Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 725237, 11 pages
doi:10.1155/2012/725237

Review Article

Myrmica Ants and Their Butterfly Parasites with Special Focus on the Acoustic Communication

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Received 30 September 2011; Accepted 18 December 2011

Academic Editor: Jean Paul Lachaud

About 10,000 arthropod species live as ants' social parasites and have evolved a number of mechanisms allowing them to penetrate and survive inside the ant nests. *Myrmica* colonies, in particular, are exploited by numerous social parasites, and the presence of their overwintering brood, as well as of their polygyny, contributes to make them more vulnerable to infestation. Butterflies of the genus *Maculinea* are among the most investigated *Myrmica* inquilines. These lycaenids are known for their very complex biological cycles. *Maculinea* species are obligated parasites that depend on a particular food plant and on a specific *Myrmica* species for their survival. *Maculinea* larvae are adopted by *Myrmica* ants, which are induced to take them into their nests by chemical mimicry. Then the parasite spends the following 11–23 months inside the ants' nest. Mimicking the acoustic emission of the queen ants, *Maculinea* parasites not only manage to become integrated, but attain highest rank within the colony. Here we review the biology of *Maculinea/Myrmica* system with a special focus on some recent breakthrough concerning their acoustical patterns.

1. Butterflies and Ants

Most myrmecophiles are commensals or mutualists, which live undisturbed or even actively protected within the foraging areas or territories of ants [1–3]. Their functional and evolutionary ecology, as well as their truly amazing diversity, have been reviewed by Wasmann [4], Donisthorpe [5], Hinton [6], Malicky [7], Hölldobler and Wilson [1], DeVries [8, 9], Fiedler [10, 11], Pierce et al. [12], and others.

The interactions that have evolved between insects and ants range from loose facultative associations to obligate dependency (as concerns butterflies, see [3, 11, 13, 14]). The nests of eu-social arthropods, including insects such as ants, bees, wasps, or termites, are aggressively defended from predators and intruders alike. As a consequence, these nests provide very safe havens for any roughly ant-sized organism having evolved the necessary adaptations to penetrate them and to become accepted as "self" by the workers' caste [4, 5, 15]. Around 10,000–15,000 insect morphospecies have evolved as social parasites of ants, thus accounting for a significant proportion of the world's biodiversity. Yet, despite the many species, most ant social parasites are exceedingly rare or localized, in comparison to the abundance and distribution not only of their ant hosts but also of other symbionts, which loosely interact with ants [1, 16, 17].

Myrmecophily is widespread among Lepidoptera, most particularly as concerns the Riodinidae and Lycaenidae [9, 12], which are often globally referred to as "lycaenoids" [10], and which make up approximately 30% of all known Papilionoidea [18]. Their relationships with ants can be mutualistic or parasitic and vary from facultative to strictly obligate. In the case of facultative myrmecophiles, the survival of butterfly larvae does not depend on the presence of attendant ants, and associations are unspecific. In other words, these lycaenoids can use ants belonging to several different species, or even subfamilies [11, 12]. On the contrary, in obligate ant associations, butterfly immatures are dependent on ants' presence, at least in some part of their life cycle and interactions are much more species specific [11, 12].

Achieving a myrmecophilous life style requires evolving numerous special adaptations, which are necessary for avoiding ant aggression and for communicating with ants. The cuticle of many myrmecophilous butterfly larvae is thicker than in other groups of Papilionoidea and the head can be retracted under a sclerotized plate [7, 19]. Frohawk [20] was the first to observe that most myrmecophilous butterfly

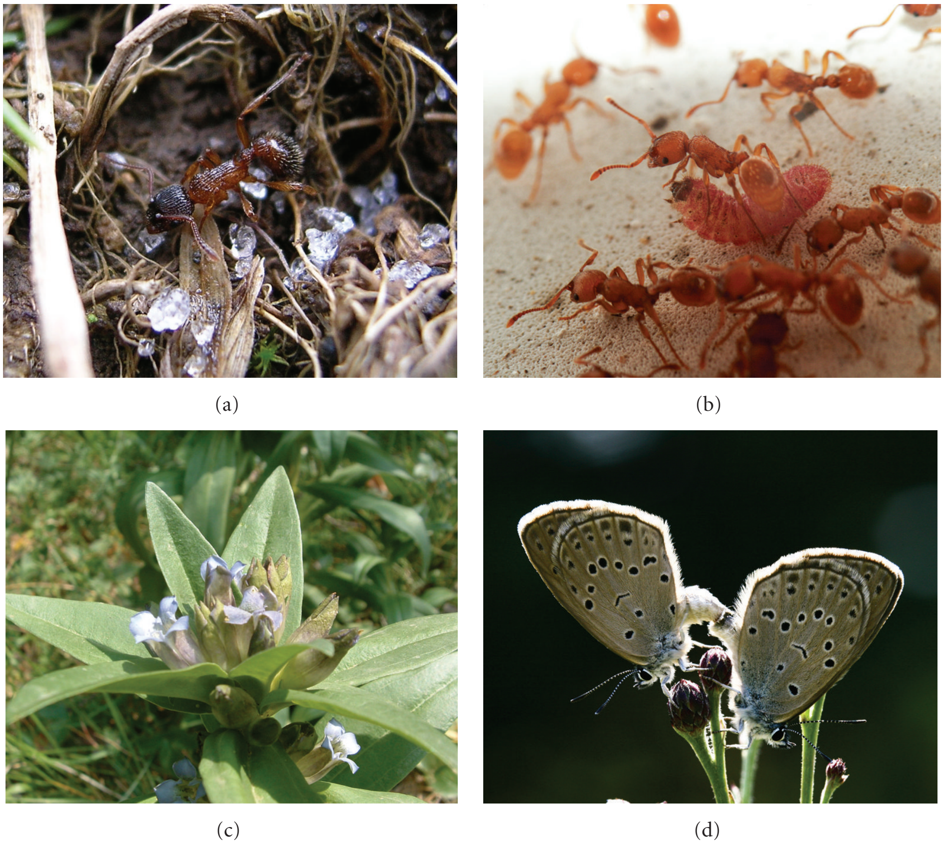

Figure 1: (a) Forager worker of *Myrmica* ant. (b) Trophallaxis between attendance worker and *Maculinea* larva. (c) *Maculinea rebeli* foodplant: *Gentiana cruciata*. (d) Mating of *Maculinea* butterflies.

larvae have dorsal nectar organs (DNOs), whose "honeydew" secretion attracts and pacifies ants, and plays an essential role in the maintenance of ant attendance [12]. Additionally, many lycaenoid caterpillars possess specialized epidermal glands, pore-cupola organs and tentacle organs, whose secretions are apparently not directly used by ants, but can somehow manipulate their behaviour [21–23]. Moreover, some butterfly species produce cohorts of other chemical and/or acoustical signals, which are involved in their interactions with ants [12].

2. The Parasites: *Maculinea* Butterflies

One of the most intensively studied systems in which both the communication channels are investigated concerns parasitic *Maculinea* butterfly larvae and their *Myrmica* host ants (Figures 1(a) and 1(b)) [24–26]. During the past decades butterflies of genus *Maculinea* (Figure 1(d)) have become "flagships" of European biodiversity conservation [24] and are perceived as umbrella species covering many grassland communities [27–29].

Some recent publications [30–32], based on both molecular and morphological data, have shown that species of *Maculinea* and *Phengaris* form a monophyletic group, where the three Chinese *Phengaris* species are basal. According to Fric et al. [32] *Maculinea* Van Eecke, 1915 should be considered a junior subjective synonym of *Phengaris* Doherty, 1891. Possible alternatives are that *Maculinea* is, as subjectively, considered subgenus of *Phengaris*, or a distinct genus in its own right.

On the other end the obligate myrmecophilous life style of *Maculinea* has attracted a vast number of studies, many of which appeared in leading scientific journals. *Maculinea* is a model organism for studies on the origin and evolution of parasitic interactions and of host-parasite communication channels [11, 24–26, 30, 33].

Maculinea have also attracted a great deal of attention from a conservationist's point of view [34–37]. For this reason some of the authors have asked the International Commission on Zoological Nomenclature to conserve the name *Maculinea* against *Phengaris* in all cases when the two are considered subjective synonyms. The decision by the ICZN is still pending and we will continue to use *Maculinea* rather than *Phengaris*, at least for the moment.

Another point is that no molecular evidence is available to distinguish *Maculinea rebeli* from *Maculinea alcon* and some authors have argued that the first of them is an ecotype of *M. alcon* [32]. Also in this case we have decided to stick to the traditional interpretation that *M. alcon* and *M. rebeli* represent separate clades (species) and in this paper we will use the name *Maculinea rebeli* to designate what might represent the xerophilous ecotype of *M. alcon*.

European *Maculinea* species need urgent conservation actions, indeed four are mentioned in the European Red List of Butterflies and three of them are included in the Annex IV of the Habitats Directive [38, 39]. These lycaenids are known for their very complex biological cycles. *Maculinea* species are all obligated parasites that depend on a particular food plant and on a specific *Myrmica* species for their survival. After having spent 10–15 days feeding on a species-specific host plant (Figure 1(c)), the 4th instar larvae of all *Maculinea* species drop to the ground and wait until they are found and carried into an ant nest by a *Myrmica* worker [40–44]. Once in the ant colony, *Maculinea* species differ in their alimentary strategy: (i) *Maculinea alcon* and *Maculinea rebeli* utilize a "cuckoo" strategy, and are mostly fed directly by attending workers (trophallaxis) [42] (Figures 1(a) and 1(b)), they are known for experiencing "contest" competition at high densities [45], (ii) *Maculinea arion* and *Maculinea teleius* are "predatory species" and directly prey on ant brood, experiencing "scramble" competition when overcrowded in the host colony [46], while (iii) the alimentary strategy of *Maculinea nausithous* has not yet been fully clarified, with some authors suggesting the coexistence of both "cuckoo" and "predatory" strategy and others considering it as a "cuckoo" species [24, 47]. *Maculinea* larvae spend 11 or 23 months inside their host colonies. In many populations two separate cohorts of larvae spending either one or two years inside the ants' nest are known to exist [33, 48–50]. The polymorphic growth pattern found in *Maculinea* populations is likely to have evolved for ergonomic, or perhaps hedge-betting reasons.

Two are the key moments in the life cycle of these butterflies: (i) the choice of an optimal food-plant on which to lay eggs and (ii) the first direct interaction with the host ants. The place where females lay their eggs is crucial for a myrmecophilous butterfly, to ensure its brood the chance to be adopted by a specific host ant. Because the worker ants' foraging range is limited, selecting an "ideal" oviposition site requires that both the phenological stage of the larval food plant (short-term larval fitness) and the presence of suitable host ants (long-term larval fitness) are taken into account. The female's selection of a valuable oviposition plant is influenced by a variety of factors. Plants are generally selected by females on the basis of their buds' phenology, while the presence of the host ants in the near surroundings of the plant may be variously insured depending on local situations and perhaps on the species. In some cases the host-plant and the *Myrmica* ant share a similar ecological niche, so that their overlap ensures population persistence [51–54]. In other cases, however, female butterflies mostly choose those plants which occur in the ants' foraging range [55–59]. To the best of the authors' knowledge, nothing is known about the mechanism providing butterfly females with the ability to discriminate among host plants placed inside/outside the foraging range of a *Myrmica* colony.

The other hot point of research on *Maculinea* butterflies is their host specificity with ants, both for its relevance in coevolutionary dynamics and as a background for conservation strategies. While *Maculinea* caterpillars induce workers of any *Myrmica* species to retrieve them by chemical and acoustical deception [26, 60], their survival till the adult stage will depend largely on which ant-species has found the larva [41–44, 61].

Before the 1970s a nonextensive study of *Maculinea* host specificity led scientists to consider all *Myrmica* species and, in some cases other ant's genera (e.g., *Lasius*), as potential host of these butterflies. In the following decades Thomas et al. [61] revealed a clear host specificity pattern involving each of the five European *Maculinea* species. In their work authors demonstrated that the survival of every *Maculinea* species was linked to single and different *Myrmica* ant species, while the adoption by a non-host species caused a large decrease in the survival rate of these butterflies. More recently, the large amount of data collected by many researchers all across Europe, confirmed these general guidelines, but demonstrated that host specificity patterns are much more complex and hosts may vary geographically all along the range of each *Maculinea* butterfly. The only species that apparently keeps a single host is *M. nausithous* [34, 62, 63], which shows a clear adaptation to *Myrmica rubra* all over its distribution [47, 61, 62, 64]. The only known exception to this occurs in Transylvania, where it exploits *M. scabrinodis* as alternative host [65]. Data on other *Maculinea* species show a much more complicated pattern, which demonstrates that host specificity occurs at the population or, at least, at the regional scale. Several works have shown that *M. teleius*, *M. arion*, *M. alcon*, and *M. rebeli* may be locally adapted to some *Myrmica* species previously considered as nonhost [29, 50, 64–72] and in the case of the latter two species have developed the ability to successfully exploit more than one host species in the same site creating real multiple host populations [25, 73].

3. The Host: *Myrmica* Ants

Myrmica ants are hosts of *Maculinea* butterflies, but their colonies are infested by numerous other social parasites such as the larvae of the hoverfly *Microdon myrmicae* (Diptera Syrphidae; see [74, 75]), or by parasitic ant species of the same genus [76]. Reasons for this apparent asymmetry are unclear, but may be related to the biological cycle of these ants. The genus *Myrmica* has a Holarctic distribution. Most of the species, however, are found in Europe and Asia, while a smaller proportion occurs in North America [77]. Colonies are widespread and can be found in various kinds of habitat, such as meadows, forests, steppes, or mountains [76]. Although the biology of many *Myrmica* species has not been studied in detail, it seems that a general life style is common to all ants of this genus [76]. Most colonies contain on average 200–500 workers, as well as from one to many functional queens [78, 79]. New nests can be either funded by a single newly mated queen or, more often, by budding pre-existing colonies [45]. Oviposition starts in early spring and lasts throughout the summer, while it stops in autumn when temperature is decreasing [76]. Part of the larvae develop rapidly but others enter diapause and overwinter. The latter

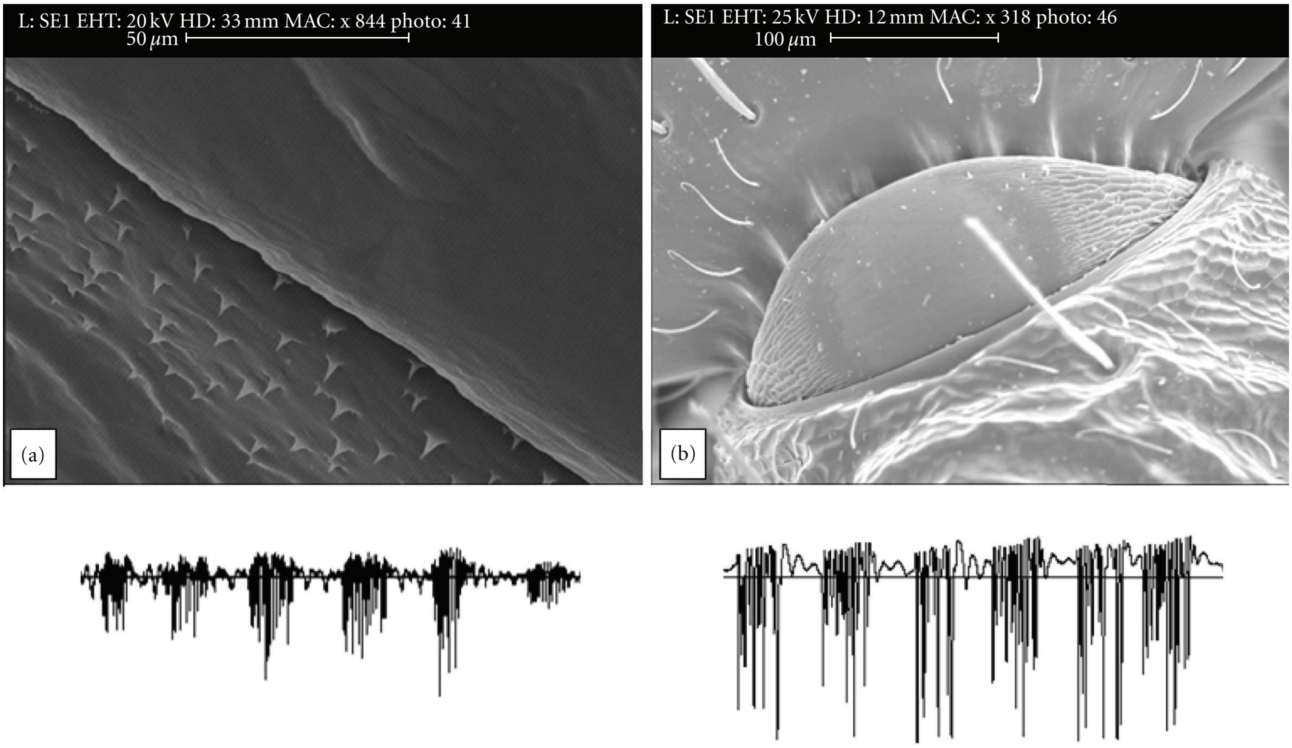

FIGURE 2: Morphology (upper part) and sounds (lower part) of the acoustical organs of (a) *Maculinea rebeli* pupa and (b) *Myrmica schencki* queen.

group includes both workers and all the gyne-potential larvae [80]. Some of these life history traits of *Myrmica* ants make them more vulnerable to infestations by social parasites. One of the most important is presence of overwintered ant larvae particularly essential for survival of the predatory *Maculinea* larvae, which start their intensive growth inside host colony at the beginning of spring and use overwintered ant brood as their food resource [49, 81]. Another significant trait that make *Myrmica* ants a proper host for many social parasites is that many *Myrmica* species live in polygynous colonies and some of them such as *M. rubra, M. ruginodis,* or *M. rugulosa* may contain a relatively high number of workers [76, 77]. This results in lower relatedness among worker nest mates [78, 82]. Many studies [83–85] showed that high genetic variance may be beneficial for social insects colonies, but it can also increase the likelihood of being infested by social parasites, because of the greater variance in nest mate recognition cues. It was indicated that *Microdon mutabilis* (Linnaeus, 1758) (Diptera: Syrphidae), a social parasite of *Formica lemani* ants, more often infests host colonies where genetic relatedness is lower [86]. A similar situation was found for colonies of *M. rubra* infested by *M. alcon* [87]. Therefore, a cost of polygyny existing in most of *Myrmica* species is that their colony communication signals (e.g., chemical or acoustical) tend to be broader and more heterogeneous than in monogynous ant species and their colonies can be more easily invaded by cheats that mimic these signals.

4. Acoustical Pattern in the *Maculinea-Myrmica* System

The more fine-tuned the host-parasite relationship is, the more intriguing studying how the host's deception can be achieved is. The communication of social insects is mainly based on chemical cues [1], but also the acoustic channel is used, thus it is clear that the parasite has to bypass the host's chemical and acoustical system to enter and live in its colonies [88].

Cuticular hydrocarbons have long been assumed to play a fundamental role in the nest mate recognition of social insects. All individuals living in the same society share a bouquet of chemicals, which serves as a "colony odour" and enables them to discriminate between nest mates and strangers. Additional variation in hydrocarbon pattern is associated with differences in sex, caste, and developmental stage [89, 90]. The fact that caterpillars of *Maculinea* butterflies use chemical mimicry to become adopted and to infiltrate colonies of their hosts was first proposed by Elmes et al. [42], while the first experimental evidence was produced by Akino et al. [43], who found that the chemical profile of *Maculinea rebeli* resembles that of its host more than those of other *Myrmica* species.

Even though sound production is not usually the dominant strategy, acoustic communication plays a fundamental role in some groups of insects [91]. Depending on the taxon, sound productions may have a number of functions, ranging from mate attraction to courtship, aggression, defence, or recruitment of foragers, at least in social insects. Recently, it has been suggested that sounds play a role in the modulation of other signals. This was demonstrated to occur at least in honey bees [92–96].

The role of stridulations in ant communication was underestimated for a long time [8, 26], also because of our scant understanding of the structures involved in the production and the reception of the acoustic signals. Stridulations, however, have long been known to occur in 4 ant subfamilies [97, 98]. In these ants, sounds are produced by a minutely ridged stridulating organ (pars stridens) positioned on the middle-dorsal part of the 4th "abdominal" segment and by a spike (plectrum) jutting from the postpetiole's rear margin [26, 99–103] (Figure 2(b)). When an ant moves its abdomen, the two parts rub on each other and emit a series of "chirps" [1, 103, 104]. Stridulations are variously defined depending on the transmitting medium. They are sounds, when transmitted by air, or vibrations, if transmitted by substrate. Myrmecologists have long believed that ants cannot "hear" the aerial component of a stridulation but perceive substrate-transmitted vibrations [105]. This notion was based on experience obtained in the early 20th century [106, 107], and has been indirectly confirmed ninety years later by the discovery of a subgenual organ in *Camponotus* ants [108]. More recently, however, a seminal paper by Hickling and Brown [105] provided fresh impulse to studies on the possible perception of air-transmitted sounds heating the debate on this subject [109, 110]. Hickling and Brown [105] maintain that ants cannot perceive the aerial component of sounds over a long distance (i.e., 1 m), but largely use short range acoustic communication (i.e., 1 cm).

Acoustic communication plays a wide range of roles in the ants' social behaviour, from reciprocal attraction to intercaste interactions. In most cases, these stimuli are effective only at small range and are mainly used as signals of alarm, for foragers' recruitment, mating requests, intimidation, and aposematic "threatening", as well as to modulate other kinds of signals [1, 92, 111–118].

Functions of stridulations have been intensively surveyed in *Atta* ants, where foragers' calls are most frequent when leaves of the highest quality for fungal cultures are found [119]. *Myrmica* workers frequently stridulate during trophallaxis, particularly the receiving worker, when food decreases [120, 121]. Intercaste acoustical communication has been recorded in only a few instances. Mating queens of *Pogonomyrmex badius* stridulate to signal to males when their spermathecae are full [111] whereas, in *Atta*, leaf-cutting workers stridulate when they are ready to return to the nest. This behaviour induces individuals of the smallest "minim" caste to climb onto the leaf fragment where from there they protect their larger sisters from attack by phorid flies during the journey home [117]. Until recently, there was no direct evidence that different members of an ant society produced distinctive caste-specific sounds to induce appropriate patterns of behaviour either in fellows or in other castes. At least two studies, however, suggested that different castes produce distinctive signals: the major workers of *Atta cephalotes* make sounds that are more intense and carry further than those of their smaller nest mates [122], while the space between the ridges of the pars stridens of queens exceeds that of workers in four *Messor* species [102].

Our own findings demonstrated that *Myrmica schencki* queens generate distinctive sounds that elicit increased benevolent responses from workers, thereby reinforcing their supreme social status [26, 123]. These findings demonstrated that acoustical communication within the vast subfamily Myrmicinae (to which *Messor* spp. and *Myrmica* spp. belong) is more variable and conveys more social information within ant colonies than was previously recognized. In this group, stridulations also fulfil the strict adaptationist definition of biological communication, in which both the signal and the response are adaptive [26, 124, 125].

Since acoustic signals convey quite complex information, not only between worker ants while outside the colony (e.g., during foraging), but also within the nest and between castes, we started research aimed at understanding whether some social parasites, such as butterfly larvae, could interfere with this communication system. Lycaenid larvae, in fact, have long been known to be able to emit stridulations even if their life cycle is not linked at any degree to the ant presence, but sounds produced by myrmecophilous species are more complex and frequent than those emitted by nonmyrmecophilous species [22]. More in general, however, studies aiming at clarifying the function of interspecific acoustic communication in myrmecophilous Lepidoptera are scarce. Most of these studies considered butterfly larva stridulations as a merely defensive signals [6, 126] or, more rarely, as aggregation messages [127]. Sounds produced by lycaenid pupae and caterpillars originate from different organs; the former from tooth-and-comb stridulatory organs between the fifth and sixth segments [12, 126, 128, 129] (Figure 2(a)), whereas caterpillar sounds may emanate from muscular contraction and air compression through the tracheae [130]. The acoustics of mutualistic lycaenid species does not obviously mimic ant stridulations, and ants attraction has been demonstrated only in the pupae of one extreme mutualist species (i.e., *Jalmenus evagoras* see [12, 131]. On the contrary, the larval calls of four *Maculinea* species are similar in pulse rate and band width to those of their hosts, although the level of apparent mimicry is to the genus *Myrmica* rather than to individual host ant species [132]. The same study showed that *Myrmica* larvae are mute, suggesting that in this trait *Maculinea* caterpillars are mimicking an adult ant cue, but no direct cause-and-effect relationship was revealed (recordings by DeVries et al. [132] were restricted to distressed worker ants and caterpillars, and were not played back to the ants). Studying the *Maculinea rebeli*/*Myrmica schencki* system, we recently demonstrated the first case of acoustical mimicry in an ant social parasite [26]. In particular we demonstrated that *Maculinea rebeli* larvae and pupae are able to mimic the sounds produced by *Myrmica schencki* queens (Figures 2(a) and 2(b)), thus obtaining a high status in the host colony hierarchy. Queens, that never come out of the nest, produce peculiar stridulations, which attract workers. Ethological experiments revealed that the acoustical signals produced by *Maculinea rebeli* larvae elicit the same benevolent responses in the worker ants as those emitted by their queen(s). When recordings of unstressed adult *M. schencki* were played back to laboratory cultures of workers, the sounds of both castes induced benign responses including aggregation and antennation at the speaker. Moreover, when workers were played their queen's sounds, they stood "on guard" on the speaker to a much greater extent than when worker sounds were played, each holding the characteristic posture adopted by a *Myrmica* worker when protecting an object of high value to the colony [26]. *Maculinea rebeli* caterpillars are rescued ahead of the ant brood when a colony is disturbed, and are fed in preference to host ant larvae when food is scarce [48]. Neither chemical mimicry nor their begging behaviour explains why *M. rebeli* caterpillars are treated in preference to host ant brood. Instead, we have suggested that acoustical cues are employed [26].

Thus it is possible that acoustical mimicry does not occur in *Maculinea rebeli* only, but rather provides another route for the infiltration of other *Maculinea* species, as well as for other myrmecophilous insects [26]. Acoustical mimicry can also be related to the level of interaction between host and parasite, or may play a role in host-specificity. In particular, in the *Maculinea/Myrmica* system the level of host's integration within the colony results from the two distinct parasites' foraging strategies. In the so-called "cuckoo" species, *Maculinea* larvae become perfectly integrated members of the colony, as they need to be tended by worker ants. Larvae of predator species, in contrast, will prey on the ants' brood and spend much of their life hidden in the remote chambers of the nest. DeVries et al. [132] showed that also the caterpillars of the predatory *Maculinea* species produce sounds that appear to mimic *Myrmica* (worker) stridulations, although in nature they are less closely integrated with their host's society [14], so that they might be less perfect acoustical mimics of their hosts. We tested [124] this hypothesis by comparing the acoustics of unstressed *Maculinea arion* caterpillars and pupae with those of the queens and workers of its host ant, *Myrmica sabuleti*, and with data obtained for *Maculinea rebeli* and *Myrmica schencki*, but found no evidence that *M. rebeli* is a closer mimic of *M. schencki* than *M. arion* is to *M. sabuleti* [26]. We also compared the worker and queen sounds of *M. sabuleti*, and those of two other ants, *Myrmica scabrinodis* and *M. schencki,* to determine whether the distinctive acoustical communication system occurring in the different castes of *M. schencki* exists in its congeners.

We found that stridulating queens from two additional *Myrmica* species (i.e., *M. sabuleti* and *M. scabrinodis*) make distinctive sounds from those of their workers by using morphologically distinct organs [124]. Interestingly, the calls produced by queen from the three *Myrmica* species were indistinguishable from each other, as were workers' stridulations even at a less extent. This suggests that acoustics plays little or no part in the cues used by *Myrmica* to distinguish between kin and nonkin, or other species of ant and members of their own society. Indeed numerous studies demonstrate the predominant role of chemical cues and the gestalt odour in colony recognition or between physiological states within an ant society [1]. However, our recent results suggest that acoustical communication, in isolation, is capable of signalling at least the caste and the status of a colony member, as well as of inducing appropriate behaviour towards it by the attending workers [124]. In other words, acoustical mimicry is genus rather than species specific, as DeVries et al. [132] concluded. We have not yet studied whether different castes of *Myrmica* ants responded differently when played the same sounds, although this seems probable, because *Myrmica schencki* queen respond aggressively when introduced to *Maculinea rebeli* pupae (which mimic queen sounds) whereas the workers tend them gently [26].

5. Concluding Remarks

To our knowledge, although 10,000 species of ant social parasites may exist [24] particularly among the Coleoptera, Diptera and Lepidoptera [1], acoustical mimicry has rarely been examined outside the case of *Maculinea*. Together with Di Giulio and his collaborators, we recently surveyed the acoustical emissions of *Paussus favieri* (Coleoptera, Paussinae), a myrmecophilous paussine beetle which lives in the nests of the ant *Pheidole pallidula* [133]. The presence of stridulatory organs in members of the myrmecophilous ground beetles tribe Paussini has long been known. However, due to the rarity of these beetles and the challenges in rearing them in captivity, sounds emitted by these organs have never been investigated, as well as their biological significance. The complexity of *P. favieri's* sound repertoire suggests that it has an important role in its interaction with *P. pallidula*.

We strongly believe that the implementation of studies on acoustic communication will bring about significant advances in our understanding of the complex mechanisms underlying the origin, evolution and stabilisation of host-parasite relationships. To improve our understanding of how important and how generalised acoustic mimicry is we also need to clarify which sensory structures are involved in sound perception processes, both in queen and worker ants. Nobody, so far, has ever investigated the possibility that the larvae and pupae of myrmecophilous lycaenids may perceive the sounds emitted by conspecifics, or by their host ants. In this respect it is worth noticing that some of the most important research on the role of filiform hairs in sound perception (e.g., [134, 135]) were carried out on *Barathra brassicae* (Lepidoptera: Noctuidae). The larvae of this moth, indeed, are able to detect the vibrations produced by a parasitoid wasp, by their thoracic hairs.

Acknowledgments

The authors would like to thank all the colleagues of the MacMan project. The research has been carried out within the project CLIMIT (Climate Change Impacts on Insects and Their Mitigation [37]) funded by DLR-BMBF (Germany), NERC and DEFRA (UK), ANR (France), Formas (Sweden), and Swedish EPA (Sweden) through the FP6 BiodivERsA Eranet as well as within the project A Multitaxa Approach to Study the Impact of Climate Change on the Biodiversity of Italian Ecosystems funded by the Italian Ministry of University and Research (MIUR).

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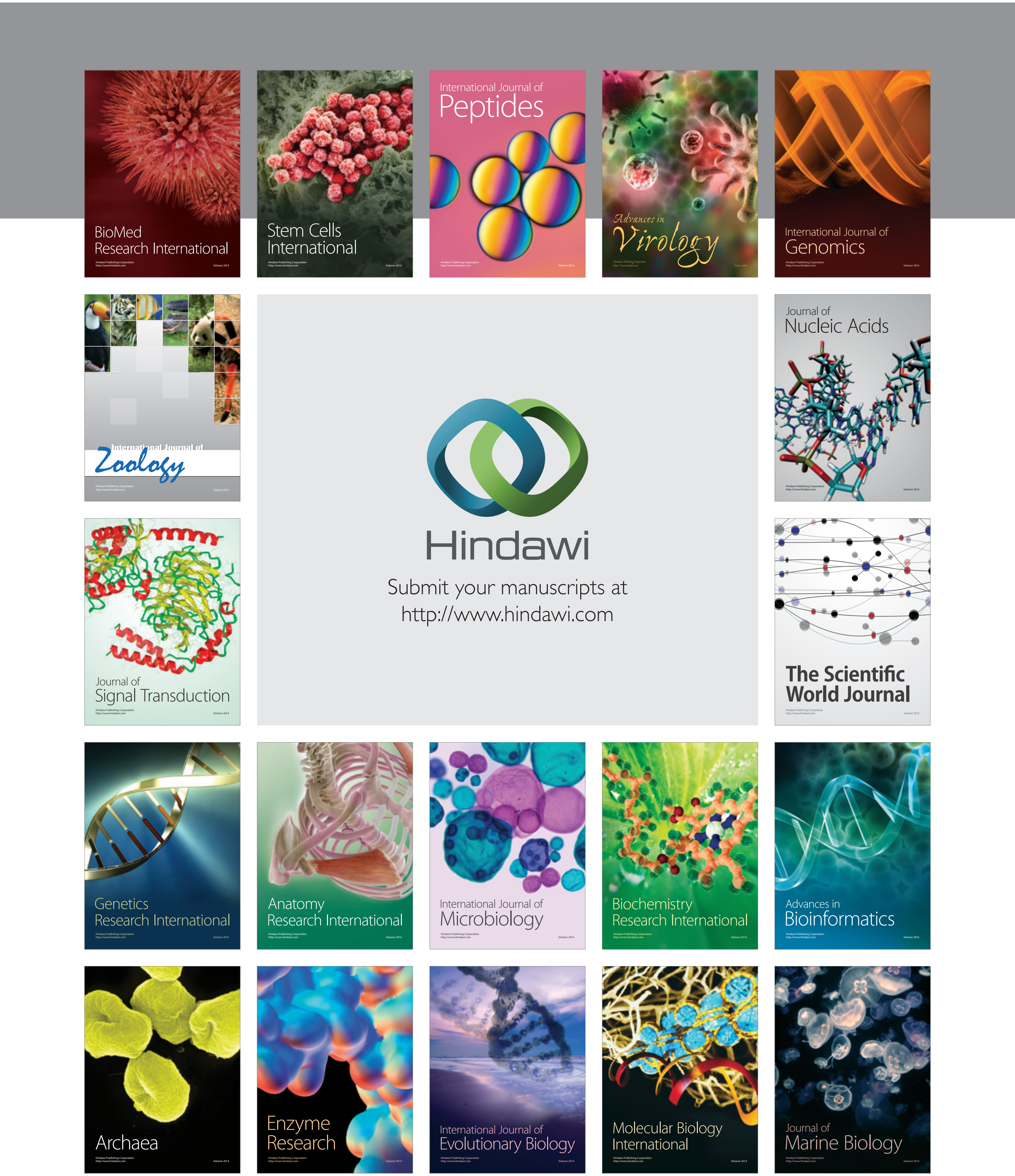
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