

## Parental care in the whitefly *Aleyrodes singularis*

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**Abstract.** 1. Patches of *Aleyrodes singularis* nymphs are characterised by a distinctive phenotype composed of the nymphs' exuviae, which are piled on the nymph, and by a covering layer of wax secreted by the adults; these characteristics have been found to confer defensive properties against natural enemies.

2. In contrast to the behaviour typical for ovipositing females of other aleyrodids, *A. singularis* females tend to remain near the patch of their progeny throughout their development. These mothers were therefore tested to show whether they exhibited active defensive behaviour towards natural enemies, beyond their contribution to passive defence achieved through the secretion of wax on the immatures.

3. The behaviour of whitefly adults differed significantly when performed in the presence of conspecific adults from their behaviour in the presence of natural enemies (either a parasitoid or a predator). The differences were expressed in the mean time devoted to some behavioural events, the frequency at which events were performed, and the number of transitions between pairs of events.

4. Most of the recorded behavioural differences were associated with departure of the natural enemies, facilitating immature survival.

5. This is the first report of active behavioural changes that convey defence of immature offspring for the family Aleyrodidae. Conditions characterising these findings and their relationship with those in which parental care is expected are discussed.

**Key words.** Aleyrodidae, defence, parasitoid, parental care, predator, whitefly.

### Introduction

Parental care, defined as any post-ovipositional behaviour that promotes survival, growth, and development of offspring, has been reported for organisms in a wide range of taxonomic groups including 13 different orders of insects (Tallamy, 1984, 1999; Tallamy & Wood, 1986). These behaviours can be classified into three groups: behaviours that protect offspring, behaviours that protect resources needed by the offspring, and behaviours that improve resources and/or facilitate resource acquisition (e.g. feeding) by offspring (Tallamy & Wood, 1986; Clutton-Brock, 1991). Following the rationale of Cody's *principle of allocation* (Cody, 1966), different behaviours within the first group can be ranked by the level of parental investment (the exact ranking should be determined by the specific currency presumably spent by parents, whether it be time, energy, or any extra risk taken): covering of eggs with

secretions, egg defence or guarding through the presence of the adult, egg defence by means of active antagonistic behaviour, and passive and active defence of young stages through development (Clutton-Brock, 1991; Fillippi-Tsukamoto *et al.*, 1995).

The whitefly *Aleyrodes singularis* (Homoptera: Aleyrodidae) is active in Israel from May to October. It feeds on composites, in particular *Lactuca serriola* L. (Compositae), which is a common weed throughout most of the country. Following mating, eggs are laid in small clusters on the underside of the younger leaves. The female remains on the leaf on or near its egg patch, and continues to lay eggs every few days. The female usually remains until the nymphs reach adulthood. Populations continue to develop on the same leaves, so from midsummer on, leaves can be found covered with the contiguous patches formed by progeny of one or several mothers, all of which may be present simultaneously.

Previous work has reported the existence of a defence mechanism of *A. singularis* nymphs towards two species of parasitoids, stemming from the influence of the unique morphology of the nymphs on parasitoid performance

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(Guershon & Gerling, 1994). The dorsum of the whitefly nymphs is covered by their preceding empty exuviae on which a wax cover, from the continuously secreting adults, has accumulated. Because the wax has been found to have a significant negative effect on the performance of parasitoids, and considering that adults usually remain on their offspring patch for a long time, provisioning their progeny continuously with fresh wax (when undisturbed, mothers may remain until adult emergence of their progeny), the existence of passive or indirect parental care for the eggs and immatures of this species was indicated. The continuous presence of adults, mainly females, prompted a check for the existence of a higher level of parental care, i.e. active agonistic behaviour displayed by whitefly adults against natural enemies.

In order to demonstrate the presence of active defence by adult whiteflies, it is necessary to study their behaviour in the presence and absence of natural enemies. When dealing with defence against predators, it may also be beneficial to differentiate self-defence, i.e. the activity of adults in the absence of progeny with parental care that would materialise only in the presence of the parent with progeny; however hundreds of field observations have never revealed whitefly females devoid of progeny. Preliminary laboratory trials were thus aimed at establishing such a situation; however all female *A. singularis* started ovipositing within 1–3 h of placement on a fresh leaf. The necessity for an acclimatisation period to be observed before behavioural experiments can be conducted prevented testing of females without progeny so only females with progeny were tested. The implications of the findings of this study in relation to defence in females without progeny are considered in the discussion.

There are three known natural enemies of *A. singularis* in Israel: the parasitoid *Encarsia inaron* (Hymenoptera: Apelinidae) and the predators *Acletoxenus formusus* (Diptera: Drosophilidae) and *Clitosthetus arcuatus* (Coleoptera, Coccinellidae). The parasitoid and the adult of one predator, *C. arcuatus*, were chosen for the experiments.

## Materials and methods

### *Insect origin*

All insects (the whitefly, the parasitoid *E. inaron*, and the coccinellid *C. arcuatus*) used in the study were collected outdoors from wild populations and reared in the laboratory on *L. serriola* plants, an annual weed that is almost the sole natural host of this whitefly. Tests were performed with individuals from the first and second generations reared in the laboratory.

### *Whitefly adult behaviour*

The behaviour of the whitefly adults was observed directly on untreated whitefly patches (including eggs, nymphs, and adults) infesting leaves of potted plants in a rearing room. The behavioural events were classified as follows: stand – standing

on the patch (while feeding, laying eggs, or performing other activities that could not be determined by the observer); flutter bout – fluttering both wings in a cyclic behaviour repeated approximately every 4 s; following three or four flutters, the abdomen was moved up and down while a last flutter was displayed; flutter – any movement of the wings that differed from the previously described bout; walk – walking on the patch or the leaf; head preen – cleaning the head and antennae with the front legs.

Each observation lasted 15 min. Behaviours were recorded using The Observer<sup>®</sup> event recorder (Noldus, 1991). Conditions during rearing and observational sets were: 26 °C, 50–60% RH, and a LD 14:10 h ratio. Behavioural observations of whitefly adults were repeated in the absence of enemies, in the presence of the parasitoid *E. inaron*, and in the presence of the predator *C. arcuatus*.

During exposure to natural enemies, a single parasitoid/predator was introduced to a leaf bearing a patch of whitefly nymphs and an adult female. The enemies had been pre-starved for 24 h (to standardise hunger) and cooled at 4 °C for 30–60 s prior to introduction for easy handling. Each scenario was replicated 10 times, with a new set-up, i.e. the nymph patch, whitefly adult, and natural enemy were renewed for each replication.

A graphical method to illustrate the behaviour is given in Fig. 1. Each event appears to be surrounded by one or several ellipses and is connected to other events by arrows. Each ellipse represents a relative quantity, and their sums represent the mean relative frequency at which the specific event occurs. The numbers inside the ellipse represent mean time (s) spent during a single performance of the annotated event. Arrows between events indicate the relative frequency of transition from one event to the other (see legend for details).

Three behavioural parameters were calculated for each scenario and used for a quantitative comparison of whitefly behaviour: mean duration of event, its frequency, and the frequency of transition between events. Duration of events was compared using a *t*-test (following square-root transformation) while frequencies of events and relative frequency of transitions between events were compared using a  $\chi^2$  analysis. Because specific events were performed at different frequencies by different whiteflies in parallel replications, in order to compare the duration, the mean duration of a specific event per whitefly was first estimated and the 10 obtained means were then used as replications for each of the three scenarios.

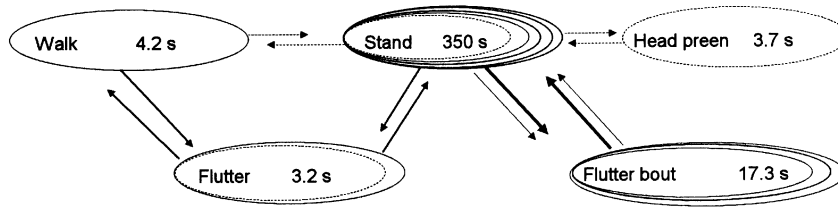
## Results

### *Whitefly behaviour*

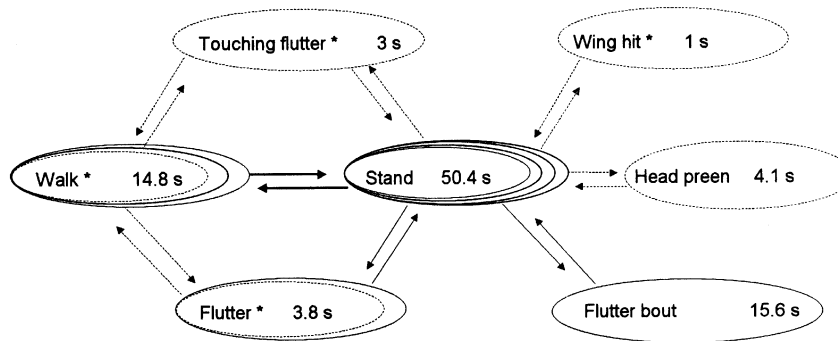
Ethograms of the observed behaviour for the three cases are shown in Fig. 1. A verbal description of whitefly behaviour under the different circumstances follows.

In the absence of enemies (Fig. 1a), whitefly behaviour was characterised mainly by the event *stand*, which was performed for lengthy durations, with the relative frequency and duration values recorded for all other events being distinctively smaller.

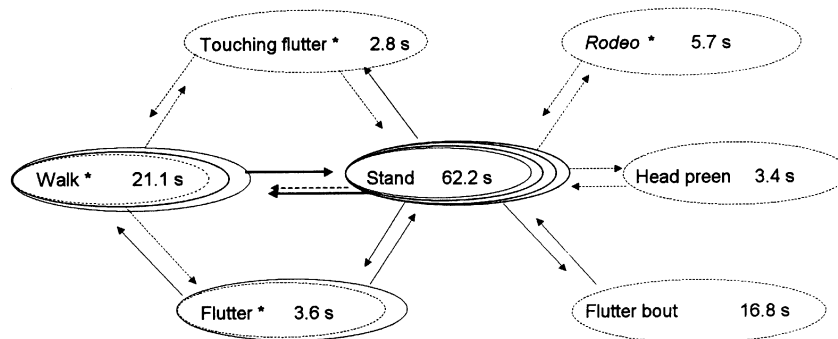
(a) In the presence of conspecifics



(b) In the presence of the parasitoid *E. inaron*



(c) In the presence of the predator *C. arcuatus*



**Fig. 1.** Ethograms of an *Aleyrodes singularis* adult when different insects are present in its patch. Each ellipse represents a relative frequency value: dotted ellipse=0.05, continuous ellipse=0.1. The sum of all ellipse values surrounding a specific event represents the relative frequency recorded for that event, e.g. three continuous ellipses around the event walk represent a proportional frequency of 0.3. The mean duration for the performance of each specified event (s) appears inside the ellipse. The sum of arrows between events indicates the relative frequency of transitions from one event to the other (dotted=0.05, continuous=0.1, bold continuous=0.2). See text for description of events.

The most frequent and visible transition between events was stand → flutter bout → stand. This was sometimes interrupted by a few flutters and by short walks.

In the presence of the parasitoid *E. inaron* (Fig. 1b), the event *stand* was again the most frequent, however this

event was interrupted repeatedly by transitions to walk and/or flutter, thus reducing its mean duration considerably. Therefore, in the presence of the parasitoid, two main transitions were observed: stand → walk → stand and stand → flutter → stand, with the previously observed stand →

flutter bout → stand no longer being the predominant sequence. In addition, some of the single *flutters* resulted in contact of the whitefly and parasitoid and were therefore classified as *touching flutters*. Moreover, a unique behaviour was performed twice by two whitefly females and was termed *wing hit*. During this event, the whitefly raised one wing, advancing its posterior edge forward, and placed it on the parasitoid being confronted. The wing thus reached a position  $\approx 180^\circ$  from its normal position, a situation never observed under any other circumstances. When the following events (marked by an asterisk in Fig. 1) were displayed by the whitefly, they ended with the desertion of the patch by the parasitoid in  $\approx 85\%$  of cases: walk (30 of 38 cases), flutter (23/27), touching flutter (9/9), and wing hit (2/2).

In the presence of the predator *C. arcuatus* (Fig. 1c), whitefly behaviour generally had a great resemblance to that described above, when the parasitoid was present. The most frequent event was stand, which was interrupted repeatedly by walk and by flutter. Thus, transitions between these two events formed the principal behavioural sequences when a predator was present. As in the encounters with the parasitoids, several of the single flutters ended in a touching flutter. In addition, a *rodeo* behaviour was observed four times, when the whitefly adult climbed on the predator's dorsum and clung to it while the predator walked rapidly on the leaf, apparently trying to shake off the whitefly. In all rodeo cases, both whitefly and predator fell from the leaf and did not return (at least during observation). A change in behaviour of the predator, accompanied by desertion of its prey, occurred in  $\approx 60\%$  of the cases when the following behaviours were observed: walk (28/46), flutter (17/28), touching flutter (6/6), rodeo (4/4).

#### Quantitative comparisons of whitefly behaviour

As noted above, three parameters were measured in the comparisons of behaviour: mean duration of event performance, mean frequency of each event, and frequency of transitions between events.

In the presence vs. absence of the parasitoid *E. inaron*, differences in mean duration were found for the event stand, which was shorter in the presence of the parasitoid, and for the event walk, which was longer ( $t = -12.679$ , d.f. = 18,  $P < 0.01$  and  $t = 5.671$ , d.f. = 18,  $P < 0.01$  respectively). Frequency of the flutter bout was lower in the presence of parasitoids, while frequency of the event walk was higher ( $\chi^2 = 10.265$  and  $\chi^2 = 4.202$ , d.f. = 2,  $P < 0.05$ ). Frequency of transition from one event to the other is summarised in Table 1. Significant differences were found for the frequency of transition between stand and flutter bout and vice versa, which occurred more in the absence of the wasp ( $\chi^2 = 11.3$  and  $10.62$  respectively, d.f. = 2,  $P < 0.05$ ), and between stand and walk, which was more frequent in the presence of the wasp ( $\chi^2 = 5.63$  and  $5.52$  respectively, d.f. = 2,  $P < 0.05$ ).

In the presence vs. absence of the predator *C. arcuatus*, the results were generally similar to those found with the parasitoids. The durations of the events stand and walk differed significantly. In the presence of the predator, the mean time devoted to each stand was shorter and the mean time for each walk was longer than in the absence of the predator ( $t = -13.32$ , d.f. = 18,  $P < 0.01$  and  $t = 7.14$ , d.f. = 18,  $P < 0.01$ ). When the predator was present, flutter bouts occurred less and walks more than in its absence ( $\chi^2 = 15.96$ , d.f. = 2,  $P < 0.05$  and  $\chi^2 = 6.277$ , d.f. = 2,  $P < 0.05$  respectively). The following transition frequencies differed when comparing whitefly behaviour in the presence and absence of the predator

**Table 1.** Comparison of the frequency of transitions between adjacent events performed by adult whiteflies with and without parasitoids on the patch. Origin = the event from which the whitefly starts, Target = the event to which the whitefly passes. P = with parasitoids, NP = without parasitoids.  $\chi^2$  values marked by an asterisk express significant differences between the frequencies ( $P < 0.05$ , d.f. = 2). Total number of transitions (N): P = 158, NP = 100.

Target:	Stand		Walk		Flutter bout		Flutter		Touching flutter		Wing hit		Head preen	
Origin	P	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P	NP
Stand			27	5	13	27	18	10	5	0	2	0	3	3
$\chi^2$			5.633*		11.3*		0.09							
Walk	24	4			0	0	9	7	4	0	0	0	0	0
$\chi^2$	5.523*						0.14							
Flutter bout	14	27	0	0			0	0	0	0	0	0	0	0
$\chi^2$	10.62*													
Flutter	17	7	8	7	0	0			0	0	0	0	0	0
$\chi^2$	0.499		0.114											
Touching flutter	6	0	3	0	0	0	0	0			0	0	0	0
Wing hit	2	0	0	0	0	0	0	0	0	0			0	0
Head preen	3	3	0	0	0	0	0	0	0	0	0	0		

(Table 2): from stand to flutter bout and back was more frequent without the coccinellid ( $\chi^2 = 15.75$  for both ways, d.f. = 2,  $P < 0.05$ ), and from stand to walk was more frequent with the coccinellid ( $\chi^2 = 7.063$  and  $10.33$  respectively, d.f. = 2,  $P < 0.05$ ).

## Discussion

The existence of passive parental care (egg guarding) has been reported previously for the Aleyrodidae *Neomaskellia bergii* (Kurosu *et al.*, 1992) and *Aleyrodes singularis* (Guershon & Gerling, 1994). The findings of this study show that a specific behavioural display performed by adult whiteflies under laboratory conditions, in the presence of their natural enemies, caused the latter to depart from the patch, enhancing the survival chances of the immature stages. These findings expand knowledge by showing that for *A. singularis*, parental care exists at a level considered to be beyond passive protection of eggs or even nymphs. In most observed cases, the specific behaviours performed by whitefly adults in the presence of natural enemies ended with the enemy leaving the patch and therefore potentially improved survival of whitefly nymphs.

As stated in the introduction, whether or not a behaviour can be considered parental care is determined by its contribution to improved offspring survival (Tallamy & Wood, 1986; Tallamy, 1999). In addition, it is of interest to determine whether the defensive behaviour of adult whitefly against predators in the absence of progeny is akin to that performed in the presence of its progeny. As reported in the introduction, the whitefly *A. singularis* does not lend itself to observations of defence without progeny. Therefore, it is only possible to extrapolate from the predator-oriented progeny-guarding behaviour performed by mothers as to the possible generality of the defensive behaviour exercised by this species. Most pertinent in this context are the flutter behaviours, especially

those ending in wing contact with the invader (touching flutters and wing hits). These are performed in relation to parasitoids that pose no danger to whitefly adults and never attack them for their own sake, and against predators that do. Thus, it is apparent that parental defence in this case is not just an extension of general defence behaviour but a directed antagonistic activity to protect the young from an intruder. On the other hand, the *rodeo* performance, in which the whitefly lands on top of the attacker and both tumble off the leaf, giving the whitefly a chance to escape, may be considered part of a more general defence repertoire.

There is an expected trade-off between parental care and oviposition potential. Parental care involves extensive investment in each individual offspring, increasing its chances of survival while contemporaneously curtailing the female's ability to produce and lay eggs (Clutton-Brock, 1991). The development of parental care therefore depends on the existence of conditions in which the production of fewer, better cared-for individuals will result in greater fitness than the production of many individuals of lesser quality. Wilson (1975) pointed out that this might occur when the environmental conditions are unfavourable (e.g. low food or poor territory quality), conditions are favourable but resources are limited in time or space, or under high selective pressures of natural enemies.

The whitefly *A. singularis* exhibits parental care by the ovipositing females, and, indeed, the number of eggs laid per female is relatively inferior to that of similar whitefly species while egg size is relatively larger (Guershon, 1997). Thus, it is interesting to examine which selective pressure appears to have directed the development of this care. Plant leaves, on which the whitefly spend their lives, appear to constitute a reliable source of food and shelter from the elements, however they offer little protection from natural enemies. Indeed, several types of defence and protection behaviours, such as cryptic colours or behaviour, ant mutualism, chemical secretions, aggregations, and parental care that potentially enhance the

**Table 2.** Comparison of the frequency of transitions between adjacent events performed by adult whiteflies with and without predators on the patch. Origin = the event from which the whitefly starts, Target = the event to which the whitefly passes. P = with predators, NP = without predators.  $\chi^2$  values marked by an asterisk express significant differences between the frequencies ( $P < 0.05$ , d.f. = 2). Total number of transitions (N): P = 169, NP = 100.

Target:	Stand		Walk		Flutter bout		Flutter		Touching flutter		Rodeo		Head preen	
Origin	P	NP	P	NP	P	NP	P	NP	P	NP	P	NP	P	NP
Stand			32	5	11	27	19	8	4	0	4	0	2	3
$\chi^2$			7.063*		15.75*		0.08							
Walk	36	4			0	0	8	7	2	0	0	0	0	0
$\chi^2$	10.33*						0.215							
Flutter bout	11	27	0	0			0	0	0	0	0	0	0	0
$\chi^2$	15.75*													
Flutter	17	7	11	7	0	0			0	0	0	0	0	0
$\chi^2$	0.313		0.011											
Touching flutter	3	0	3	0	0	0	0	0			0	0	0	0
Rodeo	4	0	0	0	0	0	0	0	0	0			0	0
Head preen	2	3	0	0	0	0	0	0	0	0	0	0		

benefits from protective properties have mainly been found and reported for leaf feeders (Wood, 1974; Kearns & Yamamoto, 1981; Tallamy & Wood, 1986). Whitefly immature stages, both eggs and nymphs, are exposed during most of their lives on the same leaf as sessile individuals, not being able to change their location or flee from predators or parasitoids. Thus, parental care could be envisaged evolving as an alternative, or addition to, other local defence mechanisms, reducing the vulnerability of these immatures to predation and parasitism. As pointed out by Gerling (1990), many of the whitefly nymphs are ornate with waxy secretions and structures whose function may be protective. The present defence mechanism, whereby the female progressively applies the waxy secretions to its progeny, can be considered a further development of a waxy protuberance strategy, visible in species of *Aleurocanthus*, *Aleurothrixus*, *Pealius*, *Siphoninus*, *Trialeurodes*, and other genera. In fact, the only parasitoid in Israel that has been found capable of penetrating the defensive wax coverage provided by the *A. singularis* adult is *Encarsia inaron*, which is also found in nature as an effective enemy of another wax-covered whitefly, *Siphoninus phyllireae* (Gould *et al.*, 1995; Rottenberg, 1995).

The reasons for parental care to appear in this species rather than in others of the family have not yet been elucidated; however biological and nutritional constraints on reproduction such as semelparity (i.e. a single reproductive event during a breeding cycle), whether apparent or functional, or other constraints on reproduction leading to limitations in oviposition, have recently been suggested as possible causes for the evolution of maternal care in insects when considering fecundity trade-offs (Tallamy & Brown, 1999). Thus, it would be interesting to speculate whether a reproductive constraint that could have led to the development of parental care exists in *A. singularis*. For example, the stenophagous host range that *A. singularis* exhibits, possibly in conjunction with the fact that it develops on an annual plant, would impose serious constraints on its development, which may favour the development of fewer, better protected, progeny. This is in contrast with most other stenophagous species that feed on perennials, or with a polyphagous range of whiteflies that feeds on annuals being able to move from one host species to the next once a host dies out.

This study represents the second reported case of parental care in whiteflies. With additional research, it is probable that more species exhibiting parental care will be found and the conditions under which they occur will shed more light on the *raison d'être* for this phenomenon.

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### References

- Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.
- Cody, M.L. (1966) A general theory of clutch size. *Evolution*, **20**, 174–184.
- Fillippi-Tsakamoto, L., Nomakuchi, S., Kuki, K. & Tojo, S. (1995) Adaptiveness of parental care in *Parastrachia japonensis* (Hemiptera: Cydnidae). *Annals of the Entomological Society of America*, **32**, 1055–1063.
- Gerling, D. (1990) Natural enemies of whiteflies: predators and parasitoids. *Whiteflies: their Bionomics, Pest Status and Management* (ed. by D. Gerling), pp. 147–185. Intercept, Andover, U.K.
- Gould, J.R., Bellows, T.S. & Paine, T.D. (1995) Preimaginal development, adult longevity and fecundity of *Encarsia inaron* (Hym. Aphelinidae) parasitizing *Siphoninus phyllireae* (Hom. Aleyrodidae) in California. *Entomophaga*, **1**, 55–68.
- Guershon, M. (1997) *Tritrophic level interactions in different phenotypes of whitefly nymphs*. PhD dissertation, Tel Aviv University, Israel. (In Hebrew with English summary.)
- Guershon, M. & Gerling, D. (1994) Defense of a sessile host against parasitoids: *Aleyrodes singularis* vs *Encarsia* spp. *Norwegian Journal of Agricultural Sciences Supplement*, **16**, 255–260.
- Kearns, R.S. & Yamamoto, R.T. (1981) Maternal behaviour and alarm response in the eggplant lace bug *Gargaphia solani* Heidemann (Tingidae: Heteroptera). *Psyche*, **88**, 215–230.
- Kurosu, U., Kudo, S. & Aoki, S. (1992) Parental care of the whitefly *Neomaskellia bergii* (Homoptera). *Japanese Journal of Entomology*, **60**, 396–400.
- Noldus, L.P.P.J. (1991) The observer: a software system for collection and analysis of observational data. *Behaviour Research Methods, Instruments and Computers*, **23**, 415–429.
- Rottenberg, O. (1995) *Population dynamics of the ash whitefly Siphoninus phyllireae (Haliday) (Homoptera: Aleyrodidae) and its natural enemies in the Tel-Aviv area*. MSc dissertation, Tel Aviv University, Israel. (In Hebrew with English summary.)
- Tallamy, D.W. (1984) Insect parental care. *BioScience*, **34**, 20–24.
- Tallamy, D.W. (1999) Child care among the insects. *Scientific American*, **1**, 72–77.
- Tallamy, D.W. & Brown, W.P. (1999) Semelparity and the evolution of maternal care in insects. *Animal Behaviour*, **57**, 727–730.
- Tallamy, D.W. & Wood, T.K. (1986) Convergence patterns in subsocial insects. *Annual Review of Entomology*, **31**, 369–390.
- Wilson, E.O. (1975) *Sociobiology: the New Synthesis*. Harvard University Press, Cambridge, Massachusetts.
- Wood, T.K. (1974) Aggregating behaviour of *Umbonia crassicornis* (Homoptera: Membracidae). *Canadian Entomologist*, **106**, 169–173.

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