

Review

Grooming Behavior as a Mechanism of Insect Disease Defense

Marianna Zhukovskaya ¹, Aya Yanagawa ^{2,*} and Brian T. Forschler ³

¹ Sechenov Institute of Evolutionary Physiology and Biochemistry, Russian Academy of Sciences, Saint-Petersburg 194223, Russia; E-Mail: mzhukovskaya@yahoo.com

² Research Institute for Sustainable Humansphere, Kyoto University, Uji 611-0011, Japan

³ Department of Entomology, University of Georgia, Athens, GA 30602, USA;
E-Mail: bfor@uga.edu

* Author to whom correspondence should be addressed; E-Mail: ayanagawa@rsh.kyoto-u.ac.jp;
Tel.: +81-774-38-3664; Fax: +81-774-38-3666.

Received: 26 July 2013; in revised form: 20 October 2013 / Accepted: 22 October 2013 /

Published: 4 November 2013

Abstract: Grooming is a well-recognized, multipurpose, behavior in arthropods and vertebrates. In this paper, we review the literature to highlight the physical function, neurophysiological mechanisms, and role that grooming plays in insect defense against pathogenic infection. The intricate relationships between the physical, neurological and immunological mechanisms of grooming are discussed to illustrate the importance of this behavior when examining the ecology of insect-pathogen interactions.

Keywords: grooming behavior; neural circuit; disease resistance; entomopathogen

1. Introduction

In vertebrates, grooming has been described in terms of mutual expression of social acceptance and indicative of familial, as well as dominance, relationships between the different members of a group. Yet grooming is not always associated with social consequences as evidenced by the fact that the majority of animal species studied devote some time to grooming activities [1]. The integument has long been considered to be a mechanical barrier and the first line of defense against infection. A chitinous exoskeleton forms the integumentary boundary between an insect's internal organs and the environment while also functioning in various other capacities including a platform for sensory and motor devices. This complex structure of epidermal origin contains numerous structural features that

call for special maintenance to keep the cuticle in proper condition. The result is that insects like all terrestrial animals display various behaviors that are generally categorized as grooming [2]. Though the functions and associations are still ambiguous, insects of most orders also devote a lot of time in grooming activities. This review focuses on the functional role of grooming in insect disease defense as well as the neurological basis for grooming behaviors to highlight promising areas for future research.

As for hygiene behavior, special behavior directed toward the care of body surfaces is known from a wide range of animal species [3,4]. Earlier studies of grooming in insects were devoted to description, classification, and sequence of movements supposedly directed at the innate ‘need’ to keep clean [5–7]. A considerable amount of work has been devoted to specific groups of insects for example locusts that use the legs as a grooming device [8–12]. A wide variety of specialized structures used in cleaning the cuticle have been described in insects and is still the focus of considerable interest [7,13–18]. The importance and influence of grooming behavior as a topic of evolutionary theory is undeniable [1,17,19–23].

There are two broad categorizations used to describe grooming of the self or others. Autogrooming (self-grooming) is a classification that includes any act by the subject related to maintenance/care of the body surface and is considered an innate behavior represented across a plethora of vertebrate and invertebrate taxa [13,24]. Allogrooming (grooming another individual) is common in social vertebrates and eusocial insects, and occasionally observed in solitary insect species [25]. Despite the diversity of taxonomic groups involved, the main functions of grooming are amazingly similar, namely removal of foreign objects from the body surface, distribution of substances across the body surface and as a displacement behavior in stressful conditions [1,3,26,27]. Care of the body surface is thought to be important for disease prevention by elimination of pathogens, parasites and parasitoids [28–32]. Hydrophobic and bacteriostatic secretions spread over the body surface are known to improve the pathogen-barrier properties of the integument and also act as chemical signatures in both vertebrates and arthropods [28,30,33–37]. Irritants and mechanical stimulation often cause simple reflex reactions aimed at removing foreign material from the integument. Induced grooming in insects has been studied using dust particles, chemical irritants and weak mechanical stimulation [13,38–42]. In contrast, grooming also has been reported as an activity executed spontaneously without apparent external stimuli [5,43–45].

The inevitable ambiguity when attempting to classify a grooming behavior such as the simple scratching sweep that is often incorporated into a more complex sequence of defense-related behaviors. This is because of a high level of plasticity in grooming-related behaviors and often-subjective observations of the behavior itself. Thus exhibition of a behavioral reaction to a simple stimulus as evoking a scratching reflex make insects an excellent model for studying the neural circuitry underlying specific behaviors [46–48]. *Euphydryas phaeton* larvae regurgitate on attacking braconid parasitoids, which react with prolonged grooming [49] while *Heliothis virescens* larvae use a head strike to apply an oral exudate to attacking *Cardiochiles nigriceps* females, which, in turn, groom [50,51]. Grooming behaviors have also been described as part of a diversity of more general behavioral routines such as the obligatory phase of host recognition [52], oviposition [53,54] and mating [55]. At a basic level grooming has been shown to eliminate extraneous amounts of the continuous efflux of cuticular hydrocarbons allowing proper operation of antennal sensilla [56]. Grooming does, however, come with an energy cost and is enhanced in satiated insects [57]. This review highlights insect grooming from the point of survival that is the protection from microbial infection.

2. Function of Grooming

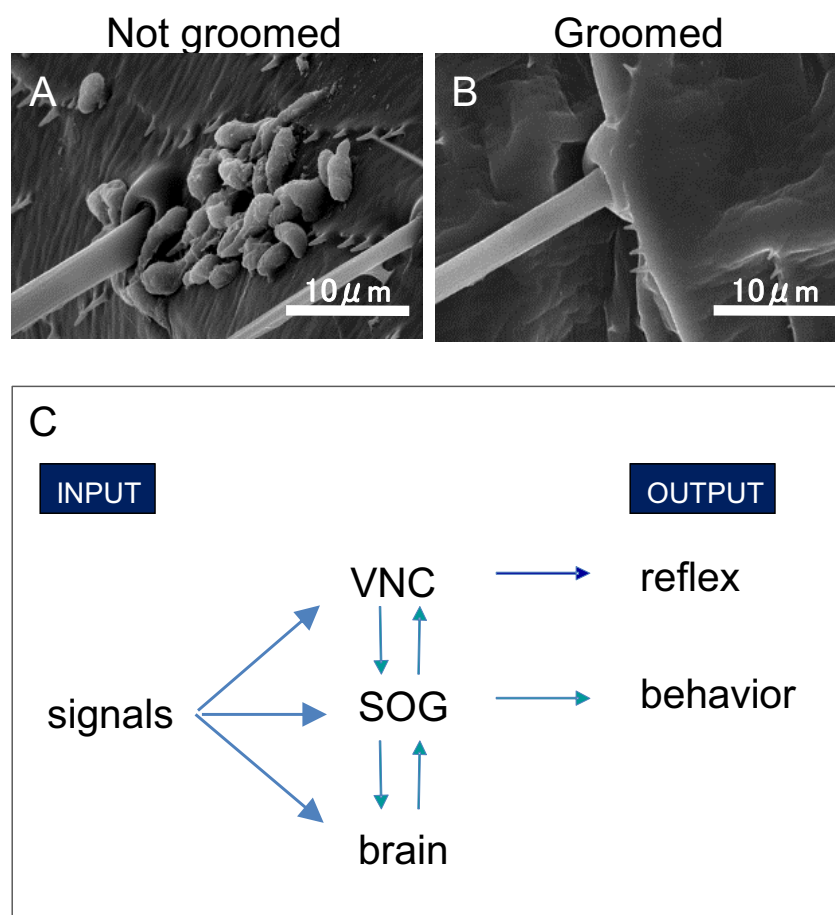
Grooming in animals is a complex, multipurpose behavior as reflected in the “microstructure” of events used to phenotype such behaviors [23]. The cleaning of various body parts is generally organized in a particular sequence of observable behaviors, often with cephalo-caudal progression [1]. Insects employ two generalized strategies for grooming that are associated with the design of the mouthparts. One strategy is a deposition of debris onto a substrate as employed by members of the Orders Diptera and Lepidoptera that possess piercing-sucking, siphoning. The other is lapping mouthparts and ingestion as displayed by members of the Orthoptera and Coleoptera that have chewing mouthparts. Some insect's combine both strategies, many hymenopterans, for example, groom their forelegs which possess a structure designed as an antennal cleaner with the mouthparts, while other body parts are rubbed against each other [17]. Another combined strategy involves honeybee allogrooming where the mouthparts are used to remove debris and parasitic mites from the body of a nestmate, but those items are not ingested [31,58]. Alternatively, the German cockroach possessing chewing mouthparts achieves antennal debris removal through the scraping action that accompanies pulling the flagellum over the glossa and most of the debris is manipulated into the hypopharynx and ingested when grooming is completed [59].

Various functions have been proposed to explain insect grooming behavior: cleaning dust particles from sensory organs [60], smearing secreted or acquired cuticular lipids that constitute a familiar chemical fingerprint for insects [61,62], parasitoid disguise [63,64], collecting pollen particles as food [65] and removing ectoparasites or pathogens [65,66]. Grooming has been shown to assist with locomotion as wings and legs are groomed to clean and flatten scales (or feathers) to diminish air resistance during the flight [20,67] or tarsi are groomed to maintain adhesion of attachment pads [18]. The importance of grooming behavior for the maintenance of sensory organ acuity has been suggested for insects as diverse as crickets, cockroaches and flea beetles [52,59,68]. Recent data shows that eucalyptol, the general odorant that causes excitation of a receptor housed in male pheromone-sensitive antennal sensilla [69,70] induces pronounced changes in frequency and duration of cockroach antennal grooming. According to work with cockroaches, hydrophobic odorant molecules get adsorbed and dissolved by the hydrocarbons on the epidermal surface and should be removed to maintain high temporal resolution of odor signals [56].

Mammals and birds display displacement activities that have been classified as locomotory behaviors, cleaning behaviors (e.g., grooming) and manipulation of objects, which are often disrupted by a variety of stressors [71–73] similar phenomena have been detected in insects [26,27]. Exposure to novelty is a traditional research approach to displacement behavior in vertebrates as it causes abnormal patterns and interrupted bouts of grooming in rodents [4,23,74]. Insecticides can trigger a biochemical xenobiotic stress response, which is believed to share some pathways with stress responses caused by other menacing circumstances [75,76]. In insects, stress-response causes drastic changes of monoamines, such as octopamine, dopamine and tyramine, which in turn, can trigger behavioral changes [77–80]. It is possible that as part of their repertoire of behavioral stress-responses insects display displacement grooming [81–86]. Understanding insect grooming may provide insights into pesticide route of entry because the oral toxicity of substances that enhance grooming should increase in insects that include ingestion in their grooming routines while sucking insects would show a decrease in toxicity. For

example, pyrethroid-resistant houseflies treated with fenvalerate (a pyrethroid insecticide), immediately initiated a vigorous grooming behavior which allowed them to remove as much as 13% of the topically applied dose which led to insecticide transfer from fly bodies to the walls of holding vials [87]. Insecticide interactions also have highlighted the role of grooming in insect resistance to infections where exposure to low concentrations of insecticide resulted in greater infection in insects simultaneously exposed to entomopathogenic fungi [85] or nematodes [88]. Grooming is an especially important behavior in social insects where such contacts are believed to be integral in reducing horizontal transmission of disease [89,90] (Figure 1A,B). Anti-fungal, anti-microbial secretions spread by grooming also serve to reduce the probability that those microorganisms can damage the integrity of the insect cuticle for both social and solitary insects [28,30,37].

Figure 1. Scanning electron microscope images of nongroomed and groomed abdomen of *Coptotermes formosanus*. Pathogenic conidia completely cover the bases of sensilla (A), groomed abdomen have no conidium on their surface (B). (C) is the basic scheme of neural circuit of insect grooming. SOG is suboesophageal ganglion. VNC is ventral nerve cord.



3. Neurobiology of Grooming

Mechanical or chemical stimulation causes movements aimed at eliminating foreign substances from the contaminated body surface [8,12,39,48,68,91–93]. It also has been shown that olfactory cues affect the pattern and frequency of grooming [94–96]. Irritant volatiles likely act through gustatory

sensilla in flies, because *Phormia regina* subjected to an irritant vapor, evert the proboscis, regurgitate a droplet onto its tip (the labellum), and proceed to wipe the labellum against the substrate [97]. These data are in accordance with electrophysiological data, showing the response of contact chemosensilla to certain volatiles [98,99]. Visual stimuli applied to only one eye cause an eye cleaning reflex [100], although the same behavior can be elicited by deflection of interommatidial mechanosensilla [68,91].

Aimed scratching, a stereotypic response to acute stimulation, has been used as a model for describing functional neuromorphology [48,92] and local control of leg movements [42,47,101]. Segmental circuits are integrated to produce complex intersegmental motor patterns [91]. In insects, the frontal ganglia (brain) is not required to produce simple aimed scratching, because the complete behaviour is executed even after transection of the connections anterior to the mesothoracic ganglion in locusts [47], and headless fly preparations [102,103]. Decapitated cockroaches are reported to groom their cercii and abdomen without special stimulation [104]. Simple scratching also has been used to describe as a process linked to non-associative learning such as habituation and dis-habituation of the cleaning reflex [105]. However not all neural circuitry related to behavior is under local control as spontaneous grooming was completely inhibited in headless flies [40]. Highly coordinated grooming, expressed by the complete repertoire of movements, is produced by the injection of parasitic wasp venom into the suboesophageal (SOG) ganglion of *Periplaneta americana* cockroaches [106,107]. SOG, which is placed below the brain and a part of central nervous system (CNS), generally controls insect movements. Segmental circuits can elicit simple sweeps that integrate into the greater intersegmental circuitry to produce higher order stereotypic actions, illustrative of neural plasticity that, at least in the cockroach, is controlled by the SOG dopaminergic network (Figure 1C). On the other hand, the absence of plasticity by feedback signals from sensilla was reported in the African praying mantis, *Sphodromantis lineola* that has mechanosensory sensilla in a femoral brush yet continue to perform eye cleaning movements after surgical removal of the brush [108]. In contrast, antennal grooming was more plastic and accomplished with a contralateral foreleg instead of the normally used ipsilateral foreleg in this species [108]. Our observations on antennal grooming in the American cockroach support these data, namely in the case of unsuccessful antennal cleaning, when after damage to the contralateral foretarsus prevent attempts to bring the antennal flagellum to the mouth subjects used both forelegs instead of the contralateral foreleg, often several times, to accomplish successful cleaning.

There is little doubt that multiple neural feedback mechanisms tune grooming behavior according to current circumstances. In the German cockroach for example, the marginal sensilla located on the antennal basal segments 20–24 respond to the bending of flagellomeres and presumably play a role in determining the duration of flagellum grooming [109] while chemoreceptors at the base of the paraglossa participate in the ingestion of debris removed from the antennae during cleaning [59,110]. Grooming therefore is a part of the behavioral repertoire executed according to a hierarchy that produces an appropriate response to various stimuli affected by physiological conditions, such as satiation, arousal and aggression. It is believed that biogenic amines mediate these observed behaviors as treatment with dopamine (DA), octopamine (OA) and tyramine (TA) and their agonists and antagonists exert effects on grooming through different pathways: DA predominantly alters motor circuits [102,103,111], while OA and TA play a modulatory role [112] through general arousal/displacement mechanisms.

4. Chemosensory Signatures

Insect behavior is often the result of a reaction to environmental signals hiding in the general background noise present in insect habitats [113]. This occurs by procedural knowledge processed from a neural circuitry that uses the difference between internally and externally generated signals to produce an appropriate behavior [114]. The importance of olfaction in host protection is highlighted by examples such as a flower that mimics olfactory and visual cues of fungi to avoid insect attack [115]. Herbivorous insects perceive the blend of odors from plants to discriminate host from non-host [116]. Blend-odor conceivably conveys essential signals also on pathogen perception in insects. Microbes vary with regard to a variety of measurable qualities such as competitive strength, attachment pattern, germination ability, and environmental adaptability [117], yet it is not clear what cues lead insects to recognize the presence of pathogens. Gripenberg *et al.* [118] suggested that insect species, which has a smaller host range, correlate with a narrower range of perceived odors. It is possible that the entomopathogen recognition process is analogous to the phytophagous insect host recognition system. Yet the importance of general odor reception as a cue for initiating behaviors should not be underestimated [119]. The simple fact that grooming enhances olfactory activity in cockroach supports the hypothesis of a critical role for grooming and entomopathogen recognition [56].

Insect olfaction seems to help protect insects from disease [120–123]. According to Pinho *et al.* [124], the volatiles of mushrooms could represent different groups of mushrooms at the species level and Mburu *et al.* [125] reported that high virulent entomopathogenic fungi shared similar volatiles. More studies are needed to clarify the interaction between odor-signal and insect perception. Integration of behavioral studies with the genetic and/or physiological pathways holds promise for a better understanding of the connection between behavior and disease resistance. The development of microRNA's opens a new door for the study of grooming related behaviors that should be exploited given the potential of using insects in loss-of-function mutants for bioassay of behaviors [126–128].

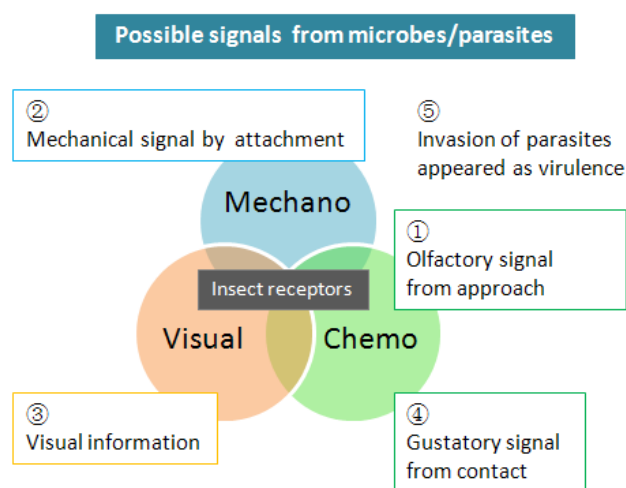
The literature on animal behavior indicates that recognition of pathogens is a common trait across taxonomic categories. The nematode *Caenorhabditis* has been shown to detect specific chemical stimuli from bacterial pathogens [129], and display associative learning by avoiding indications of pathogenic bacteria using olfactory stimuli [130–132]. In vertebrates like rats, interactions between the immune system, sensory physiology and behavior can be affected by an immune response [133]. It is also well documented that vertebrates are capable of associative learning using taste aversive conditioning paradigms [134–139]. While, in insects, more studies are required to illustrate behavior as an integral strategy to cope with pathogens [66,140].

5. Detection of Pathogens

Insect perception of pathogens has long been thought to begin after contact [86,141,142]. Recently, however, numerous studies with social insects highlight the phenomenon of identifying pathogens prior to infection (Figure 2). Fouks *et al.* [143] reported that honey bees can detect parasite-contaminated flowers. Ants and honeybees demonstrate a communicated response to pathogens and groom more frequently in a contaminated environment in addition to grooming or removing infected larva [144–147]. *Formica podzolica* even display a response to their infected aphid mutualist partners [148].

The sensitivity of insects towards chemosensitive odors and tastes has been discussed in the context of food, sex or social interactions [149–152] but not in relation to disease. The hypothesis that chemoreception is involved in disease prevention may provide insights into how grooming behavior has evolved within different groups of insects [17], because it predicts that grooming should be related to selection pressure against certain pathogens in a given environment. It has been suggested that insects may have evolved specific chemoreceptors to detect pathogens [153–155]. *Drosophila* possess olfactory receptors that detect 1-octen-3-ol, a typical fungal odor [156,157], and it is not unreasonable to assume that the same selection pressure that preserves a host seeking behavior could also promote avoidance. A few papers examining full transcriptoms note that microbial infections are associated with changes in expression of olfactory-related genes like odorant binding proteins [158,159].

Figure 2. Microbes/parasites, which invade their host through insect cuticle are cleared due to grooming behavior. Olfaction will be the first signal from microbe [123,143,164], then physical [8,39] and gustatory [142,148,149] signals will be received by contact/attachments. Some hosts will be able to receive visual signals [31]. At the last stage, host insects probably find an invasion of pathogens by smell or behavior of infected individuals [163].



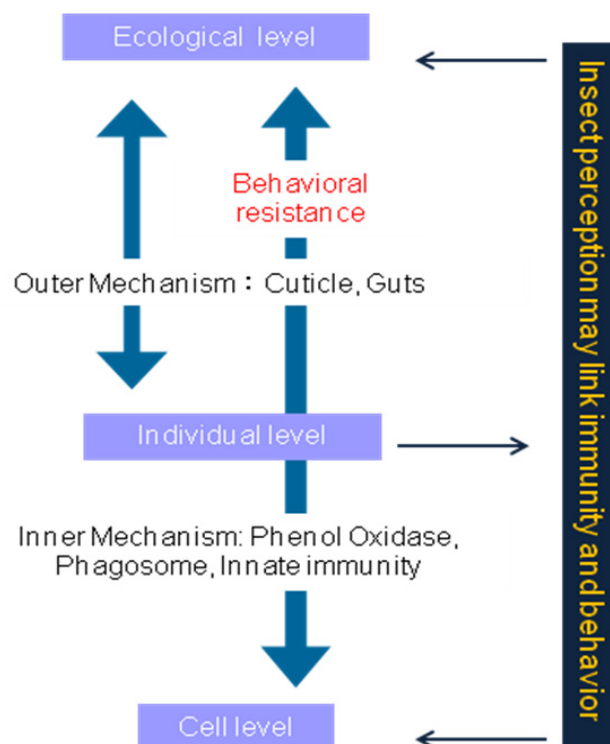
Termite hygiene behaviors are likely triggered by chemical information, because most termites are blind and therefore represent a good model system to test the hypothesis of chemoreceptive avoidance behavior. Several studies have reported that insects are repelled by the odor of strongly virulent entomopathogenic fungi [125,160–162]. Recent studies have revealed that termite antennae are sensitive to the odors of entomopathogenic fungi [95,163] this sensitivity varies according to the conditions of the bioassay [164]. Termites have been shown to avoid highly virulent *Metarhizium anisopliae* conidia more than less-virulent conidia [160,161]. It is possible that termites avoid aversive odors, not simply the most virulent pathogen; a categorization based on speed of mortality rather than overall pathogenic affects [165]. Future studies should examine more pathogens and fungal isolates that measure not just high virulence but factors such as decreased fecundity and mortality over an extended time frame [166].

There is still a long way to go to recognize behavior as an integral part of the strategies used by insects to cope with pathogens [66,140,167] and another area of exciting research is the initiation of humoral responses to pathogens [168,169].

6. Disease Prevention

Insect defenses against pathogens have been studied from the point of view of an overall immune response [140,142]. Vertebrates possess adaptive immunity yet debate continues on whether insect immunity has an adaptive component [170–174]. The known antimicrobial defense mechanisms include maintenance of physical barriers (epithelia), secretion of humoral mediators (antimicrobial peptides, reactive oxygen species), activation of proteolytic cascades leading to melanization and cellular functions including phagocytosis and encapsulation [142] (Figure 3). The regulation of antimicrobial peptide gene expression during systemic infection has shown that production of antimicrobial peptides by the fat body, analogous to the mammalian liver, are orchestrated through two signaling modules: the Toll and Imd pathways respond to microbial infection and lead to activation of NF- κ B-like factors [142]. The strategies available to individual insects to withstand pathogen infections also have been viewed from the perspective of a cost/benefit trade-off [90,175]. Few studies have examined the role of behavior in insect disease defense [24,176–178]. However the role of insect grooming and hygienic activities is gaining recognition in the field of insect pathology [140].

Figure 3. Interaction between Resistant Level Insects employing strategies to fight against microbial infection at cell, individual and ecological levels. Behavioral resistance is often the first defense in the infection stage.



Insects employ several strategies to fight back against microbial infection at cell, individual and ecological levels. Behavioral resistance will be one of the most initial defense in the infection stage.

Hygienic behavior has been shown to play a key role in disease prevention in insects [86,144,179]. It has also been documented that suppression of grooming behavior increases mortality in insect-pathogen bioassays [84,180–183]. Although grooming activities can be induced by aversive

stimuli (mechanical or chemical), they also occur after oviposition or situations involving contact with potentially contaminated food, therefore there are few data supporting the specific hypothesis that grooming plays a role in the defense of insects against microbial infection [54,184–187].

Autogrooming can prevent infection from various microorganisms, especially in species like flies that live in an environment littered with bacteria, fungi and other microorganisms developing on decaying material [184,188]. Considering that many entomopathogenic fungi disperse as airborne conidia that penetrate the insect cuticle upon germination it is reasonable to hypothesize the same sensory neurons important in triggering grooming activities in response to dust particles [60] play a role in insect immunity to fungal infection.

The trigger(s) that initiate insect behavioral reaction to pathogens is currently not well described. Increased grooming was noticed in the presence of parasitic nematodes for both earwigs and Japanese beetle larvae [189,190], however no data were collected to elucidate the sensory stimuli involved in such behavior. It is known that *Drosophila* spend a considerable amount of time grooming and that grooming systematically occurs after egg-laying [54,191]. Our unpublished observations also support the hypothesis that pathogen contact initiates grooming because most of the *Beauveria bassiana* conidia deposited on adult *Drosophila* are actively removed by grooming. There are reports that insect contact with pathogens can result in up/down regulation of gene expression, drive immune reaction and alter behavior [24,175,192]. In addition, toll-deficient *Drosophila* mutants show increased susceptibility to *B. bassiana* while infection leads to the expression of the antifungal peptide genes *Drosomycin* and *Metchnikowin* [193,194]. There are exciting opportunities to study the interaction between behavioral defense and humoral/cellular immune response in solitary insects and the trigger can be one of the most essential cues to clarify the associations. While, there are limited data in the literature on the question of whether insects respond to chemical or mechanical signals from microorganism by evoking grooming behavior.

Horizontal disease transmission can be significantly more serious in eusocial insects because colony members are closely related and frequently interact, often under conditions of high population densities [144,195–197]. The high risk of disease transmission within colonies is counterbalanced by cooperative behavioral defenses, often termed social immunity, that complement the immune response of individual group members [90,143,198]. It has often been reported that social insects such as ants [181,199], termites [29,177] and honeybees [65], help protect the colony from infection using allogrooming behaviors. Although a recent model suggests that allogrooming is less important than nest hygiene or immunity in social insect disease resistance [200].

Allogrooming is a well-known social behavior exhibited by numerous animal species that serves both hygienic and social functions [201]. Reduced allogrooming has been reported to be important in termite and ant social immunity in regard to removing pathogenic fungal conidia [29,36,85,159,202–205]. Allogrooming has also been implicated in the spread of glandular secretions or other antimicrobial substances such as the metapleural gland in ants [206–212] or gram-negative bacteria binding proteins in termites [169]. Ants have been shown to increase grooming of eggs and brood after exposure to pathogens [146]. In bees, autogrooming functions to remove external parasites such as *Varroa* mites [213] after which they conduct a ‘grooming dance’ that elicits allo-grooming from nestmates [31,65,214–220]. Social insects provide a compelling, comparative model for the study of grooming behavior in immunity and disease resistance.

7. Discussion and Conclusions

Maintenance of the cuticle, that physical barrier between an animal and the environment, can be considered the first line of defense against disease. The grooming behavior displayed by vertebrates and insects serve multiple functions, such as care and maintenance of the body surface and sensory organs. In insects mechano- and chemosensory sensitivity play an important role in the discovery of pathogenic organisms toward initiating grooming behaviors. Antimicrobial secretions spread by grooming provide insects with an additional role for this behavior. Sensory recognition can also trigger mobilization of immune response to compliment a suite of behavioral mechanisms, such as avoidance, self-medication and grooming [221]. Grooming behaviors vary by insect species and recognition of these behaviors is often not connected to disease defense although observations suggest that displacement grooming—well documented in mammals—also may be characteristic for stressed insects. The efficiency of grooming alone in protecting insects from disease is considered limited especially in solitary insects [222] yet there is ample evidence that the grooming component of social immunity is an effective tool in social insect disease defense [221].

Grooming behavior has long been observed and reported in many insects [13]. Future research should identify and classify these behaviors to aid in the systematic exploration of the physiological, neurological and pharmacologic basis of grooming. Occasional failures have been observed in biological control using microbial agents, which could be controlled by eliminating the agent with this behavior, but there are many other possible relevant factors. A better understanding of grooming should provide new insight toward the development of management practices using entomopathogens, leading to less damage to beneficial insects and consequently new possibilities for sustainable agricultural activity.

Acknowledgments

Authors thank to F. Marion-Poll (CNRS, France), B. Lemaitre (EPFL, Switzerland) and C. Neyen (EPFL, Switzerland) for their fruitful discussions and important suggestions. Authors are supported by RFBR Grant Number 13-04-00610a and JSPS KAKENHI Grant Number 24880019.

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Mooring, M.S.; Blumstein, D.T.; Stoner, C.J. The evolution of parasite-defence grooming in ungulates. *Biol. J. Linn. Soc.* **2004**, *81*, 17–37.
2. Sachs, B.D. The development of grooming and its expression in adult animals. *Ann. N. Y. Acad. Sci.* **1988**, *525*, 1–17.
3. Borchelt, P.L. Care of the Body Surface (COBS). In *Comparative Psychology: An Evolutionary Analysis of Animal Behavior*; Denny, M.R., Ed.; John Wiley & Sons Inc.: New York, NY, USA, 1980; pp. 363–384.
4. Kalueff, A.V.; Tuohimaa, P. Grooming analysis algorithm for neurobehavioural stress research. *Brain Res. Prot.* **2004**, *13*, 151–158.

5. Szebenyi, A.L. Cleaning behaviour in *Drosophila melanogaster*. *Anim. Behav.* **1969**, *17*, 641–651.
6. Valentine, B.D. Grooming behavior in Coleoptera. *Coleopts. Bull.* **1973**, *27*, 63–73.
7. Goldman, L.J.; Callahan, P.S.; Carlysle, T.C. Tibial combs and proboscis cleaning in mosquitoes. *Annu. Rev. Entomol. Soc. Am.* **1972**, *65*, 1299–1302.
8. Newland, P.L. Avoidance reflexes mediated by contact chemoreceptors on the legs of locusts. *J. Comp. Physiol. A* **1998**, *183*, 313–324.
9. Newland, P.L.; Rogers, S.M.; Gaaboub, I.; Matheson, T. Parallel somatotopic maps of gustatory and mechanosensory neurons in the central nervous system of an insect. *J. Comp. Neurol.* **2000**, *425*, 82–96.
10. Rogers, S.M.; Newland, P.L. Local movements evoked by chemical stimulation of the hind leg in the locust *Schistocerca gregaria*. *J. Exp. Biol.* **2000**, *203*, 423–433.
11. Dürr, V.; Matheson, T. Graded limb targeting in an insect is caused by the shift of a single movement pattern. *J. Neurophysiol.* **2003**, *90*, 1754–1765.
12. Page, K.L.; Matheson, T. Wing hair sensilla underlying aimed hindleg scratching of the locust. *J. Exp. Biol.* **2004**, *207*, 2691–2703.
13. Hlavac, T.F. Grooming systems of insects: Structure, mechanics. *Ann. Entomol. Soc. Am.* **1975**, *68*, 823–826.
14. Schönlitzer, K.; Renner, M. The function of the antenna cleaner of the honeybee (*Apis mellifica*). *Apidologie* **1984**, *15*, 23–32.
15. Walker, E.D.; Archer, W.E. Sequential organization of grooming behaviors of the mosquito *Aedes triseriatus*. *J. Insect Behav.* **1988**, *1*, 97–109.
16. Basibuyuk, H.H.; Quicke, D.L.J. Morphology of the antenna cleaner in the Hymenoptera with particular reference to non-aculeate families (Insecta). *Zool. Scr.* **1995**, *28*, 152–177.
17. Basibuyuk, H.H.; Quicke, D.L.J. Grooming behaviours in the Hymenoptera (Insecta): Potential phylogenetic significance. *Zool. J. Linn. Soc.* **1999**, *125*, 349–382.
18. Hosoda, N.; Gorb, S.N. Friction force reduction triggers feet grooming behavior in beetles. *Proc. R. Soc. B* **2011**, *278*, 1748–1752.
19. Farish, D.J. The evolutionary implications of qualitative variation in the grooming behavior of the Hymenoptera (Insecta). *Anim. Behav.* **1972**, *20*, 662–676.
20. Thelen, E.; Farish, D.J. Analysis of grooming behaviour of wild and mutant strains of *Bracon hebetor* (Braconidae-Hymenoptera). *Behaviour* **1977**, *62*, 70–102.
21. Valentine, B.D.; Glorioso, M.J. Grooming behavior in Diplura (Insecta: Apterygota). *Psyche* **1978**, *85*, 191–200.
22. Lefebvre, L. Grooming in crickets: Timing and hierarchical organization. *Anim. Behav.* **1981**, *29*, 973–984.
23. Smolinsky, A.N.; Bergner, C.L.; LaPorte, J.L.; Kalueff, A.V. Analysis of grooming behavior and its utility in studying animal stress, anxiety, and depression. *Neuromethods* **2009**, *42*, 21–36.
24. Roy, H.E.; Steinkraus, D.C.; Eilenberg, J.; Hajek, A.E.; Pell, J.K. Bizarre interactions and endgames: Entomopathogenic fungi and their arthropod hosts. *Annu. Rev. Entomol.* **2006**, *51*, 331–357.
25. Valentine, B.D. Mutual grooming in cucujoid beetles (Coleoptera: Silvanidae). *Insecta Mundi* **2007**, Paper 54. Available online: <http://digitalcommons.unl.edu/insectamundi/54/> (accessed on 8 April 2013).

26. Hefetz, A.; Soroker, V.; Dahbi, A.; Malherbe, M.C.; Fresneau, D. The front basitarsal brush in *Pachycondyla apicalis* and its role in hydrocarbon circulation. *Chemoecology* **2001**, *11*, 17–24.
27. Root-Bernstein, M. Displacement activities during the honeybee transition from waggle dance to foraging. *Anim. Behav.* **2010**, *79*, 935–938.
28. Kovac, D.; Maschwitz, U. Secretion-Grooming in aquatic beetles (Hydradephaga): A chemical protection against contamination of the hydrofuge respiratory region. *Chemoecology* **1990**, *1*, 131–138.
29. Yanagawa, A.; Shimizu, S. Resistance of the termite, *Coptotermes formosanus* Shiraki to *Metarhizium anisopliae* due to grooming. *BioControl* **2007**, *52*, 75–85.
30. Lusebrink, I.; Dettner, K.; Seifert, K. Stenusine, an antimicrobial agent in the rove beetle genus *Stenus* (Coleoptera, Staphylinidae). *Naturwissenschaften* **2008**, *95*, 751–755.
31. Peng, Y.S.; Fang, Y.; Xu, S.; Ge, L.; Nasr, M.E. The resistance mechanism of the Asian honey bee, *Apis cerana* Fabr, to an ectoparasitic mite *Varroa jacobsoni* Oudemans. *J. Invertebr. Pathol.* **1987**, *49*, 54–60.
32. Vincent, C.M.; Bertram, S.M. Crickets groom to avoid lethal parasitoids. *Anim. Behav.* **2010**, *79*, 51–56.
33. Elder, W.H. The oil gland of birds. *Wilson Bull.* **1954**, *66*, 6–31.
34. Jacob, J.; Ziswiler, V. The uropygial gland. *J. Avian Biol.* **1982**, *6*, 199–324.
35. Moyer, B.; Rock, A.N.; Clayton, D.H. Experimental test of the importance of preen oil in rock doves (*Columba livia*). *Auk* **2003**, *120*, 490–496.
36. Graystock, P.; Hughes, W.O.H. Disease resistance in a weaver ant, *Polyrhachis dives*, and the role of antibiotic-producing glands. *Behav. Ecol. Sociobiol.* **2011**, *65*, 2319–2327.
37. Baracchi, D.; Mazza, G.; Turillazzi, S. From individual to collective immunity: The role of the venom as antimicrobial agent in the Stenogastrinae wasp societies. *J. Insect Physiol.* **2012**, *58*, 188–193.
38. Gratwick, M. The contamination of insects of different species exposed to dust deposits. *Bull. Entomol. Res.* **1957**, *48*, 741–753.
39. Reingold, S.C.; Camhi, J.M. Abdominal grooming in the cockroach: Development of an adult behavior. *J. Insect Physiol.* **1978**, *24*, 101–110.
40. Vandervorst, P.; Ghysen, A. Genetic control of sensory connections in *Drosophila*. *Nature* **1980**, *86*, 65–67.
41. El-Awami, I.O.; Dent, D.R. The interaction of surface and dust particle size on the pick-up and grooming behaviour of the German cockroach *Blattella germanica*. *Entomol. Exp. Appl.* **1995**, *77*, 81–87.
42. Matheson, T. Hindleg targeting during scratching in the locust. *J. Exp. Biol.* **1997**, *200*, 93–100.
43. Hay, D.A. Genetical and maternal determinants of the activity and preening behaviour of *Drosophila melanogaster* reared in different environments. *Heredity* **1972**, *28*, 311–336.
44. Ashton, K.; Wagoner, A.P.; Carrillo, R.; Gibson, G. Quantitative trait loci for the monoamine-related traits heart rate and headless behavior in *Drosophila melanogaster*. *Genetics* **2001**, *157*, 283–294.
45. Spruijt, B.; van Hooff, J.; Gispen, W. Ethology and neurobiology of grooming behavior. *Physiol. Rev.* **1992**, *72*, 825–852.

46. Eaton, R.C.; Farley, R.D. The neural control of cercal grooming behaviour in the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **1969**, *15*, 1047–1065.
47. Berkowitz, A.; Laurent, G. Local Control of Leg Movements and motor patterns during grooming in locusts. *J. Neurosci.* **1996**, *16*, 8067–8078.
48. Canal, I.; Acebes, A.; Ferrus, A. Single neuron mosaics of the *Drosophila gigas* mutant project beyond normal targets and modify behavior. *J. Neurosci.* **1998**, *18*, 999–1008.
49. Stamp, N.E. Interactions of parasitoids and checkerspot caterpillars *Euphydryas* spp. (Nymphalidae). *J. Res. Lepid.* **1984**, *23*, 2–18.
50. Hays, D.B.; Vinson, S.B. Acceptance of *Heliothis virescens* (F.) as a host by the parasite *Cardiochiles nigriceps* viereck (Hymenoptera, Braconidae). *Anim. Behav.* **1971**, *19*, 3–52.
51. Gross, P. Insect behavioral and morphological defenses against parasitoids. *Annu. Rev. Entomol.* **1993**, *38*, 251–273.
52. Henderson, A.E.; Hallett, R.H.; Soroka, J.J. Prefeeding behavior of the crucifer flea beetle, *Phyllotreta cruciferae*, on host and nonhost crucifers. *J. Insect Behav.* **2004**, *17*, 17–39.
53. Qiu, Y.; van Loon, J.J.A.; Roessingh, P. Chemoreception of oviposition inhibiting terpenoids in the diamondback moth *Plutella xylostella*. *Entomol. Exp. Appl.* **1998**, *87*, 143–155.
54. Yang, C.-H.; Belawat, P.; Hafen, E.; Jan, L.Y.; Jan, Y.-N. *Drosophila* egg-laying site selection as a system to study simple decision-making processes. *Science* **2008**, *319*, 1679–1683.
55. Wuellner, C.T.; Porter, S.D.; Gilbert, L.E. Eclosion, mating, and grooming behavior of the parasitoid fly *Pseudacteon curvatus* (Diptera: Phoridae). *Fla. Entomol.* **2002**, *85*, 563–566.
56. Böröczky, K.; Wada-Katsumata, A.; Batchelor, D.; Zhukovskaya, M.; Schal, C. Insects groom their antennae to enhance olfactory acuity. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 3615–3620.
57. Jacquet, M.; Lebon, C.; Lemperiere, G.; Boyer, S. Behavioural functions of grooming in male *Aedes albopictus* (Diptera: Culicidae), the Asian tiger mosquito. *Appl. Entomol. Zool.* **2012**, *47*, 359–363.
58. Bozic, J.; Valentincic, T. Quantitative analysis of social grooming behavior of the honey bee *Apis mellifera carnica*. *Apidologie* **1995**, *26*, 141–147.
59. Robinson, W.H. Antennal Grooming and Movement Behavior in the German Cockroach, *Blattella germanica* (L.). In Proceedings of the Second International Conference on Urban Pests, Edinburgh, UK, July 1996; pp. 361–369.
60. Phillis, R.W.; Bramlage, A.T.; Wotus, C.; Whittaker, A.; Gramates, L.S.; Seppala, D.; Farahanchi, F.; Caruccio, P.; Murphey, R.K. Isolation of mutations affecting neural circuitry required for grooming behavior in *Drosophila melanogaster*. *Genetics* **1993**, *133*, 581–592.
61. Carlin, N.F.; Holldobler, B.; Gladstein, D.S. The kin recognition system of carpenter ants (*Camponotus* spp.). *Behav. Ecol. Sociobiol.* **1986**, *20*, 219–227.
62. Ozaki, M.; Wada-Katsumata, A.; Fujikawa, K.; Iwasaki, M.; Yokohari, F.; Satoji, Y.; Nisimura, T.; Yamaoka, R. Ant nestmate and non-nestmate discrimination by a chemosensory sensillum. *Science* **2005**, *309*, 311–314.
63. Dettner, K.; Liepert, C. Chemical mimicry and camouflage. *Ann. Rev. Entomol.* **1994**, *39*, 129–154.
64. Seid, M.A.; Brown, B.V. A new host association of *Commoptera solenopsidis* (Diptera: Phoridae) with the ant *Pheidole dentata* (Hymenoptera: Formicidae) and behavioral observations. *Fla. Entomol.* **2009**, *92*, 309–313.

65. Rath, W. Co-Adaptation of *Apis cerana* Fabr and *Varroa jacobsoni* Oud. *Apidologie* **1999**, *30*, 97–110.
66. Boucias, D.G.; Pendland, J.C. *Principles of Insect Pathology*; Kluwer Academic Publisher: Boston, MA, USA, 1998; p. 537.
67. Elphick, C.; Dunning, J.B.; John, B. Behaviour. In *The Sibley Guide to Bird Life & Behaviour*; Elphick, C., Dunning, J.B., Sibley, D., Eds.; Christopher Helm: London, UK, 2001; pp. 58–59.
68. Honegger, H.-W.; Reif, H.; Müller, W. Sensory mechanisms of eye cleaning behavior in the cricket *Gryllus campestris*. *J. Comp. Physiol.* **1979**, *129*, 247–256.
69. Fujimura, K.; Yokohari, F.; Tateda, H. Classification of antennal olfactory receptors of the cockroach, *Periplaneta americana* L. *Zool. Sci.* **1991**, *8*, 243–255.
70. Zhukovskaya, M.I. Modulation by octopamine of olfactory responses to nonpheromone odorants in the cockroach, *Periplaneta americana* L. *Chem. Senses* **2012**, *37*, 421–429.
71. Tinbergen, N. *The Study of Instinct*; Clarendon: Oxford, UK, 1951; p. 228.
72. Wilz, K.J. The disinhibition interpretation of the “displacement” activities during courtship in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* **1970**, *18*, 682–687.
73. Anselme, P. Abnormal patterns of displacement activities: A review and reinterpretation. *Behav. Process.* **2008**, *79*, 48–58.
74. File, S.E.; Mabbutt, P.S.; Walker, J.H. Comparison of adaptive responses in familiar and novel environments: Odulatory factors. *Ann. N. Y. Acad. Sci.* **1988**, *525*, 69–79.
75. David, J.P.; Boyer, S.; Mesneau, A.; Ball, A.; Ranson, H.; Dauphin-Villemant, C. Involvement of cytochrome P450 monooxygenases in the response of mosquito larvae to dietary plant xenobiotics. *Insect Biochem. Mol. Biol.* **2006**, *36*, 410–420.
76. King-Jones, K.; Horner, M.A.; Lam, G.; Thummel, C.S. The DHR96 nuclear receptor regulates xenobiotic responses in *Drosophila*. *Cell Metab.* **2006**, *4*, 37–48.
77. Davenport, A.; Evans, P.D. Stress-Induced changes in the octopamine levels of insect haemo-lymph. *Insect Biochem.* **1984**, *14*, 135–143.
78. Woodring, J.P.; Meier, O.W.; Rose, R. Effect of development, photoperiod, and stress on octopamine levels in the house cricket, *Acheta domesticus*. *J. Insect Physiol.* **1988**, *34*, 759–765.
79. Hirashima, A.; Nagano, T.; Takeya, R.; Eto, M. Effect of larval density on whole-body biogenic amine levels of *Tribolium freemani* Hinton. *Comp. Biochem. Physiol.* **1993**, *106*, 457–461.
80. Libersat, F.; Pflueger, H.J. Monoamines and the orchestration of behavior. *BioScience* **2004**, *54*, 17–25.
81. Cox, R.L.; Wilson, W.T. Effects of permethrin on the behavior of individually tagged honey bees, *Apis mellifera* L. (Hymenoptera, Apidae). *Environ. Entomol.* **1984**, *13*, 375–378.
82. Wiles, J.A.; Jepson, P.C. Sub-Lethal effects of deltamethrin residues on the within-crop behaviour and distribution of *Coccinella septempunctata* Entomol. *Exp. Appl.* **1994**, *72*, 33–45.
83. Longley, M.; Jepson, P.C. Effects of honeydew and insecticide residues on the distribution of foraging aphid parasitoids under glasshouse and field conditions. *Entomol. Exp. Appl.* **1996**, *81*, 189–198.
84. Boucias, D.G.; Stokes, C.; Storey, G.; Pendland, J.C. The effects of imidacloprid on the termite *Reticulitermes flavipes* and its interaction with the mycopathogen *Beauveria bassiana*. *Pflanzensch. Nachr. Bayer* **1996**, *49*, 103–144.

85. Neves, P.M.; Alves, S.B. Grooming capacity inhibition in *Cornitermes cumulans* (Kollar) (Isoptera: Termitidae) inoculated with entomopathogenic fungi and treated with imidacloprid. *An. Soc. Entomol. Bras.* **2000**, *29*, 537–545.
86. James, R.R.; Xu, J. Mechanisms by which pesticides affect insect immunity. *J. Invertebr. Pathol.* **2012**, *109*, 175–182.
87. Golenda, C.F.; Forgash, A.J. Grooming behavior in response to fenvalerate treatment in pyrethroid-resistant house flies. *Entomol. Exp. Appl.* **1986**, *40*, 169–175.
88. Koppenhöfer, A.M.; Grewal, P.S.; Kaya, H.K. Synergism of imidacloprid and entomopathogenic nematodes against white grubs: The mechanism. *Entomol. Exp. Appl.* **2000**, *94*, 283–293.
89. Rosengaus, R.; Traniello, J. Disease susceptibility and the adaptive nature of colony demography in the dampwood termite *Zootermopsis angusticollis*. *Behav. Ecol. Sociobiol.* **2001**, *50*, 546–556.
90. Hughes, W.O.H.; Eilenberg, J.; Boomsma, J.J. Trade-Offs in group living: Transmission and disease resistance in leaf-cutting ants. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **2002**, *269*, 1811–1819.
91. Hensler, K. Intracellular recordings of neck muscle motoneurons during eye cleaning behaviour of the cricket. *J. Exp. Biol.* **1986**, *120*, 153–172.
92. Phillis, R.; Statton, D.; Caruccio, P.; Murphey, R.K. Mutations in the 8 kDa dynein light chain gene disrupt sensory axon projections in the *Drosophila* imaginal CNS. *Development* **1996**, *122*, 2955–2963.
93. Reingold, S.C.; Camhi, J.M. A quantitative analysis of rhythmic leg movements during three different behaviors in the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **1977**, *23*, 1407–1420.
94. Östrand, F.; Anderbrant, O.; Jönsson, P. Behaviour of male pine sawflies, *Neodiprion sertifer*, released downwind from pheromone sources. *Entomol. Exp. Appl.* **2000**, *95*, 119–128.
95. Yanagawa, A.; Yokohari, F.; Shimizu, S. The role of antennae in removing entomopathogenic fungi from cuticle of the termite, *Coptotermes formosanus*. *J. Insect Sci.* **2009**, *9*, 1–9.
96. Zhukovskaya, M.I. Odorant-Dependent changes of the antennal surface secretions in the cockroach, *Periplaneta americana*. *Sensornye. Syst.* **2011**, *25*, 78–86. (in Russian)
97. Eisner, T.; Deyrup, M.; Jacobs, R.; Meinwald, J. Necrodols: Anti-Insectan terpenes from defensive secretion of carrion beetle (*Necrodes surinamensis*). *J. Chem. Ecol.* **1986**, *12*, 1407–1415.
98. Dethier, V.G. Sensitivity of the contact chemoreceptors of the blowfly to vapors. *Proc. Nat. Acad. Sci. (Wash.)* **1972**, *69*, 2189–2192.
99. Städler, E.; Hanson, F.E. Olfactory capabilities of the “gustatory” chemoreceptors of the tobacco hornworm larvae. *J. Comp. Physiol.* **1975**, *104*, 97–102.
100. Maldonado, H.; Levin, L. Distance estimation and the monocular cleaning reflex in praying mantis. *Z. Vergl. Physiol.* **1967**, *56*, 258–267.
101. Page, K.L.; Zakotnik, J.; Dürr, V.; Matheson, T. Motor control of aimed limb movements in an insect. *J. Neurophysiol.* **2008**, *99*, 484–499.
102. Torres, G.; Horowitz, J.M. Activating properties of cocaine and cocaethylene in a behavioral preparation of *Drosophila melanogaster*. *Synapse* **1998**, *29*, 148–161.
103. Yellman, C.; Tao, H.; He, B.; Hirsh, J. Conserved and sexually dimorphic behavioral responses to biogenic amines in decapitated *Drosophila*. *Proc. Natl. Acad. Sci. USA* **1997**, *94*, 4131–4136.
104. Schaefer, P.L.; Ritzmann, R.E. Descending influences on escape behavior and motor pattern in the cockroach. *J. Neurobiol.* **2001**, *49*, 9–28.

105. Corfas, G.; Dudai, Y. Habituation and dishabituation of a cleaning reflex in normal and mutant *Drosophila*. *J. Neurosci.* **1989**, *9*, 56–62.
106. Weisel-Eichler, A.; Haspel, G.; Libersat, F. Venom of a parasitoid wasp induces prolonged grooming in the cockroach. *J. Exp. Biol.* **1999**, *202*, 957–964.
107. Gal, R.; Rosenberg, L.A.; Libersat, F. Parasitoid wasp uses a venom cocktail injected into the brain to manipulate the behavior and metabolism of its cockroach prey. *Arch. Insect Biochem. Physiol.* **2005**, *60*, 198–208.
108. Zack, S. The effects of foreleg amputation on head grooming behaviour in the praying mantis, *Sphodromantis lineola*. *J. Comp. Physiol.* **1978**, *125*, 253–258.
109. Campbell, F.L. A new antennal sensillum of *Blattella germanica* (Dictyoptera: Blattellidae) and its presence in other Blattaria. *Ann. Entomol. Soc. Am.* **1972**, *65*, 888–892.
110. Frings, H.; Frings, M. The loci of contact chemoreceptors in insects. *Am. Mid. Nat.* **1949**, *41*, 602–658.
111. Mustard, J.A.; Pham, P.M.; Smith, B.H. Modulation of motor behavior by dopamine and the D1-like dopamine receptor AmDOP2 in the honey bee. *J. Insect Physiol.* **2010**, *56*, 422–430.
112. Fussnecker, B.L.; Smith, B.H.; Mustard, J.A. Octopamine and tyramine influence the behavioral profile of locomotor activity in the honey bee (*Apis mellifera*). *J. Insect Physiol.* **2006**, *52*, 1083–1092.
113. Schröder, R.; Hilker, M. The relevance of background odor in resource location by insects: A behavioral approach. *BioScience* **2008**, *58*, 308–316.
114. Webb, B. Cognition in insects. *Phil. Trans. R. Soc. B* **2012**, *367*, 2715–2722.
115. Teichert, H.; Dötterl, S.; Frame, D.; Kirejtshuk, A.; Gottsberger, G. A novel pollination mode, saprocantharophily, in *Duguetia cadaverica* (Annonaceae): A stinkhorn (Phallales) flower mimic. *Flora* **2012**, *207*, 522–529.
116. Bruce, T.J.A.; Pickett, J.A. Perception of plant volatile blends by herbivorous insects—Finding the right mix. *Phytochemistry* **2011**, *72*, 1605–1611.
117. Clarkson, J.M.; Charnley, A.K. New insights into the mechanisms of fungal pathogenesis in insects. *Trends Microbiol.* **1996**, *4*, 197–203.
118. Gripenberg, S.; Mayhew, P.J.; Parnell, M.; Roslin, T. A meta-analysis of preference-performance relationships in phytophagous insects. *Ecol. Lett.* **2010**, *13*, 383–393.
119. Cunningham, J.P. Can mechanism help explain insect host choice? *J. Evol. Biol.* **2012**, *25*, 244–251.
120. Floyd, M.; Evans, D.A.; Howse, P.E. Electrophysiological and behavioural studies on naturally occurring repellents to *Reticulitermes lucifugus*. *J. Insect Physiol.* **1976**, *22*, 697–701.
121. Dong, C.; Zhang, J.; Chen, W.; Huang, H.; Hu, Y. Characterization of a newly discovered China variety of *Metarhizium anisopliae* (*M. anisopliae* var. *dechyium*) for virulence to termites, isoenzyme, and phylogenetic analysis. *Microbiol. Res.* **2007**, *162*, 53–61.
122. Sun, J.; Fuxa, J.R.; Richter, A.; Ring, D. Interactions of *Metarhizium anisopliae* and tree-based mulches in repellence and mycoses against *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Environ. Entomol.* **2008**, *37*, 755–763.
123. Carey, A.F.; Carlson, J.R. Insect olfaction from model system to disease control. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 12987–12995.

124. Pinho, P.G.D.; Ribeiro, B.; Gonçalves, R.F.; Baptista, P.; Valentão, P.; Seabra, R.M.; Andrade, P.B. Correlation between the pattern volatiles and the overall aroma of wild edible mushrooms. *J. Agric. Food Chem.* **2008**, *56*, 1704–1712.
125. Mburu, D.M.; Maniania, N.K.; Hassanali, A. Comparison of volatile blends and nucleotides sequences of two *Beauveria bassiana* isolates of different virulence and repellency towards the termite *Macrotermes michealseni*. *J. Chem. Ecol.* **2013**, *39*, 101–108.
126. Pasquinelli, A.E.; Hunter, S.; Bracht, J. MicroRNAs: A developing story. *Curr. Opin. Gen. Dev.* **2005**, *15*, 200–205.
127. Vreugdenhil, E.; Berezikov, E. Fine-Tuning the brain: microRNAs. *Front. Neuroendocrinol.* **2010**, *31*, 128–133.
128. Abbott, A.L. Uncovering new functions for MiRNAs in *Caenorhabditis elegans*. *Curr. Biol.* **2011**, *21*, 668–671.
129. Pradel, E.; Zhang, Y.; Pujol, N.; Matsuyama, T.; Bargmann, C.I.; Ewbank, J.J. Detection and avoidance of a natural product from the pathogenic bacterium *Serratia marcescens* by *Caenorhabditis elegans*. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 2295–2300.
130. Zhang, Y.; Lu, H.; Bargmann, C.I. Pathogenic bacteria induce aversive olfactory learning in *Caenorhabditis elegans*. *Nature* **2005**, *438*, 179–184.
131. Zhang, Y. Neuronal mechanisms of *Caenorhabditis elegans* and pathogenic bacteria interactions. *Curr. Opin. Microbiol.* **2008**, *11*, 257–261.
132. Song, B.-M.; Faumont, S.; Lackery, S.; Avery, L. Recognition of familiar food activities feeding via an endocrine serotonin signal in *Caenorhabditis elegans*. *eLife* **2013**, *2*, e00329.
133. Hendricks, S.J.; Sollars, S.I.; Hill, D.L. Injury-Induced functional plasticity in the peripheral gustatory system. *J. Neurosci.* **2002**, *22*, 8607–8613.
134. Cross-Mellor, S.K.; Hoshoooley, J.S.; Kavaliers, M.; Ossenkopp, K.P. Immune activation paired with intraoral sucrose conditions oral rejection. *Neuroreport* **2004**, *15*, 2287–2291.
135. Cross-Mellor, S.K.; Kavaliers, M.; Ossenkopp, K.-P. Comparing immune activation (lipopolysaccharide) and toxin (lithium chloride)-induced gustatory conditioning: Lipopolysaccharide produces conditioned taste avoidance but not aversion. *Behav. Brain Res.* **2004**, *148*, 11–19.
136. Cross-Mellor, S.K.; Kavaliers, M.; Ossenkopp, K.-P. The effects of lipopolysaccharide and lithium chloride on the ingestion of a bitter-sweet taste: Comparing intake and palatability. *Brain Behav. Immun.* **2005**, *19*, 564–573.
137. Pacheco-Lopez, G.; Niemi, M.-B.; Kou, W.; Harting, M.; Fandrey, J.; Schedlowski, M. Neural substrates for behaviorally conditioned immunosuppression in the rat. *J. Neurosci.* **2005**, *25*, 2330–2337.
138. Niemi, M.-B.; Harting, M.; Kou, W.; del Rey, A.; Besedovsky, H.O.; Schedlowski, M.; Pacheco-Lopez, G. Taste-Immunosuppression engram: Reinforcement and extinction. *J. Neuroimmunol.* **2007**, *188*, 74–79.
139. Pacheco-Lopez, G.; Niemi, M.B.; Engler, H.; Engler, A.; Riether, C.; Doenlen, R.; Espinosa, E.; Oberbeck, R.; Schedlowski, M. Weaken taste-LPS association during endotoxin tolerance. *Physiol. Behav.* **2008**, *93*, 261–266.
140. Vega, F.E.; Kaya, H.K. *Insect Pathology*, 2nd ed.; Academic Press: San Diego, CA, USA, 2012; p. 508.

141. Tanada, Y.; Kaya, H.K. *Insect Pathology*; Academic Press: San Diego, CA, USA, 1993; p. 666.
142. Lemaitre, B.; Hoffmann, J. The host defense of *Drosophila melanogaster*. *Annu. Rev. Immunol.* **2007**, *25*, 697–743.
143. Fouks, B.; Michae, H.; Lattorff, G. Recognition and avoidance of contaminated flowers by foraging bumblebees (*Bombus terrestris*). *PLoS One* **2011**, *6*, e26328.
144. Swanson, J.A.I.; Torto, B.; Kells, S.A.; Mesce, K.A.; Tumlinson, J.H.; Spivak, M. Odorants that induce hygienic behaviour in honeybees: Identification of volatile compounds in chalkbrood-infected honeybee larvae. *J. Chem. Ecol.* **2009**, *35*, 1108–1116.
145. Ugelvig, L.V.; Kronauer, D.J.C.; Schrempf, A.; Heinze, J.; Cremer, S. Rapid anti-pathogen response in ant societies relies on high genetic diversity. *Proc. R. Soc. B* **2010**, *277*, 2821–2828.
146. Scharf, I.; Modlmeier, A.P.; Beros, S.; Foitzik, S. Ant societies buffer individual-level effects of parasite infections. *Am. Nat.* **2012**, *180*, 671–683.
147. Tragust, S.; Mitteregger, B.; Barone, V.; Konrad, M.; Ugelvig, L.V.; Cremer, S. Ants disinfect fungus-exposed brood by oral uptake and spread of their poison. *Curr. Biol.* **2013**, *23*, 76–82.
148. Nielsen, C.; Anurag, A.; Agrawal, A.A.; Hajek, A.E. Ants defend aphids against lethal disease. *Biol. Lett.* **2010**, *23*, 205–208.
149. Schoonhoven, L.M.; van Loon, J.J.A. An inventory of taste in caterpillars: Each species its own key. *Acta Zool. Acad. Sci. Hung.* **2002**, *48*, 215–263.
150. Chapman, R.F. Contact chemoreception in feeding by phytophagous insects. *Annu. Rev. Entomol.* **2003**, *48*, 455–484.
151. Dahanukar, A.; Hallem, E.A.; Carlson, J.R. Insect chemoreception. *Curr. Opin. Neurobiol.* **2005**, *15*, 423–430.
152. Hallem, E.A.; Dahanukar, A.; Carlson, J.R. Insect odor and taste receptors. *Annu. Rev. Entomol.* **2006**, *51*, 113–135.
153. Clark, A.G.; Eisen, M.B.; Smith, D.R.; Bergman, C.M.; Oliver, B.; Markow, T.A.; Kaufman, T.C.; Kellis, M.; Gelbart, W.; Iyer, V.N.; *et al.* Evolution of genes and genomes on the *Drosophila* phylogeny. *Nature* **2007**, *450*, 203–218.
154. McBride, C.S. Rapid evolution of smell and taste receptor genes during host specialization in *Drosophila sechellia*. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 4996–5001.
155. McBride, C.S.; Arguello, J.R. Five drosophila genomes reveal nonneutral evolution and the signature of host specialization in the chemoreceptor superfamily. *Genetics* **2007**, *177*, 1395–1416.
156. Steiner, S.; Erdmann, D.; Steidle, J.; Ruther, J. Host habitat assessment by a parasitoid using fungal volatiles. *Front. Zool.* **2007**, *4*, 3.
157. De Bruyne, M.; Baker, T. Odor detection in insects: Volatile codes. *J. Chem. Ecol.* **2008**, *34*, 882–897.
158. Bartholomay, L.C.; Cho, W.L.; Rocheleau, T.A.; Boyle, J.P.; Beck, E.T.; Fuchs, J.F.; Liss, P.; Rusch, M.; Butler, K.M.; Wu, R.C.C.; *et al.* Description of the transcriptomes of immune response-activated Hemocytes from the mosquito vectors *Aedes aegypti* and *Armigeres subalbatus*. *Infect. Immun.* **2004**, *72*, 4114–4126.
159. Aguilar, R.; Jedlicka, A.E.; Mintz, M.; Mahairaki, V.; Scott, A.L.; Dimopoulos, G. Global gene expression analysis of *Anopheles gambiae* responses to microbial challenge. *Insect Biochem. Mol. Biol.* **2005**, *35*, 709–719.

160. Myles, T.G. Alarm, aggregation, and defense by *Reticulitermes flavipes* in response to a naturally occurring isolate of *Metarhizium anisopliae*. *Sociobiology* **2002**, *40*, 243–255.
161. Mburu, D.M.; Ochola, L.; Maniania, N.K.; Njagi, P.G.N.; Gitonga, L.M.; Ndung'u, M.W.; Wanjoya, A.K.; Hassanali, A. Relationship between virulence and repellency of entomopathogenic isolates of *Metarhizium anisopliae* and *Beauveria bassiana* to the termite *Macrotermes michaelseni*. *J. Insect Physiol.* **2009**, *55*, 774–780.
162. Ennis, D.E.; Dillon, A.B.; Griffin, C.T. Pine weevils modulate defensive behavior in response to parasites of different virulence. *Anim. Behav.* **2010**, *80*, 283–288.
163. Yanagawa, A.; Yokohari, F.; Shimizu, S. Influence of fungal odor on grooming behavior of the termite, *Coptotermes formosanus* Shiraki. *J. Insect Sci.* **2010**, *10*, 141.
164. Yanagawa, A.; Fujiwara-Tsujii, N.; Akino, T.; Yoshimura, T.; Yanagawa, T.; Shimizu, S. Behavioral changes in the termite, *Coptotermes formosanus* (Isoptera), inoculated with six fungal isolates. *J. Invertebr. Pathol.* **2011**, *107*, 100–106.
165. Yanagawa, A.; Fujiwara-Tsujii, N.; Akino, T.; Yoshimura, T.; Yanagawa, T.; Shimizu, S. Musty odor of entomopathogens enhances disease-prevention behaviors in the termite *Coptotermes formosanus*. *J. Invertebr. Pathol.* **2011**, *108*, 1–6.
166. Hesketh, H.; Roy, H.E.; Eilenberg, J.; Pell, J.K.; Hails, R.S. Challenges in modelling complexity of fungal entomopathogens in semi-natural populations of insects. *BioControl* **2010**, *55*, 55–73.
167. Jackson, M.A.; Dunlop, C.A.; Jaronski, A.T. Ecological considerations in producing and formulating fungal entomopathogen for use in insect biocontrol. *BioControl* **2010**, *55*, 129–145.
168. Gendrin, M.; Welchman, D.P.; Poidevin, M.; Herve, M.; Lemaitre, B. Long-Range activation of systemic immunity through peptidoglycan diffusion in *Drosophila*. *PLoS Pathog.* **2009**, *5*, e1000694.
169. Bulmer, M.S.; Bachelet, I.; Raman, R.; Rosengaus, R.B.; Sasisekharan, R. Targeting an antimicrobial effector function in insect immunity as a pest control strategy. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 12652–12657.
170. Hauton, C.; Smith, V.J. Adaptive immunity in invertebrates: A straw house without a mechanistic foundation. *BioEssays* **2007**, *29*, 1138–1146.
171. Chou, P.-H.; Chang, H.-S.; Chen, I.-T.; Lin, H.-Y.; Chen, Y.-M.; Yang, H.-L.; Wang, K.C.H.-C. The putative invertebrate adaptive immune protein *Litopenaeus vannamei* Dscam (LvDscam) is the first reported Dscam to lack a transmembrane domain and cytoplasmic tail. *Dev. Comp. Immunol.* **2009**, *33*, 1258–1267.
172. Arala-Chaves, M.; Sequeira, T. Is there any kind of adaptive immunity in invertebrates? *Aquaculture* **2000**, *191*, 247–258.
173. Kurtz, J.; Armitage, S.A.O. Alternative adaptive immunity in invertebrates. *Trends Immunol.* **2006**, *27*, 493–496.
174. Walker, T.N.; Hughes, W.O.H. Adaptive social immunity in leaf-cutting ants. *Biol. Lett.* **2009**, *5*, 446–448.
175. Yek, S.H.; Boomsma, J.J.; Schiøtt, M. Differential gene expression in *Acromyrmex* leaf-cutting ants after challenges with two fungal pathogens. *Mol. Ecol.* **2013**, *22*, 2173–2187.
176. Cotter, S.C.; Kilner, R.M. Personal immunity *versus* social immunity. *Behav. Ecol.* **2010**, *21*, 663–668.
177. Cremer, S.; Armitage, S.A.O.; Schmid-Hempel, P. Social immunity. *Curr. Biol.* **2007**, *17*, R693–R702.

178. Cremer, S.; Sixt, M. Analogies in the evolution of individual and social immunity. *Phil. Trans. R. Soc. B* **2009**, *364*, 129–142.
179. Oi, D.H.; Pereira, R.M. Ant behaviour and microbial pathogens (Hymenoptera: Formicidae). *Fla. Entomol.* **1993**, *76*, 63–75.
180. Yanagawa, A.; Shimizu, S. Defense strategy of the termite, *Coptotermes formosanus* Shiraki to entomopathogenic fungi. *Jpn. J. Environ. Entomol. Zool.* **2005**, *16*, 17–22.
181. Galvanho, J.P.; Carrera, M.P.; Moreira, D.O.; Erthal, M., Jr.; Silva, C.P.; Samuels, R.I. Imidacloprid inhibits behavioral defences of the leaf-cutting ant *Acromyrmex subterraneus subterraneus* (Hymenoptera: Formicidae). *J. Insect. Behav.* **2013**, *26*, 1–13.
182. Kramm, K.R.; West, D.F. Termite pathogens: Effects of ingested *Metarhizium*, *Beauveria*, and *Glucosporium* conidia on worker termite (*Reticulitermes* sp.). *J. Invertebr. Pathol.* **1982**, *40*, 7–11.
183. Shimizu, S.; Yamaji, M. Effect of density of the termite, *Reticulitermes speratus* Kolbe (Isoptera: Rhinotermitidae), on the susceptibilities to *Metarhizium anisopliae*. *Appl. Entomol. Zool.* **2003**, *38*, 125–130.
184. Rohlf, M. Clash of kingdoms or why *Drosophila* larvae positively respond to fungal competitors. *Front. Zool.* **2005**, *2*, doi:10.1186/1742-9994-2-2.
185. Aubert, A.; Richard, F.J. Social management of LPS-induced inflammation in *Formica polyctena* ants. *Brain Behav. Immun.* **2008**, *22*, 833–837.
186. Wilson-Rich, N.; Spivak, M.; Fefferman, N.H.; Starks, P.T. Genetic, individual, and group facilitation of disease resistance in insect societies. *Annu. Rev. Entomol.* **2009**, *54*, 405–423.
187. Libersat, F.; Delago, A.; Gal, R. Manipulation of host behavior by parasitic insects and insect parasites. *Annu. Rev. Entomol.* **2009**, *54*, 189–207.
188. Rohlf, M.; Obmann, B.; Petersen, R. Competition with filamentous fungi and its implication for a gregarious lifestyle in insects living on ephemeral resources. *Ecol. Entomol.* **2005**, *30*, 556–563.
189. Hodson, A.K.; Friedman, M.L.; Wu, L.N.; Lewis, E.E. European earwig (*Forficula auricularia*) as a novel host for the entomopathogenic nematode *Steinernema carpocapsae*. *J. Invertebr. Pathol.* **2011**, *107*, 60–64.
190. Wang, Y.; Campbell, J.F.; Gaugler, R. Infection of entomopathogenic nematodes *Steinernema glaseri* and *Heterorhabditis bacteriophora* against *Popillia japonica* (Coleoptera: Scarabaeidae) larvae. *J. Invertebr. Pathol.* **1995**, *66*, 178–184.
191. Rieger, D.; Fraunholz, C.; Popp, J.; Bichler, D.; Dittmann, R.; Helfrich-Forster, C. The fruit fly *Drosophila melanogaster* favors dim light and times its activity peaks to early dawn and late dusk. *J. Biol. Rhythm.* **2007**, *22*, 387–399.
192. Thompson, G.J.; Crozier, Y.C.; Crozier, R.H. Isolation and characterization of a termite transferrin gene up-regulated on infection. *Insect Mol. Biol.* **2003**, *12*, 1–7.
193. Lemaitre, B.; Reichhart, J.M.; Hoffmann, J.A. *Drosophila* host defense: Differential induction of antimicrobial peptide genes after infection by various classes of microorganisms. *Proc. Natl. Acad. Sci. USA* **1997**, *94*, 14614–14619.
194. Gottar, M.; Gobert, V.; Matskevich, A.A.; Reichhart, J.M.; Wang, C.S.; Buft, T.M.; Belvin, M.; Hoffmann, J.A.; Ferrandon, D. Dual detection of fungal infections in *Drosophila* via recognition of glucans and sensing of virulence factors. *Cell* **2006**, *127*, 1425–1437.
195. Alexander, R.D. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **1974**, *5*, 324–383.

196. Yoshimura, T.; Takahashi, M. Termiticidal performance of an entomogenous fungus, *Beauveria brongniartii* (Saccardo) Petch in laboratory tests. *Jpn. J. Environ. Entomol. Zool.* **1998**, *9*, 16–22.
197. Wilson, K.; Knell, R.; Boots, M.; Koch-Osborne, J. Group living and investment in immune defense: An interspecific analysis. *J. Anim. Ecol.* **2003**, *72*, 133–143.
198. Rosengaus, R.B.; Jordan, C.; Lefebvre, M.L.; Traniello, J.F.A. Pathogen alarm behavior in termite: A new form of communication in social insects. *Naturwissenschaften* **1999**, *86*, 544–548.
199. Ugelvig, L.V.; Cremer, S. Social prophylaxis: Group interaction promotes collective immunity in ant colonies. *Curr. Biol.* **2007**, *17*, 1967–1971.
200. Fefferman, N.H.; Traniello, J.F.A.; Rosengaus, R.B.; Calleri, D.V., II. Disease prevention and resistance in social insects: Modeling the survival consequences of immunity, hygienic behavior, and colony organization. *Behav. Ecol. Sociobiol.* **2007**, *61*, 565–577.
201. Radford, A.N. Post-Allogrooming reductions in self-directed behaviour are affect by role and status in the green woodhoopoe. *Biol. Lett.* **2012**, *8*, 24–27.
202. Rosengaus, R.B.; Maxmen, A.B.; Coates, L.E.; Traniello, J.F.A. Disease resistance: A benefit of sociality in the dampwood termite *Zootermopsis angusticollis* (Isoptera: Termopsidae). *Behav. Ecol. Sociobiol.* **1998**, *44*, 125–134.
203. Chouvenc, T.; Su, N.-Y.; Robert, A. Inhibition of *Metarhizium anisopliae* in the alimentary tract of the eastern subterranean termite *Reticulitermes flavipes*. *J. Invertebr. Pathol.* **2009**, *101*, 130–136.
204. Okuno, M.; Tsuji, K.; Sato, H.; Fujisaki, K. Plasticity of grooming behavior against entomopathogenic fungus *Metarhizium anisopliae* in the ant *Lasius japonicus*. *J. Ethol.* **2012**, *30*, 23–27.
205. Little, A.E.F.; Murakami, T.; Mueller, U.G.; Currie, C.R. Defending against parasites: Fungus-Growing ants combine specialized behaviours and microbial symbionts to protect their fungus garden. *Biol. Lett.* **2006**, *2*, 12–16.
206. Fernandez-Marin, H.; Zimmerman, J.; Rehner, S.; Weislo, W. Active use of the metapleural glands by ants in controlling fungal infection. *Proc. R. Soc. Lond. B* **2006**, *273*, 1689–1695.
207. Beattie, A.J.; Turnbull, C.L.; Hough, T.; Knox, R.B. Antibiotic production—A possible function for the metapleural glands of ants (Hymenoptera, Formicidae). *Ann. Entomol. Soc. Am.* **1986**, *79*, 448–450.
208. Bot, A.N.M.; Obermayer, M.L.; Holldobler, B.; Boomsma, J.J. Functional morphology of the metapleural gland in the leaf-cutting ant *Acromyrmex octospinosus*. *Insect Soc.* **2001**, *48*, 63–66.
209. Hölldobler, B.; Wilson, E.O. *The Ants*; Belknap Press: Cambridge, MA, USA, 1990; p. 746.
210. Mackintosh, J.A.; Trimble, J.E.; Jones, M.K.; Karuso, P.H.; Beattie, A.J.; Veal, D.A. Antimicrobial mode of action of secretions from the metapleural gland of *Myrmecia gulosa* (Australian bull ants). *Can. J. Microbiol.* **1995**, *41*, 136–144.
211. Schlüns, H.; Crozier, R.H. Molecular and chemical immune defenses in ants (Hymenoptera: Formicidae). *Myrmecol. News* **2009**, *12*, 237–249.
212. Veal, D.A.; Trimble, J.E.; Beattie, A.J. Antimicrobial properties of secretions from the metapleural glands of *Myrmecia gulosa* (The Australian bull ants). *J. Appl. Bacteriol.* **1992**, *72*, 188–194.
213. Moretto, G.; Gonçalves, L.S.; de Jong, D. Heritability Africanized and European honey bee defensive behavior against the mite *Varroa jacobsoni*. *Braz. J. Genet.* **1993**, *16*, 71–77.
214. Büchler, R. Rate of damaged mites in natural mite fall with regard to seasonal effects and infestation development. *Apidologie* **1993**, *24*, 492–493.

215. Büchler, R. Design and success of a German breeding program for *Varroa* tolerance. *Am. Bee J.* **2000**, *140*, 662–665.
216. Bienefeld, K.; Zautkea, F.; Proninb, D.; Mazeedc, A. Recording the proportion of damaged *Varroa jacobsoni* Oud. in the debris of honey bee colonies (*Apis mellifera*). *Apidologie* **1999**, *30*, 249–256.
217. Hoffman, S. The occurrence of damaged mites in cage test and under field conditions in hybrids of different carniolan lines. *Apidologie* **1993**, *24*, 493–495.
218. Rosenkranz, P.; Fries, I.; Boecking, O.; Stürmer, M. Damaged *Varroa* mites in the debris of honey bee (*Apis mellifera* L.) colonies with and without hatching brood. *Apidologie* **1997**, *28*, 427–437.
219. Arechavaleta-Velasco, M.E.; Guzman-Novoa, E. Relative effect of four characteristics that restrain the population growth of the mite *Varroa destructor* in honey bee (*Apis mellifera*) colonies. *Apidologie* **2001**, *32*, 157–174.
220. Stanimirovic, Z.; Stevanovic, J.; Cirkovic, D. Behavioural defenses of the honey bee ecotype from Sjenica-Pester against *Varroa destructor*. *Acta Vet.* **2005**, *55*, 69–82.
221. Roode, J.C.; Lefèvre, T. Behavioral immunity in insects. *Insects* **2012**, *3*, 789–820.
222. Clemente, C.J.; Bullock, J.M.R.; Beale, A.; Federle, W. Evidence-Self-Cleaning in fluid-based smooth and hairy adhesive systems of insects. *J. Exp. Biol.* **2009**, *213*, 635–642.

© 2013 by the authors; licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).