THE QUARTERLY JOURNAL OF EXPERIMENTAL PSYCHOLOGY, 1992, *44B* (3/4) 165–178

Preimaginal Induction of Adult Behaviour in Insects

Yves Caubet, Pierre Jaisson, and Alain Lenoir
Université Paris-Nord, Villetaneuse, France

This review illustrates the role of preimaginal experiences in four main aspects of insect life: feeding, habitat choice, host selection, and social relationships. After an illustration of the two former aspects with examples taken from various species, special attention is paid to the two latter aspects. First, an experiment is described, which demonstrates the existence of preimaginal induction involved in host selection by the solitary parasitoid wasp *Dinarmus basalis* (Hymenoptera: Pteromalidae). Then, a review of preimaginal induction in ants' behaviour is presented; orientation of social behaviour, particularly altruism, is mainly determined by preimaginal imprinting. All the examples developed in this review clearly show that insects can no longer be considered as strictly, rigidly "pre-programmed" beings. Their complex behavioural development and plasticity is clearly documented.

For centuries, insects were considered as admirably miniaturized "machine animals", in which behavioural plasticity, common in vertebrates, was replaced by a highly elaborated and programmed stereotypy. This thinking was supported by considerations about the size and relative simplicity of insect brains, which were not supposed to contain enough neuronal "wiring" to permit complex developmental behavioural mechanisms.

Although insects are not comparable to higher vertebrates, their behaviour appears to be far more complex, plastic, and flexible than previously thought. In fact, the increasing impact of insects on agriculture has focused interest on studies of the determinants of host recognition in phytophagous[1] as well as entomophagous[2] species. This concern has had a major influence on the evolution of thought about insect behaviour. Another influence, partly also motivated by economic considerations, was the growing interest in bee biology. Indeed, discoveries made by Karl von

---

Requests for reprints should be sent to P. Jaisson, Laboratoire d'Ethologie et Sociobiologie, URA CNRS n° 667, Université Paris-Nord, 93430 Villetaneuse, France.

[1] Qualifies an organism which feeds on plants.

[2] Qualifies an organism which feeds on insects

Frisch and his German students documented the learning capabilities of social Hymenoptera. More recently, kinship theory opened a new era in the investigation of developmental mechanisms involved in kin recognition and discrimination behaviour.

From many of these studies, it appears that two preimaginal (in a wide sense) stages[3] may be susceptible to external stimulation, producing further imaginal, mature behaviour: larval and teneral[4] (or neoimaginal) stages. In this survey, we will consider successively significant examples of such induction phenomena involved in feeding, egg-laying, habitat choice and social behaviour in insects.

ROLE OF PREIMAGINAL LEARNING ON FEEDING BEHAVIOUR

In 1939, Thorpe showed that adult *Drosophila* flies proceeding from larvae reared in a peppermint-scented medium displayed a preference for a perfumed over a non-perfumed medium. Conversely, adult *Drosophila* flies born from larvae reared in a standard non-scented medium showed a spontaneous avoidance for a peppermint-scented milieu when given a choice involving a non-scented one. These results were confirmed by further authors (e.g. Cushing, 1941; Hershberger & Smith, 1967; Manning, 1971). Also, preimaginal learning phenomena were widely documented in phytophagous insects, particularly in lepidopteran and dipteran larvae: olfactory conditioning in larvae determines the host selection in adults ("Hopkins' effect") (see reviews by Hanson, 1983; Papaj & Prokopy, 1986, 1989). For example, *Colias* butterfly caterpillars familiarized to a particular fabaceous plant develop adult behavioural and physiological specializations adapted to this plant (Karowe, 1989). Evidence of specific food preference induction in lepidopterous larvae was demonstrated earlier by Jermy, Hanson, and Dethier (1968).

PREIMAGINAL INDUCTION OF HABITAT CHOICE

Following previous unconvincing attempts made by various authors, Alloway (1972) trained grain beetle larvae (*Tenebrio molitor*) in a T-maze using food reward, and observed a high degree of facilitation of learning in imago (adult beetles) resulting from these larvae and retested on the same task. They learned to orientate themselves in the maze more easily than imagos from inexperienced control larvae.

---

[3] *Preimaginal* includes all stages during which insects still do not present adult (imago) characteristics.

[4] *Teneral* represents the state of an adult (imago) insect immediately after moulting, during which it is soft, not very mobile, and generally immature in colouring.

More recently, learning of environmental cues was investigated in newly emerged imago insects. In *Drosophila*, this learning phenomenon seems to be involved in evolutionary genetics at the population level, where it complicates the patterns of host utilization in these phytophagous species (Hoffmann, 1988; Jaenike, 1983). Taylor (1986) demonstrated that habitat choice in *D. pseudoobscura* adults was influenced by early exposures to different temperature or light conditions; and the observed effect depended on the flies' genetic strain. However, the experimental design made it impossible to specify the period during which the stimulation operated.

In Formicine ants (*Formica polyctena* and *Camponotus vagus*), Jaisson (1980a) demonstrated that, in a nest-relocation situation, the presence of aromatic thyme (*Thymus vulgaris*) was actively preferred by mature workers that had been forced to spend their teneral stage (the first three or four weeks of an imago life lasting about two years) in the presence of thyme twigs. However, thyme was spontaneously repellent for mature workers collected in the field or for workers from thyme-less laboratory colonies. In these examples, social behaviour is actively involved through the decision made by scout ants seeking a nest location and subsequently recruiting the rest of the group to enter the new nest site.

In the primitive Ponerine ant *Neoponera villosa*, Dejean (1990) discovered preimaginal learning involved in habitat selection, which depended on exposure to a host plant during the larval stage. In the study area (Yucatan Peninsula, Mexico), these predatory ants nest within big Bromeliacea epiphytes, *Aechmea bracteata*. Young *N. villosa* ants reared in laboratory colonies in the presence of another plant, *Schomburgkia tibicinis* (Orchidacea), showed a clear preference for the latter when they were given a nesting choice between both plants. Individuals proceeding from laboratory nests in the absence of any plant chose randomly between the two plants. More investigation would be needed to understand why, in natural conditions, *Neoponera villosa* generally occupies only one epiphyte species in this region.

PREIMAGINAL LEARNING IN HOST SELECTION FOR EGG-LAYING

Early Learning in Parasitoid Wasps

Parasitoid wasps, including the ancestors of the social Hymenoptera (social bees, wasps, and ants) present an array of behavioural adaptations in their relations with their host species. The main difference between "true" parasites and parasitoids is that the latter's parasitic life is restricted to immature stages only. The host species are generally other insects, sometimes spiders. The parasitized stage may be one or more of the host's developmental stages, from the egg to the adult. In most cases, target hosts are phytophagous insects, which gives economical importance to parasitoids, as they often attack pests in the field or storage areas.

The host–parasitoid tandem involves co-evolutionary processes (see reviews by Vinson, 1975, 1984), which are often accompanied by a parallel co-evolution between the host and its host plant (see review by Smith, 1973). Here, researchers are facing tri-trophic level models with high complexity in adaptive phenomena. This is clearly illustrated by the examples of hyperparasitism where a parasitoid species becomes a potential host for an over-parasitoid species (Espelie & Brown, 1990). The specificity of parasitoid wasps for their host can be strict (specialist species) or rather low (generalist species).

When emerging from the host on which she developed, a young adult parasitoid female must seek a new potential host population. In many species, she rarely meets a suitable host near the eclosion site. In this context, natural selection favoured behavioural processes improving a rapid recognition of new egg-laying sites soon after ovarian maturation (mating takes place in early imaginal life). Several experimental studies have documented the importance of the first search for a host, or oviposition experiences, in further choices made by adult female parasitoids (Vinson, Barfield, and Henson, 1977; Vet & Schoonmann, 1988; Drost & Cardé, 1989). The experience of the host's plant early after emergence may also be important (see reviews by Vinson, 1981, 1984, 1985; Godfray & Waage, 1988). In its host seeking behaviour the parasitoid may successively use induced preferences for the host habitat (Carton, 1976; Vet, Dejong, Van Giessen, & Visser, 1990), for the damaged plant and host by-products (frass, exsuvies), and finally for the host itself (Dmoch, Lewis, Martin, & Nordlund, 1985; Lewis & Tumlinson, 1988).

Only a few works have analysed precisely the role of preimaginal learning in the induction of adult preference for a specific host stimulus (Thorpe, 1939; Smith & Cornell, 1979; Debolt, 1989; Caubet & Jaisson, 1991) or for a stimulus related to the presence of the preferred host (Thorpe & Jones, 1937; Arthur, 1965). We propose to illustrate these processes by the model of the Pteromalid wasp *Dinarmus basalis* Rondani, previously studied by two of us (Caubet & Jaisson, 1991).

The *Dinarmus basalis* model

This tiny wasp originates from eastern countries and has spread throughout Europe, Africa, and America, being confined to grain-storage units in the last two continents but also found in the field in the former. She parasitizes the immature stages of several bruchid (bean weevil) species (Coleoptera) feeding on stored or field seeds. Using a powerful sting apparatus, the *D. basalis* female perforates the grain integuments and paralyzes the host larva or pupa living inside. Then she lays eggs near the host's body. After eclosing, the parasitoid larva eliminates supernumerary parasitoid eggs and feeds on the host's body (ectoparasitism). Once her development has been completed, she starts an eight-day metamorphosis within the chamber previously burrowed by the host larva into the grain. Finally, the adult wasp emerges from the seed, using her mandibles to cut through the grain integument. Frequently the young parasitoid female mates soon after escaping from the grain and begins to search for a suitable host to parasitize. However, the teneral wasp stays in the host chamber for several hours after the imaginal moult before finally freeing from the seed.

D. basalis is potentially able to parasitize several species of bruchids. This led us to study the possibility of inducing host preference in females whose developmental stages were manipulated. For this purpose, we used two bruchid species, both potential wasp hosts, and reared on kidney beans (*Phaseolus vulgaris*): *Acanthoscelides obtectus* and *Zabrotes subfasciatus*. Wasps derived from the same population were reared on both species, and their mated daughters were tested for their first spontaneous host preference three days after emergence. They were given a choice between two beans, one infested by *Acanthoscelides* and the other by *Zabrotes*. The results showed a clear difference according to their host origins: females that developed on *Zabrotes* chose this same host type in almost all tests, whereas those reared on *Acanthoscelides* made choices not significantly different from random. This demonstrated that the developmental origin of the parasitoid wasp influences her spontaneous preference in the first situation for host selection. However, the asymmetry in the results suggested a likely constraint on learning through an endogenous predisposition to learn features of one host species more easily than those of the other. In this case, predispositions would favour *Zabrotes* cues over *Acanthoscelides* ones.

In a second experiment, *D. basalis* pupae were manipulated in order to locate the sensitive period during which familiarization takes place: old parasitoid pupae reared on one host species were moved beside the remains of an individual of the other host species. It showed that only one period was involved: the teneral stage, which occurs during the few hours of confinement spent in the host chamber, just beside the host's remains. Therefore, the host the parasitoid larva had fed on did not affect further host selection behaviour as an adult. Hence, this acquisition of host preference appears to differ from the classical preimaginal conditioning through host consumption, as described in "Hopkins' host selection effect" (Hopkins, 1917). Conclusively, the imago female who escapes from the seed is already trained for a clear host preference only if, as a teneral wasp, she was exposed to *Zabrotes* remains.

Starting from these results, we investigated possible differences in the oviposition behaviour between wasps from different host origins. The data presented below concern female wasps proceeding from either *Zabrotes* or *Acanthoscelides* hosts and exposed to bean seeds infested by *Zabrotes*. A significant difference between the two kinds of tested wasps appeared in the time latency before entering into contact with one of the bean seeds. Parasitoid females reared on *Acanthoscelides* (Group *A*) spent more time before choosing any bean than did the *Zabrotes* originating wasps (Group *Z*). After choosing a bean, the antennal exploration of the seed surface took longer for Group *A* females, whereas those of Group *Z* began more rapidly to drill the grain integument with their ovipositors.

The duration of the first complete ovipositor insertion was shorter for Group *Z* females. This first insertion is known to be the stage during which the parasitoid female recognizes the host larva and evaluates its suitability by collecting information through the ovipositor *sensilla* (King & Fordy, 1970; Weseloh, 1971). The duration of following insertions (which correspond to egg-laying) was longer for parasitoid females proceeding from *Zabrotes* hosts. The general tendency of these data is to show that adult parasitoid females proceeding from a *Zabrotes* host behave with greater "confidence" when they are engaged in the egg-laying behaviour sequence in the presence of *Zabrotes* hosts. This probably means that their reproductive investment is higher.

Dinarmus basalis constitutes an excellent model for experimenting on preimaginal learning as well as for theoretical considerations about behavioural development or behavioural ecology in higher insects. In fact, it represents a significant example of behavioural plasticity during immature stages and illustrates the role of endogenous constraints favoured by natural selection and acting directly upon individual responsiveness to stimulation experienced during the preimaginal life.

PREIMAGINAL INDUCTION OF SOCIAL BEHAVIOUR

It is difficult to affirm definitively that susceptibility to environmental influences in the ethogenesis of parasitoid Hymenoptera constitutes a preadaptation that favours the evolution of sociality in this taxonomic group. The idea is well supported by finding more than one example in which a young social Hymenoptera (mainly ants and social wasps) integrates information from nestmates or from nest material during the larval stage and then uses this to determine its behaviour during its mature stage. Two periods seem to be important in these developmental processes: the larval stage (examples known in ants) and the teneral (young callow) stage (examples known in ants and social wasps). Their importance has been documented in three distinct behavioural situations: species-specific recognition, colony recognition, and environment recognition (this last reviewed above).

Early Induction of Species-specific Recognition

Social parasitism in ants (see recent reviews by Buschinger, 1986, and Davies, Bourke, & de Brooke, 1989) is known in about 2% of all living species. The more complex form of permanent social parasitism, *slave-making*, is only shown by species belonging to two advanced subfamilies of ants among the twelve represented in the present-day fauna: Myrmicinae and Formicinae. This is possibly related to the higher capability of social learning in advanced ants than in more primitive subfamilies (Jaisson, 1991). A slave-maker colony consists of two social groups living together and forming an integrated interspecific society in which one group (the social parasite) exploits for its own benefit the resources provided by the other (the social host). Enslaved individuals are collected by the slave-maker species through repeated raids during summertime. Attention was paid to the fact that in the raids made by Formicinae slave-makers, only pupae (exceptionally teneral workers) are captured. One current interpretation is that this choice made by the raiding slave-makers was selected because pupae do not need to be fed. Another interpretation (Jaisson, 1973, 1975a), compatible with the former, considers that selective raiding on pupae is more adaptive because it uses, in an interspecific context, behavioural characteristics already present in many advanced species: the ability to learn the colony chemical visa during the early moments of imaginal life (teneral stage). In advanced species, there is a rule of thumb based on a total reliance between members of the colony, which might be expressed as: "display care for any member of the colony you emerged in". Consequently, the most important trick used in the slave-maker strategy would be the deception of the enslaved individuals as soon as they emerge from the pupae. In fact, teneral workers of the host Formicine *Serviformica fusca* could be experimentally induced to recognize pupae of a variety of genera (including the *Raptiformica* slave-maker as well as *Formica*, *Camponotus*, or *Lasius* species, which are neither slave-makers nor slaves) as their own if they were kept in their presence during the few days after the imaginal moult (Jaisson, 1973, 1975b). This was confirmed in other related *Serviformica* species (e.g. Le Moli & Mori, 1985, 1987). Moreover, *Formica polyctena*, which is never enslaved, shows the same training capacities to recognize allospecific cocoons, although it is never found in natural mixed colonies. Mature *Serviformica* workers from a pure *Serviformica* colony consistently refuse to tend offered *Raptiformica* cocoons, which are considered as prey. Hence, the evolution of early learning capabilities, apparently related to the total reliance between members of the colony, seems to have strongly favoured the evolution of cheating species (Jaisson, in press). However, little is known still about the individual ethogenesis of worker ants enslaved in Myrmicinae colonies.

Such studies will surely take place in the next few years, and it can be expected that they will somewhat confirm those results obtained with Formicinae slave and slave-making species.

Artificial mixed nests of ants have been formed and studied since the end of the nineteenth century (see reviews by Breed & Bennett, 1987; Carlin, 1988; Jaisson, 1985, 1991). As for natural mixed colonies, early learning processes are involved in the successful establishment of artificial colonies. However, in natural conditions parasite and host species are phylogenetically closely related, as predicted by Emery's rule (1909), and there are never more than two species in one nest. In the laboratory, more "fantasy" is possible than in the "natural laboratory", and in optimal conditions it is possible to rear six species together without observing any aggression. The feasibility of an artificial, queenless, mixed colony depends on the optimal combination of two variables: the age of the individual ants and the phylogenetic distance between their species (Jaisson, 1980b). In other words if the species are phylogenetically distant (e.g. belonging to distinct subfamilies), it is essential to use very young teneral workers, within a few hours after eclosing; conversely, two sibling species can be successfully joined together even if workers are several days old (Errard, 1984). Thus, the limits of the sensitive period during which the establishment of a mixed colony is feasible between two allospecific worker groups depends on their phylogenetic distance. It is highly probable that genetic characteristics of each species determine chemical recognition cues secreted by cuticular glands on the body surface. Moreover, there are several pieces of evidence supporting cuticular hydrocarbons as good candidates for recognition substances (Blum, 1987; Bonavita-Cougourdan, Clément, & Lange, 1987; Morel, Vander Meer, & Lavine, 1988; Nowbahari et al., 1990). In heterospecific queenless groups, workers are able to produce recognition cues. But in small queenright groups the queens would constitute the main source of colony visa (Carlin & Hölldobler, 1986, 1987). It seems that passive adsorption of hydrocarbons between members of the mixed colony occurs, whereas an active familiarization learning takes place in small groups (Errard & Jallon, 1987). Moreover, the hypothesis that individual ants are able to synthesize actively chemicals characterizing a partner species when they are reared in mixed groups has been recently proposed with some supporting evidence (Bagnères et al., 1991; Errard & Jaisson, 1991).

Early Induction of Colony Recognition

In ants, development of colony recognition seems to follow the same general mechanisms as for species-specific recognition. Generally speaking, recognition between adult nestmates seems stricter than colony–brood recognition. Consequently, a colony is far more tolerant towards an alien conspecific brood than towards non-nestmate conspecific adults (Jaisson, 1985; Crosland, 1988). Here also, early familiarization processes take place. Moreover, it was demonstrated in two *Camponotus* species that adult worker assistance during the eclosion of a new ant from the cocoon is important for the further social integration of this newly emerged callow (Morel, 1983, 1988).

In two Formicine genera at least, the development of colony recognition occurs during the larval stage. This was demonstrated experimentally by Isingrini, Lenoir, and Jaisson (1985) with the northern Mediterranean species *Cataglyphis cursor*. Workers of *C. cursor* responded preferentially to nestmate larvae when given a choice between nestmate and alien conspecific larvae presented simultaneously. *C. cursor* eggs were transferred from their natal nest to an adoptive conspecific colony where they developed to pupation. These pupae were then returned to the natal nest. Five days after emergence, the resulting workers showed a significant preference for carrying and licking non-sister larvae from the adoptive colony presented together with sister larvae. Familiarization took place during the larval stage and was retained through metamorphosis. Carlin and Schwartz (1989) obtained a similar result in slightly different experimental conditions with the carpenter ant *Camponotus floridanus*. Here, larvae were reared from the first instar to pupation in an adoptive colony, and the callow ants were transferred soon after emergence to a group of workers and pupae from a foreign colony. When they were 5–7 days old, experimental workers, when given a choice test, preferred to lick pupae from the colony known during the larval stage. This together with experiments on *Cataglyphis*, supports the idea that nestmate brood recognition documented in various ant genera (see reviews by Carlin, 1988, and Jaisson, 1991) could depend on a widely spread preimaginal learning process, at least in Formicine species. Its biological meaning is unclear; we may speculate that it plays a role in within-colony recognition. In fact, young worker nurses influenced by their own larval experience might clump together the larvae according to their own odour, which would provide, by return, preimaginal experience to these larvae (Carlin & Schwartz, 1989).

Preimaginal learning does not affect intra- or inter-specific aggression, which is determined by imprinting during and soon after emergence (see review by Jaisson, 1991). Recently it was suggested that queen recognition could be learned during larval life in *Cataglyphis cursor*: callow workers adopted by a new alien queen for two months were still attracted to their old familiar mother queen whom they had experienced as larvae (Berton, Lenoir, Nowbahari, & Barreau, 1991).

CONCLUSIONS

The examples presented in this review show that preimaginal and more generally early learning phenomena are far more common than previously expected for insects. They mainly occur in the following situations: habitat choice, feeding preferences, search for an oviposition site, and orientation of social behaviour. Hence, insects no longer appear to be inflexible "pre-programmed automatons", and early learning processes seem to be found as often as they are investigated. Nevertheless, many limits appear as in hygienic behaviour (Rothenbuhler, 1964) and topographic orientation capacities (Lauer & Lindauer, 1971) of honey bees and in recognition of homospecific brood by slave-making species of ants (Jaisson, 1985), where endogenous mechanisms do operate.

We must also keep in mind that early behavioural plasticity is very probably closely linked to neurophysiological plasticity during larval and neoimaginal stages (Blaney, Schoonhoven, & Simmonds, 1986; Palka, 1984; Vet et al., 1990). This point has rarely been explored experimentally. However, Gascuel and Masson (1987) observed that olfactory deprivation in honey bees during the pupae stage and the first 10 days of adult life induced a 27% decrease in the synaptical density in the glomeruli. This clearly means that the adult olfactory system develops through epigenetic mechanisms and, according to the authors, probably with a synaptic selective stabilization process comparable to the vertebrates. It is suspected that only few neurones persist through metamorphosis in insects. Nevertheless, these neurones can memorize early experiences. As early learning is also maintained through metamorphosis in amphibians (Miller & Berk, 1977), one may hypothesize that mnemonic storage could have common basis in insects and in some vertebrates.

REFERENCES

Alloway, T.M. (1972). Retention of learning through metamorphosis in the grain beetle (*Tenebrio molitor*). *American Zoologist, 12*, 471–477.

Arthur, A.P. (1965). Absence of preimaginal conditioning in *Itoplectis conquisitor* (Hym., Ichneumonidae). *Canadian Entomologist, 97*, 1000–1001.

Bagnères, A.G., Errard, C., Mulheim, C., Joulié, C., & Lange, C. (1991). Induced mimicry of colony odours in ants. *Journal of Chemical Ecology, 17*, 1641–1664.

Berton, F., Lenoir, A., Nowbahari, E., & Barreau, J. (1991). Ontogeny of queen attraction to workers in the ant *Cataglyphis cursor* (Hym. Formicidae). *Insectes Sociaux, 38*, 293–305.

Blaney, W.M., Schoonhoven, L.M., & Simmonds, M.S.J. (1986). Sensitivity in insect chemoreceptors; a review. *Experientia, 42*, 13–19.

Blum, M.S. (1987). The bases and evolutionary significance of recognitive olfactory acuity in insect societies. In J.M. Pasteels & J.-L. Deneubourg (Eds.), *From individual to collective behaviour in social insects* (pp. 277–294). Basel: Birkhäuser Verlag.

Bonavita-Cougourdan, A., Clément, J.L., & Lange, C. (1987). Nest-mate recognition: Cuticular hydrocarbons and colony odour in the ant *Camponotus vagus* Scop. *Journal of Entomological Science, 22*, 1–10.

Breed, M., & Bennett, B. (1987). Kin recognition in highly eusocial insects. In D.J.C. Fletcher & C.D. Michener (Eds.), *Kin recognition in animals* (pp. 243–285). New York: Wiley.

Buschinger, A. (1986). Evolution of social parasitism in ants. *Trends in Ecology and Evolution, 1*, 155–160.

Carlin, N.F. (1988). Species, kin and other forms of recognition in the brood discrimination behavior of ants. In J. Trager (Ed.), *Advances in myrmecology* (pp. 267–295). Leiden: E.J. Brill.

Carlin, N.F., & Hölldobler, B. (1986). The kin recognition system in carpenter ants (*Camponotus spp.*). I. Hierarchical cues in small colonies. *Behavioral Ecology and Sociobiology, 19*, 123–134.

Carlin, N.F., & Hölldobler, B. (1987). The kin recognition system in carpenter ants (*Camponotus spp.*). II. Larger colonies. *Behavioral Ecology and Sociobiology, 20*, 209–217.

Carlin, N.F., & Schwartz, P.H. (1989). Pre-imaginal experience and nestmate brood recognition in the carpenter ant, *Camponotus floridanus*. *Animal Behaviour, 38*, 89–95.

Carton, Y. (1976). Attraction de *Cothonaspis sp.* par le milieu trophique de son hôte *Drosophila melanogaster*. *Colloques Internationaux. Centre National de la Recherche Scientifique, 265*, 285–303.

Caubet, Y., & Jaisson, P. (1991). A post-eclosion early learning involved in host recognition by *Dinarmus basalis* Rondani (Hymenoptera: Pteromalidae). *Animal Behaviour, 42*, 977–980.

Crosland, M. (1988). Inability to discriminate between related and unrelated larvae in the ant *Rhytidoponera confusa* (Hymenoptera; Formicidae). *Annals of the Entomological Society of America, 81*, 844–850.

Cushing, M.D. (1941). An experiment on olfactory conditioning in *Drosophila guttifera*. *Proceedings of the National Academy of Sciences, Washington, 27*, 496–499.

Davies, N.B., Bourke, A.F.G., & de Brooke, M.L. (1989). Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. *Trends in Ecology and Evolution, 4*, 274–278.

Debolt, J.W. (1989). Host preference and acceptance by *Leiophron uniformis* (Hymenoptera, Braconidae): Effects of rearing on alternate *Lygus* (Heteroptera, Miridae) species. *Annals of the Entomological Society of America, 82*, 399–402.

Dejean, A. (1990). Influence de l'environnement pré-imaginal et précoce dans le choix du site de nidification de *Pachycondyla* (= *Neoponera*) *villosa* (Fabr.) (Formicidae, Ponerinae). *Behavioral Processes, 21*, 107–125.

Dmoch, J., Lewis, W.J., Martin, P.B., & Nordlund, D.A. (1985). Role of host-produced stimuli and learning in host selection behavior of *Cotesia* (=*Apanteles*) *marginiventris* (Braconidae). *Journal of Chemical Ecology, 11*, 453–463.

Drost, Y.C., & Cardé, R.T. (1989). Influence of experience on the sequential and temporal organization of host-acceptance behavior in *Brachymeria intermedia* (Chalcididae), an endoparasitoid of gypsy moth. *Journal of Insect Behaviour, 3*, 647–661.

Emery, C. (1909). Über der ursprung der dulotischen, parasitischen und myrmecophilen ameisen. *Biologisches Zentralblatt, 29*, 352–362.

Errard, C. (1984). Evolution, en fonction de l'âge, des relations sociales dans les colonies mixtes hétérospécifiques chez les fourmis des genres *Camponotus* et *Pseudomyrmex*. *Insectes Sociaux, 31*, 185–198.

Errard, C., & Jaisson, P. (1991). Les premières étapes de la reconnaissance interspécifique chez les fourmis *Manica rubida* et *Formica selysi* (Hymenoptera, Formicidae) élevées en colonies mixtes. *Comptes Rendus des Séances. Académie des Sciences. Série 3. Sciences de la Vie, 313*, 73–80.

Errard, C., & Jallon, J.-M. (1987). An investigation of the development of chemical factors in ants intrasociety recognition. In J. Eder & H. Rembold (Eds.), *Chemistry and biology of social insects* (p. 478). München: Peperny Verlag.

Espelie, K.E., & Brown, J.J. (1990). Cuticular hydrocarbons of species which interact on four trophic level: Apple, *Mallus pumila* ill.; codling moth, *Cydia pomonella* L.; a hymenopteran parasitoid, *Ascogaster quadridentata* Wesmael; and an hyperparasite, *Perilampus fulvicornis* Ashmead. *Comparative Biochemistry & Physiology. B. Comparative Biochemistry, 95B*, 131–136.

Gascuel, J., & Masson, C. (1987). Influence of olfactory deprivation on synapse frequency in developing antennal lobe of the honeybee *Apis mellifera. Neuroscience Research Communications, 1*, 173–180.

Godfray, H.C.J., & Waage, J.K. (1988). Learning in parasitic wasps. *Nature, 331*, 211.

Hanson, F.E. (1983). The behavioral and neurophysiological basis of food plant selection by lepidopterous larvae. In Sami-Ahmad (Ed.), *Herbivorous insects: Host-seeking behavior and mechanisms* (pp. 3–26). New York: Academic Press.

Hershberger, W.A., & Smith, M.P. (1967). Conditioning in *Drosophila melanogaster. Animal Behaviour, 15*, 259–262.

Hoffmann, A.A. (1988). Early adult experience in *Drosophila melanogaster. Journal of Insect Physiology, 34*, 197–204.

Hopkins, A.D. (1917). Discussions of C.G. Hewitt's paper on insect behaviour. *Journal of Economic Entomology, 10*, 92–93.

Isingrini, M., Lenoir, A., & Jaisson, P. (1985). Preimaginal learning as a basis of colony-brood recognition in the ant *Cataglyphis cursor. Proceedings of the National Academy of Sciences, USA, 82*, 8545–8547.

Jaenike, J. (1983). Induction of host preference in *Drosophila melanogaster. Oecologia, 58*, 320–325.

Jaisson, P. (1973). L'imprégnation dans l'ontogenèse du comportement de soins aux cocons chez les formicines. In *Proceedings of the VIIth International Conference, IUSSI, London*, pp. 176–180.

Jaisson. P. (1975a). L'imprégnation dans l'ontogenèse du comportement de soin aux cocons chez la jeune fourmi rousse (*Formica polyctena* Först.). *Behaviour, 52*, 1–37.

Jaisson, P. (1975b). *Contribution à l'étude de l'expérience chez les fourmis*. Doctoral thesis, Université Pierre-et-Marie Curie, Paris.

Jaisson, P. (1980a). Environmental preference induced experimentally in ants (Hymenoptera: Formicidae). *Nature, 286*, 388–389.

Jaisson, P. (1980b). Les colonies mixtes plurispécifiques: un modèle pour l'étude des fourmis. *Biologie Ecologie Méditerranéenne, 7*, 163–166.

Jaisson, P. (1985). Social behaviour. In G.A. Kerkut & L.I. Gilbert (Eds.), *Comprehensive insect physiology, biochemistry and pharmacology* (pp. 673–694). London: Pergamon Press.

Jaisson, P. (1991). Kinship and fellowship in ants and social wasps. In P.G. Hepper (Ed.), *Kin recognition* (pp. 60–93). Cambridge: Cambridge University Press.

Jaisson, P. (in press). *La fourmi et le sociobiologiste*. Paris: Odile Jacob.

Jermy, T., Hanson, F.E., & Dethier, V.G. (1968). Induction of specific food preference in lepidopterous larvae. *Entomologia Experimentalis et Applica, 11*, 211–230.

Karowe, D.N. (1989). Facultative monophagy as a consequence of prior feeding experience: behavioral and physiological specialization in individual *Colias philodice* larvae. *Oecologia, 78*, 106–111.

King, P.E., & Fordy, M.R. (1970). The external morphology of the "pore" structures on the tips of the ovipositor in Hymenoptera. *Entomologists Monthly Magazine, 106*, 65–66.

Lauer, J., & Lindauer, M. (1971). Genetisch fixierte Lerndispositionen bei der Honigbiene. *Abhandlungen Akademie Wissenschaften und der Literatur*, 1–87.

Le Moli, F., & Mori, A. (1985). The influence of the early experience of worker ants on enslavement. *Animal Behaviour, 33*, 1384–1387.

Le Moli, F., & Mori, A. (1987). The problem of enslaved ant species: origin and behavior. In J.M. Pasteels & J.-L. Deneubourg (Eds.), *From individual to collective behaviour in social insects* (pp. 333–363). Basel: Birkhäuser Verlag.

Lewis, W.J., & Tumlinson, J.H. (1988). Host detection by chemically mediated associative learning in a parasitic wasp. *Nature, 331*, 257–259.

Manning, A. (1971). Pre-imaginal conditioning in *Drosophila. Nature, 216*, 338–340.

Miller, R.R., & Berk, A.M. (1977). Retention over metamorphosis in the African claw-toed frog. *Journal of Experimental Psychology, Animal Behaviour Processes, 3*, 343–356.

Morel, L. (1983). Relation entre comportement agressif et privation sociale précoce chez les jeunes fourmis immatures de la fourmi *Camponotus vagus* Scop. (Hymenoptera: Formicidae). *Comptes Rendus Hebdomadaires des Séances. Académie des Sciences. Série D, 296*, 449–452.

Morel, L. (1988). Ontogenèse de la reconnaissance des membres de la société chez *Camponotus floridanus* (Hymenoptera: Formicidae). Rôle de l'expérience sociale précoce. *Biologie du Comportement, 13*, 59–72.

Morel, L., Vander Meer, R.K., & Lavine, B.K. (1988). Ontogeny of nestmate recognition cues in the red carpenter ant (*Camponotus floridanus*). *Behavioral Ecology and Sociobiology, 22*, 175–183.

Nowbahari, E., Lenoir, A., Clément, J.L., Lange, C., Bagnères, A.G., & Joulié, C. (1990). Individual geographical and experimental variation of cuticular hydrocarbons of the ant *Cataglyphis cursor* (Hymenoptera: Formicidae): Their use in nest and subspecies recognition. *Biochemical Systematus and Ecology, 18*, 63–73.

Palka, J. (1984). Precision and plasticity in the insect nervous system. *Trends in Neurosciences, 7*, 455–456.

Papaj, D.R., & Prokopy, R.J. (1986). Phytochemical basis of learning in *Rhagoletis pomonella* and other herbivorous insects. *Journal of Chemical Ecology, 12*, 1125–1143.

Papaj, D.R., & Prokopy, R.J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology, 34*, 315–350.

Rothenbuhler, W.C. (1964). Behavior genetics of nest cleaning in honey-bees. IV Responses of F1 and backcross generations to diseasekilled brood. *American Zoologist, 4*, 111–123.

Smith, C.C. (1973). The coevolution of plants and seeds predators. In L.E. Gilbert & P.H. Raven (Eds.), *Coevolution of animals and plants* (pp. 53–77). Boulder, CO: Colorado University Press.

Smith, M.A., & Cornell, H.V. (1979). Hopkins host selection in *Nasonia vitripennis* and its implications for sympatric speciation. *Animal Behaviour, 27*, 365–370.

Taylor, C.E. (1986). Habitat choice by *Drosophila pseudoobscura*: the roles of genotypes and of experience. *Behavior Genetics, 16*, 271–280.

Thorpe, W.H. (1939). Further studies on preimaginal conditioning in insects. *Proceedings of the Royal Society of London B. Biological Sciences, 127*, 424–433.

Thorpe, W.H., & Jones, F.G.W. (1937). Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. *Proceedings of the Royal Society of London B. Biological Sciences, 124*, 56–81.

Vet, L.E.M., De Jong, R., Van Giessen, W.A., & Visser, J.H. (1990). A learning-related variation in electroantennogram responses of a parasitic wasp. *Physiological Entomology, 15*, 243–247.

Vet, L.E.M., & Schoonmann, G. (1988). The influence of previous foraging experience on microhabitat acceptance in *Leptopilina heterotoma. Journal of Insect Behaviour, 1*, 387–392.

Vinson, S.B. (1975). Biochemical coevolution between parasitoids and their hosts. In P.W. Price (Ed.), *Evolutionary strategies of parasitic insects and mites* (pp. 14–18). New York: Plenum Press.

20 ex

Vinson, S.B. (1981). Habitat location. In D.A. Norlund, R.L. Jones, & W.J. Lewis (Eds.), *Semiochemicals: Their role in pest control* (pp. 51–77). New York: Wiley.

Vinson, S.B. (1984). Parasitoid-host relationship. In W.J. Bell & R.T. Cardé (Eds.), *Chemical ecology of insects* (pp. 205–233). New York: Chapman & Hall.

Vinson, S.B. (1985). The behavior of parasitoids. In G.A. Kerkut & L.I. Gilbert (Eds.), *Comprehensive insect physiology, biochemistry and pharmacology* vol. 9 (pp. 417–469). London: Pergamon Press.

Vinson, S.B., Barfield, C.S., & Henson, R.D. (1977). Ovipositional behavior of *Bracon mellitor*, a parasitoid of the boll weevil (*Anthonomus grandis*): Associative learning. *Physiological Entomology, 2*, 157–164.

Weseloh, R.M. (1971). Sense organs of the hyperparasite *Cheiloneura naxius* important in host selection processes. *Annals of the Entomological Society of America, 65*, 41–46.

Manuscript received August 1991

Expérience pré-imaginale et comportement adulte chez les insectes

Cet articles illustre le rôle de l'expérience pré-imaginale sous quatre des principaux aspects du comportement des insectes: comportement alimentaire, choix de l'habitat, sélection de l'hôte et interactions sociales. Après une illustration des deux premiers thèmes chez diverses espèces, nous abordons les deux derniers aspects avec une attention toute particulière. Tout d'abord, une expérience est présentée, démontrant l'existence d'une induction pré-imaginale impliquée dans la sélection de l'hôte par la guêpe solitaire parasitoïde *Dinarmus basalis* (Hyménoptère, Pteromalidae). Ensuite, une revue actualisée de l'influence de l'induction pré-imaginale sur le comportement des fourmis est présentée. L'orientation des comportements sociaux, en particulier les comportements altruistes, est fortement déterminée par l'empreinte pré-imaginale. Tous les examples développés dans cette revue montrent indubitablement que les insectes ne peuvent êntre considérés plus longtemps comme des automates "pré-programmés". La complexité de leur développement comportemental et sa plasticité sont, maintenant, clairement démontrées.

Inducción pre-imaginal de comportamiento adulto en insectos

Presentamos una revisión del rol de las experiencias pre-imaginales en cuatro aspectos de la vida de los insectos: alimentación, selección de habitat, selección de huéspedes y relaciones sociales. Luego de ilustrar los primeros dos aspectos con ejemplos de diversas especies, se presta especial atención a los últimos dos aspectos. Primeramente describimos un experimento que demuestra la existencia de inducción pre-imaginal en la selección de huéspedes por la avispa parasitoide solitaria *Dinarmus basilis* (Himenóptera: Pteromalidae). Luego presentamos una revisión de inducción pre-imaginal en hormigas: la orientación del comportamiento social, especialmente de altruísmo, es determinada principalmente por acuñamiento pre-imaginal. Todos los ejemplos en esta revisión demuestran que los insectos no pueden ser considerados como seres estricta y rígidamente pre-programados. Se demuestra el complejo desarrollo comportamental y la plasticidad de los insectos.