximate the colony-specific chemical signature and thereby reduce aggressive responses from nestmate workers. Such chemical matching may facilitate long-term persistence within socially regulated nest environments and contribute to ecological integration within host societies. Maintenance of this

acquired chemical similarity may therefore represent a key mechanism underlying host tolerance toward socially integrated beetles (Leonhardt *et al.*, 2017; Nehring *et al.*, 2017; Perez-Lachaud *et al.*, 2017; Kuo *et al.*, 2020).

Myrmecophilous beetles belonging to the family Staphylinidae frequently exhibit morphological and chemical adaptations that facilitate their integration within ant colonies. Such adaptations may include behavioral interactions and the acquisition of host-derived cuticular hydrocarbons, which enable guest organisms to approximate the colony-specific chemical profile. Chemical similarity achieved through socially mediated CHC transfer may reduce host aggression and promote tolerance toward socially integrated organisms. These mechanisms may contribute to the persistence of guest species within protected nest environments and support long-term ecological integration within ant societies (von Beeren *et al.*, 2012; Nehring *et al.*, 2016; Guillem *et al.*, 2017b).

Behavioral tolerance toward socially integrated beetles may depend on the stability of transferred recognition cues across different colony environments. Guest organisms interacting with *Camponotus* and *Lasius* workers may maintain chemical similarity through grooming-mediated hydrocarbon acquisition. These interactions may facilitate persistence inside socially regulated nest zones. Maintenance of transferred

compounds may therefore regulate the survival of beetles under ecological constraints. Host-mediated chemical similarity may influence the ecological stability of guest organisms (Helanterä *et al.*, 2016; Martin *et al.*, 2016; Guillem *et al.*, 2017a; Hefetz, 2019).

Spatial persistence of beetles inside ant colonies may be influenced by microhabitat occupation across brood chambers and foraging tunnels. Transfer of recognition cues during routine host interactions may

facilitate acceptance of socially integrated organisms. Maintenance of host-derived hydrocarbons may therefore regulate tolerance under colony conditions. These mechanisms may influence the ecological integration of beetles across different ant species. Persistence inside nest environments may depend on chemical similarity with host workers (Figure 4) (Leonhardt *et al.*, 2016; Martin *et al.*, 2016; Fouks and d’Ettorre, 2020a; Fouks and d’Ettorre, 2020b).

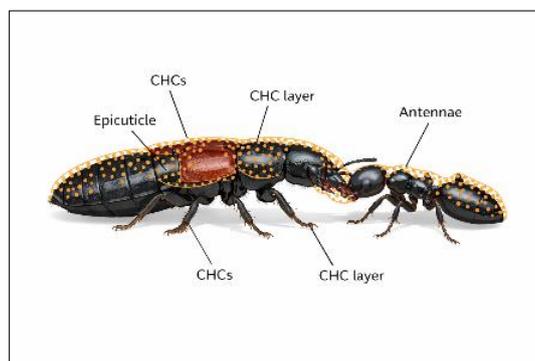


Figure 4: Maintenance of transferred host-derived hydrocarbons contributes to beetle physiological stability under desiccation risk within subterranean nest chambers. Grooming-mediated acquisition of CHCs promotes tolerance toward socially integrated guest organisms. Sustained chemical similarity facilitates persistence of beetles within protected nest environments

Physiological stability of beetles occupying subterranean nest chambers may be associated with the maintenance of transferred hydrocarbons under desiccation risk. Grooming-mediated acquisition of host-derived compounds may influence tolerance toward guest organisms under socially regulated conditions. These interactions may facilitate the persistence of socially integrated beetles inside protected nest environments. Maintenance of chemical similarity may therefore regulate the survival of guest organisms. Host–guest interactions may reflect ecological integration mechanisms (Helanterä *et al.*, 2016; Gibbs, 2016; Martin *et al.*, 2016; Hefetz, 2019).

Maintenance of transferred hydrocarbons under desiccation risk may contribute to the physiological stability of beetles inhabiting subterranean nest chambers. Such host–guest interactions may facilitate the persistence of socially integrated organisms inside protected nest microhabitats. Repeated acquisition of colony-specific CHCs may stabilize the chemical identity of guest organisms over time. Consequently, socially mediated chemical integration may represent a key ecological mechanism underlying the survival of myrmecophilous beetles within ant societies (Figure 5) (Guillem *et al.*, 2017a; Wagner *et al.*, 2017; Hefetz, 2019; Fouks and d’Ettorre, 2020a).



Figure 5: Direct physical contact between ants and myrmecophilous beetles enables the transfer of host Cuticular Hydrocarbons (CHCs) onto the beetle epicuticle. Such socially mediated interactions may facilitate chemical matching with the host colony profile. This process promotes tolerance and persistence within socially regulated nest environments

Closely interacting myrmecophilous beetles and their ant hosts may also share microbial symbionts through repeated physical contact within socially structured nest environments. Comparative analyses have shown that socially integrated guest species frequently harbor bacterial communities dominated by taxa such as *Rickettsia* Rocha-Lima, 1916 (Rickettsiales: Rickettsiaceae), *Rickettsiella* Philip, 1956 (Legionellales: Coxiellaceae), and *Weissella* Collins *et al.* 1994 (Lactobacillales: Lactobacillaceae), *Wolbachia* Hertig 1936 (Approved Lists 1980) (Rickettsiales:

Ehrlichiiaceae), which may also occur in ant larvae and workers. The occurrence of identical bacterial genotypes across phylogenetically distinct host species suggests that microbial transmission may occur between socially integrated organisms inhabiting the same nest environment. Such microbial overlap may reflect ecological integration mechanisms associated with close interspecific interactions and host-guest tolerance (Figure 6) (Lenoir *et al.*, 2017; Schmid-Hempel, 2017; Valdivia *et al.*, 2023).

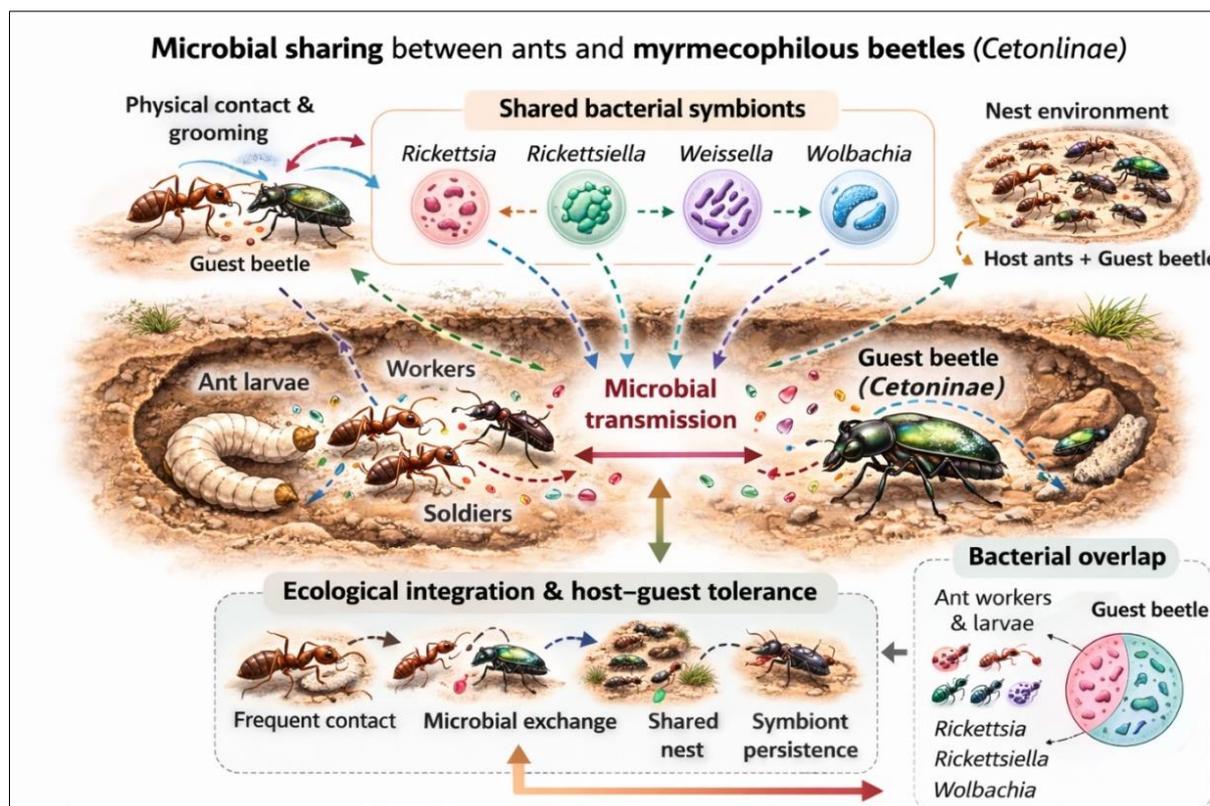


Figure 6: Microbial overlap between myrmecophilous beetles and their ant hosts. Schematic representation of shared bacterial symbionts between socially integrated beetles and host ants within nest environments. Microbial transmission through physical contact may contribute to ecological integration and host-guest tolerance

Beetles belonging to the subfamily Cetoniinae (Coleoptera: Scarabaeidae) have also been reported to occupy the nests of social insects, where they may exploit sheltered microhabitats and available nutritional resources throughout both larval and adult stages. Although cohabitation between Cetoniine beetles and ant hosts has been documented in multiple systems, the ecological and physiological mechanisms underlying these associations remain poorly understood. Occupation of ant nest environments may lead to distinct interaction

outcomes, including antagonistic effects resulting in host colony mortality, guest mortality, or stable coexistence between host and guest organisms. Such variability in interaction dynamics suggests that nest integration in ant-beetle systems may involve context-dependent ecological and chemical mechanisms that regulate long-term persistence within socially structured environments (Figure 7) (Parmentier *et al.*, 2016; Rodrigues and Puker, 2019).

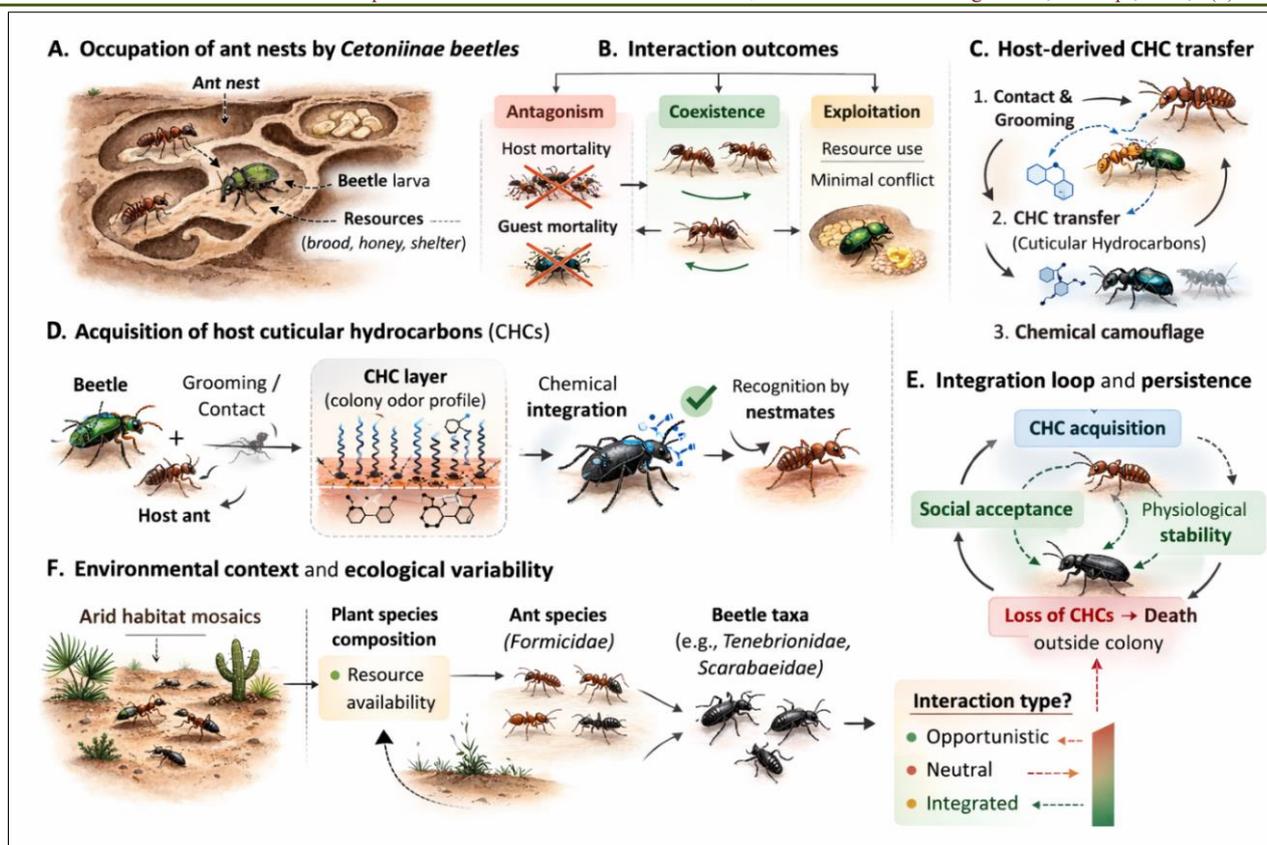


Figure 7: Schematic representation of Cetoniinae beetle larvae inhabiting ant nest chambers and exploiting sheltered microhabitats and available nutritional resources such as brood and stored organic material. Nest occupation may result in different ecological outcomes, ranging from antagonistic interactions to stable coexistence between host ants and guest beetles

Beyond immediate recognition avoidance, the acquisition and maintenance of host-derived hydrocarbons may also confer ecological advantages related to long-term persistence within socially structured nest environments. Myrmecophilous beetles may exploit host colony chemical cues through the acquisition of CHCs via direct physical contact and socially mediated interactions such as grooming. This process enables guest organisms to approximate the colony-specific odor profile and thereby reduce detection by nestmate workers. Chemical similarity resulting from host-derived CHC transfer may influence tolerance thresholds within socially regulated nest environments (Helanterä *et al.*, 2016; Guillem *et al.*, 2017b; Hefetz, 2019).

Chemical acquisition of host-derived cuticular hydrocarbons may impose a functional constraint on socially integrated beetles by linking nestmate recognition to desiccation resistance under colony conditions. In certain myrmecophilous systems, suppression of endogenous hydrocarbon biosynthesis may require continuous grooming interactions with host workers to maintain chemical congruence and

physiological stability. This dependency may generate a host-mediated integration loop in which survival outside the colony becomes constrained by loss of transferred compounds. Such mechanisms may reflect stabilization of social parasitism through chemically enforced reliance on host-derived recognition cues (Martin *et al.*, 2016; Wagner *et al.*, 2017; Hefetz, 2019; Fouks and d’Ettorre, 2020b).

Chemical integration mechanisms observed in beetle–ant associations may ultimately influence the ecological persistence of socially integrated guests across multiple Formicidae systems. Acquisition of host-derived hydrocarbons may regulate behavioral acceptance under socially constrained nest environments. Maintenance of transferred recognition cues may therefore facilitate stable integration inside host colonies. These processes may influence the survival of guest organisms interacting with different ant species. Such interactions may reflect adaptive strategies for persistence within eusocial environments (Figure 8) (Helanterä *et al.*, 2016; Leonhardt *et al.*, 2016; Martin *et al.*, 2016; Hefetz, 2019).

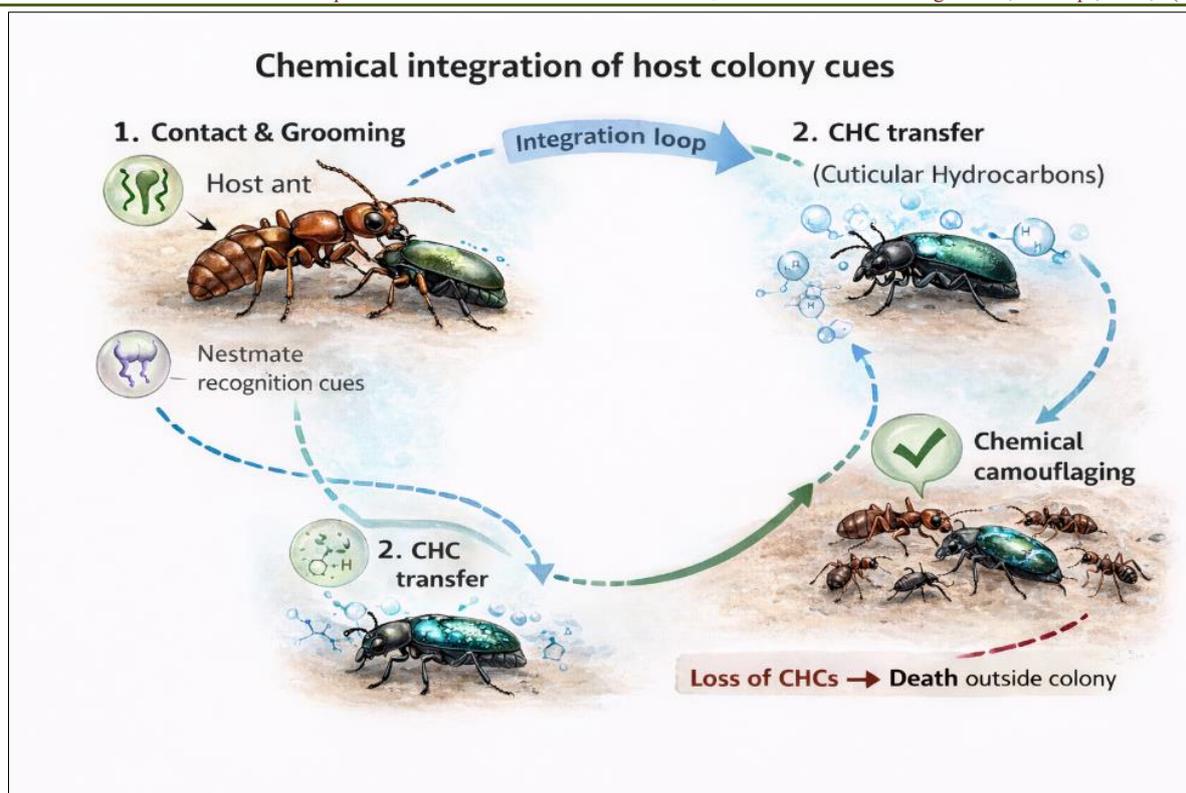


Figure 8: Chemical integration of Cetoniinae beetle larvae within ant colonies. Acquisition of host-derived Cuticular Hydrocarbons (CHCs) through contact and grooming with worker ants. Chemical transfer reduces nestmate detection and facilitates larval persistence within host colonies

Ant-beetle associations in myrmecophilous Coleoptera may represent a continuum of ecological interactions rather than discrete symbiotic categories. Recent conceptual frameworks suggest that guest species occupying ant nest environments may exhibit varying degrees of integration, ranging from opportunistic nest cohabitation to highly specialized host-dependent relationships. These associations may involve behavioral, chemical, or physiological adaptations that facilitate persistence within socially structured nest environments. Such variability in integration strategies highlights the importance of considering myrmecophily as a dynamic ecological process shaped by host specificity, environmental context, and interspecific interactions (Parmentier *et al.*, 2017; Perez-Lachaud *et al.*, 2019; Parker *et al.*, 2020).

Associations between ants and beetles are not restricted to classical myrmecophilous lineages such as Staphylinidae and Scarabaeidae but may also occur in ecologically co-occurring taxa such as Tenebrionidae inhabiting arid environments. Differences in vegetation structure and abiotic conditions may influence the spatial distribution and community composition of both ants and darkling beetles across heterogeneous landscapes. Variability in resource availability associated with distinct plant assemblages may affect the distribution patterns of these taxa and potentially facilitate indirect ecological interactions within shared habitats. Such patterns suggest that ant-beetle associations may also emerge through environmentally mediated mechanisms in systems where direct social integration has not been established (Figure 9) (Flores and Carrara, 2013; Scharf and Martin, 2018).

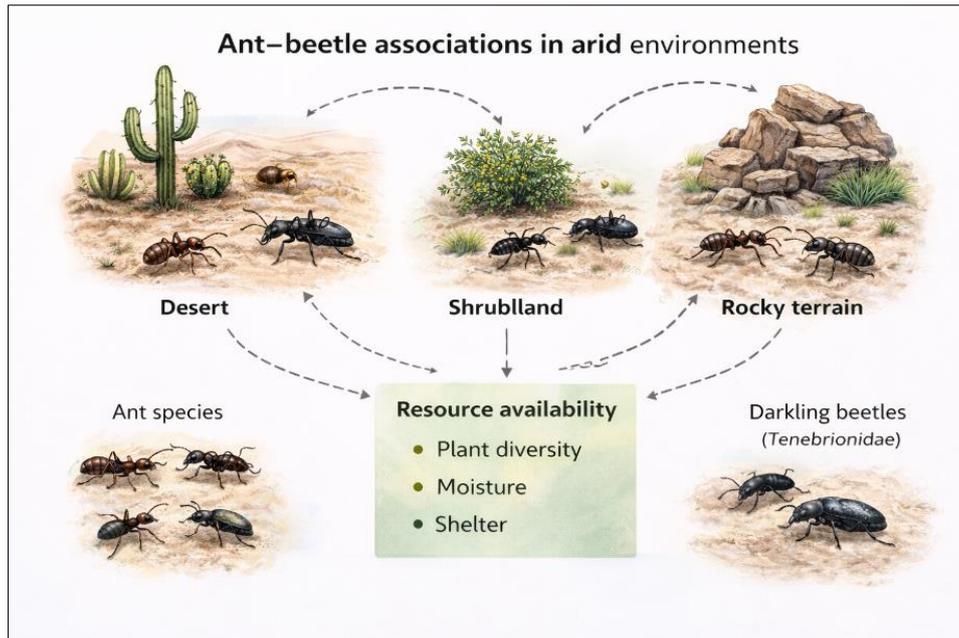


Figure 9: Environmentally mediated ant-beetle associations in arid ecosystems. Schematic representation of co-occurrence between ants and Tenebrionidae beetles across heterogeneous habitats influenced by vegetation structure and abiotic conditions. Variation in resource availability may facilitate indirect ecological interactions in the absence of direct social integration

Taken together, these findings suggest that ant-beetle associations may arise through multiple integration pathways, ranging from socially mediated chemical mimicry in highly specialized myrmecophiles to environmentally structured co-occurrence in ecologically associated taxa. Such variability indicates that host-guest interactions in ant societies may reflect a dynamic continuum of integration shaped by behavioral,

chemical, microbial, and environmental factors. Understanding this spectrum of interaction strategies may therefore provide a broader ecological framework for interpreting the persistence and evolution of ant-associated beetle lineages across diverse habitats (Figure 10) (Parmentier *et al.*, 2017; Akino, 2019; Perez-Lachaud *et al.*, 2019).

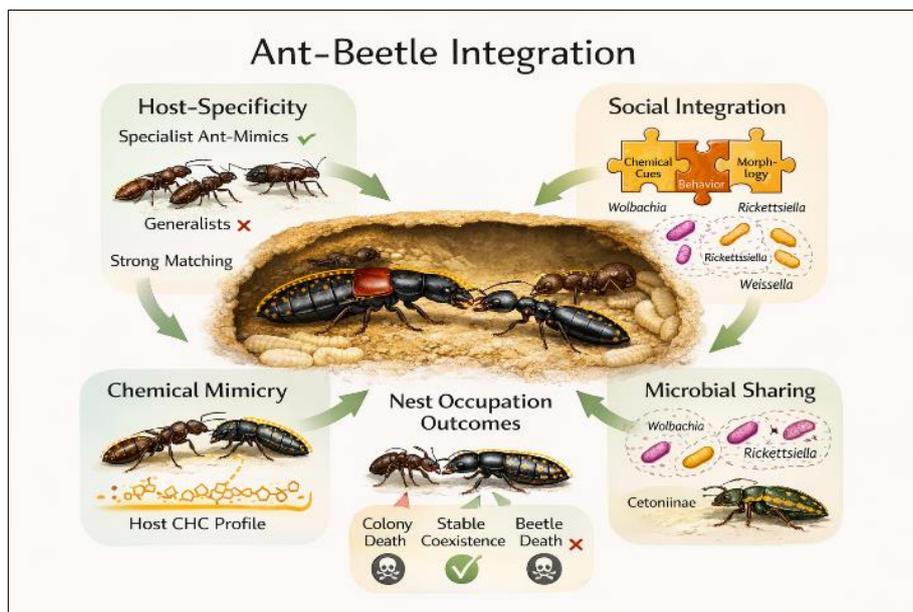


Figure 10: Behavioral, morphological, and chemical integration mechanisms may determine the degree of host specificity in myrmecophilous beetles. Specialist species often achieve accurate CHC matching with host ants, facilitating social acceptance within nest environments. In contrast, generalists display lower chemical resemblance and reduced levels of social integration

5.0. CONCLUSION

Chemical integration mechanisms in beetle–ant associations may regulate behavioral tolerance and ecological persistence of socially integrated guests inside eusocial colonies. Acquisition of host-derived cuticular hydrocarbons through grooming interactions can influence nestmate recognition and access to protected nest environments across multiple Formicidae systems. Maintenance of transferred chemical profiles may contribute to physiological stability under desiccation constraints imposed by social integration. These interactions may facilitate persistence of myrmecophilous beetles inside colony microhabitats regulated by host contact frequency and spatial organization. Understanding these mechanisms provides insight into biological and ecological processes underlying chemical camouflage in socially integrated arthropods interacting with different ant species.

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