Title: Sex differences in foraging behaviour and oviposition site preference in an insect predator, Orius sauteri

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Sex differences in foraging behaviour and oviposition site preference in an insect predator *Orius sauteri*
Abstract

The effects of patch quality on the foraging behaviour of an anthocorid predator *Orius sauteri* (Poppius) were compared between sexes. Prior experience in patches was also studied to determine whether this was a factor affecting oviposition decisions. Patch quality affected patch residence time differently for the two sexes; females stayed much longer in a patch with prey (*Thrips palmi* larvae) than a patch without prey, while males did not remain in any patch for extended periods. Most of the females remained in or moved to patches with prey, whereas males dispersed irrespective of patch quality. Both females released in patches with prey and females released in patches without prey deposited more eggs per hour in patches with prey than in patches without prey. Females released in patches without prey laid eggs in patches with prey at higher rates than did females released in patches with prey. Causes for the sex difference in patch residence time and allocation are discussed in relation to optimal foraging theory. The significance of selective oviposition and the role of experience in oviposition decisions within heterogeneous environments are also discussed.
Introduction

Searching for resources is one of the most important activities of animals (Hassell & Southwood, 1978; Bell, 1990, 1991). According to classical foraging theory, foragers maximise energetic gains by selectively exploiting patches rich in resources and by minimising foraging time in poor patches (Stephens & Krebs, 1986). A male’s reproductive success generally increases as it mates with more females, whereas females do not usually increase offspring production through multiple mating (Bateman, 1948; Trivers, 1972). From Bateman’s principle, it is predicted that factors limiting female and male reproductive success are food and mate acquisition rates, respectively. This disparity between sexes suggests that female dispersion should be influenced primarily by food resources while male dispersion should be influenced primarily by the presence of potential mates (Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977). Theoretical models predict that optimal male searching tactics are influenced by female distribution and density (Sandell & Liberg, 1992; Forchhammer & Boomsma, 1998).

Adult females of predatory insects can increase their egg production with prey consumption (e.g. Dixon, 1959; Ives, 1981; Mills, 1981; Coll & Ridgway, 1995; Nakashima & Hirose, 1999a). In addition, offspring survival rates may increase with number of prey in the patches chosen for oviposition by adult females. Thus, remaining longer in a better-quality patch (i.e. a patch with more prey) leads to higher female fitness. In contrast, although males also need prey to survive and reproduce, selecting a high density prey-patch does not directly increase male fitness if the patch lacks potential mates. Males, therefore, forage for prey under constraints created by the need to find mates.

Many studies on foraging behaviour of predacious insects have been conducted to detect
behavioural responses when predators encounter prey (Dixon, 1959; Marks, 1977; Nakamuta, 1982; Murakami & Tsubaki, 1984; Ettiffouri & Ferran, 1993). Differences in foraging behaviour between the sexes have been ignored in most studies although Inoue & Matsura (1983) and Hemptinne et al. (1996) demonstrated that female searching patterns were flexible and dictated by prey availability whereas males did not respond to differences in patch quality in food. Thus, we tested for sex differences in foraging responses of an insect predator to patches with rich or poor food resources.

Oviposition site preference by insect predators in response to prey availability should also be an important female fitness factor. However, only a few workers (Evans & Dixon, 1986; Kan, 1988a,b; Hemptinne et al., 1992) have focused on this subject, reporting selective oviposition for some coccinellid and syrphid predators in response to prey availability. These studies also revealed that predators are able to assess patch quality and lay more eggs in more profitable patches.

How previous experience by female predators influences their oviposition decisions in new patches has not, however, been investigated. In the field, insect predators usually live in temporally and spatially heterogeneous environments. They, therefore, encounter patches of various prey density, and quality of patches previously visited by females may affect patterns of their oviposition in the following patches. A dynamic state variable model examines the effects of the resource distribution on the oviposition behaviour (clutch size) of the insects (Mangel, 1987). The model predicts that higher probability of encounter with resource leads to a small frequency of large clutches (Mangel, 1987). Thus, we tested whether variability in patch quality affects oviposition patterns of an insect predator.

Species of Orius (Anthocoridae) are known to be effective biological control agents of thrips in greenhouses (van den Meiracker & Ramakers, 1991; Jacobson, 1993; van de Veire &
Degheele, 1993). For example, *Orius sauteri* (Poppius), a native of Japan that inhabits row crops and vegetables (Yasunaga, 1997; Yasunaga & Kashio, 1993), is an effective biological control agent against *Thrips palmi* Karny, a serious pest of vegetable crops both in the field (Nagai 1993ab; Ohno & Takemoto, 1997) and greenhouses (Kawai, 1995).

The main objectives of the work reported here are (1) to assess female and male *O. sauteri* responses in foraging behaviour to patches of different prey availability (patch quality), (2) to examine oviposition site selection by *O. sauteri* in response to prey availability in patches, and (3) to determine the effects of quality of a previously encountered patch on female oviposition decisions in the subsequent patch.

In the patch with prey, handling time of a predator is likely to increase with the number of consumed prey in a patch. If the number differs between sexes, this may cause a difference in patch residence time between them. We, therefore, conducted a laboratory experiment to estimate daily prey requirements of both sexes. To determine how female oviposition sites affect offspring development, we examined the effects of prey availability on nymphal survival.

**Materials and methods**

*Rearing.* An *O. sauteri* colony was initiated with adults collected from eggplant gardens in Hisayama Town, Fukuoka Prefecture in summer 1996. A *T. palmi* colony was established by insects collected from an eggplant field in Sanyo Town, Okayama Prefecture in the summer of 1993. Both colonies were maintained at 25 °C with a LD 16 : 8 h. *T. palmi* was reared on kidney bean plants and *O. sauteri* was reared on kidney bean plants infested by *T. palmi*, both in plastic boxes (50 cm x 70 cm x 46 cm)
Effects of patch quality on searching and oviposition behaviour. This experiment was designed to determine patch residence times of *O. sauteri* females and males and their dispersal upon release, whether females oviposition rates depend on prey availability in patches, and whether ovipositing females can assess patch quality based on experience in previous patches.

Five-day-old mated *O. sauteri* females and males were used. Newly emerged females and males were held individually in a glass vial (2.5 cm diameter x 7.0 cm height) with about 30 *T. palmi* second-instar larvae. A piece of filter paper (1.5 x 1.5 cm) and a leaflet of kidney bean (1.5 x 1.5 cm) were also placed in the vial. One day after emergence, pairs (a female and male) were each confined in a vial with about 60 larvae of *T. palmi*, filter paper, and a leaflet of kidney bean for 24 h. This procedure ensures successful mating (Nakashima et al., 1996; Honda et al., 1998). They were then held individually in vials as described above until testing. Prey, kidney bean leaves, and filter paper were replaced daily.

Four kidney bean plants, each grown in 10-cm pots, were housed in a plastic cage (50 x 70 x 46 cm) and served as an experimental unit (Fig. 1). Each plant was designated as either an *O. sauteri* prey-containing (PC) patch or a prey-deficient (PD) patch. A PC patch contained 60 second instar *T. palmi* larvae. The four plants were placed as shown such that *Orius* individuals could move freely among the plants by walking on the leaves (Fig. 1).

An *O. sauteri* female or male was released in a PC patch or a PD patch, using a fine brush. The release was replicated 12 times for each patch quality regime and each sex. After release, each predator was checked every hour to assess its movement among the patches or dispersion from patches to plastic cage walls. A test was terminated after 10 h or if the predator left any patches. Predators and kidney bean plants were used only once. The experiment was conducted at 25°C.

To examine oviposition site selection of females in response to patch quality, the number of eggs laid in a PC patch or PD patch was counted at the end of each test. As the predator eggs
were deposited in plant tissue (stem or leaf vein), we counted their eggs using a microscope.

The female and male residence times in a released patch were analysed using a two-way-ANOVA with sex and patch type as main effects. Numbers of eggs laid in PC and PD patches were analysed using Wilcoxon’s signed rank test and Mann-Whitney *U* test.

Prey requirement for Orius sauteri. This experiment was designed to estimate daily prey requirement for *O. sauteri* females and males because prey requirements may affect patch residence time in a PC patch. Two-day-old mated female and male *O. sauteri* were maintained individually as described above. The number of prey consumed was counted daily over a 7-day period. Fourteen females and 14 males were tested. The number of prey consumed by adults was corrected by Abbott’s (1925) method using mortality data for prey unexposed to predators. After 7-days, the body length of females and males (from the tylus to the end of the wing) was measured under a binocular microscope because prey requirement for these predators may correlate with their body size. The experiment was conducted at 25°C and with a LD 16 : 8 h photoperiod. The differences in body size and number of consumed prey between sexes were analysed using Mann-Whitney *U* test.

*Prey availability and nymphaI survival of O. sauteri.* The purpose of this experiment was to determine effects of prey availability on survival of predator nymphs. Newly hatched *O. sauteri* nymphs were reared at different prey densities using 0, 5, 10, and 30-second instar *T. palmi* larvae per vial. Prey density 0 was added to treatments because there is a possibility that *Orius* nymphs can feed on plant tissue and develop as suggested by Coll (1996). They were reared individually in vials until they died or developed to adults, with filter paper and a leaflet as described above. Nymphal survival was checked daily. Prey larvae and the other materials were renewed every day.
Twenty-five replicates were tested in each class of prey densities. The survival rates were analysed using Fisher’s exact probability test with correction (the sequential Bonferroni method; Rice, 1989).

**Results**

**Effects of patch quality on searching and oviposition behaviour.** Time spent in patches where females or males were released is shown in Fig. 2. A two-way ANOVA of patch residence time indicated that effects of both sex and prey availability on patch residence time were highly significant (for sex, $F = 10.07$, 1 and 44 d.f., $P < 0.01$; for prey availability, $F = 11.25$, 1 and 44 d.f., $P < 0.01$). Although the difference in mean time spent in PD patches for females and males was less than 1 h, the difference in mean time spent in PC patches was more than 6 h for the two sexes. Thus, in the analysis, the interaction between sex and prey availability was highly significant ($F = 13.15$; 1 and 44 d.f.; $P < 0.01$). This result indicates that the response of predators to different prey availability differs between sexes (Fig. 2).

Predator movement patterns in response to quality of the patches in which they were released are shown in Table 1. Females and males released in each of the two patch types, i.e. PC and PD patches, showed three categories of responses: remaining in the patch, dispersing to another patch (a PC or PD patch) and dispersing from all four patches (leaving the plants). These responses of *O. sauteri* adults to a PC or PD patch differed significantly between sexes (Fisher’s exact probability test: for PC patches, $\chi^2 = 20.31$, d. f. = 1, $P < 0.01$; for PD patches, $\chi^2 = 16.70$, d. f. = 1, $P < 0.01$). Of females released in PC patches, 75% did not disperse but 25% moved to PD patches or dispersed from patches; in contrast, only 8.3% of females released in PD patches remained, and over 80% of females dispersed to PC patches (Table 1). Males behaved differently;
most individuals dispersed regardless of prey availability in the patches where they were released (Table 1). These results indicate that predator dispersal in response to patch quality differs between sexes; female dispersal depends on prey availability but males disperse regardless of patch quality.

Females showed oviposition site preferences for high quality patches. They laid eggs at higher rates in PC patches than in PD patches regardless of where they were originally released (Fig. 3). Females released in PC patches did not lay any eggs in PD patches but they laid about 0.3 eggs per hour in PC patches, a highly significant difference (Wilcoxon’s signed rank test, $z = 2.68$, $P < 0.01$). Females released in PD patches laid eggs in both PD and PC patches, however the oviposition rates were significantly higher in PC patches than in PD patches (Wilcoxon’s signed rank test, $z = 2.09$, $P < 0.05$).

Prey availability in previously visited patches affects subsequent oviposition rates elsewhere (Fig. 4). Among the females released in PD patches, one female remained in a PD patch and another female left the experimental arena (Table 1). Thus, these two females did not move from PD patches to PC patches. To analyse effects of experience in PD patches on oviposition rates in the following PC patches, they were excluded from the analyses. Females released in PD patches laid eggs in PC patches at significantly higher rates than females released in PC patches (Fig. 4, Mann-Whitney $U$ test, $z = 2.38$, $P < 0.05$; Fig. 4).

Prey requirement for *Orius sauteri*. The numbers of prey consumed by females and males per day differed significantly; females: $15.0 \pm 0.2$, males: $11.5 \pm 0.3$ (mean $\pm$ SE) (Mann-Whitney $U$ test, $z = 4.37$, $P < 0.01$). Body lengths of females and males were $2.16 \pm 0.01$ and $2.00 \pm 0.01$ mm (mean $\pm$ SE) respectively. Females were significantly larger than males (Mann-Whitney $U$ test, $z = 4.46$, $P < 0.01$).

*Prey availability and nymphal survival of O. sauteri.* Nymphal survival rates at the
densities of 0, 5, 10, and 30 prey larvae per vial were 0, 32, 40 and 88% (Fig. 5). Survival rates at
the densities of 5 and 10 prey were statistically indistinguishable, but were significantly higher
than the rate at density 0 and significantly lower than the rate at density 30 (Fisher’s exact
probability test with the sequential Bonferroni method, $P < 0.05$).

Discussion

Sexual asymmetries in behavioural responses to patch quality. The responses of O. sauteri adults
to patches of different food quality differed markedly between the sexes. When released in
prey-rich patches, female O. sauteri stayed there about 6 h longer on average than male O. sauteri,
whereas the time spent by females in a patch was similar to that of males when they were released
in prey-deficient patches. These results indicate that females detect high-quality patches and stay
longer where more prey are available. Males could detect the higher prey density but the latter
does not induce behavioural change. Staying longer in prey-rich patches can be advantageous to
females in three ways: increased individual survival, higher reproductive rates, and increased
offspring survival.

In contrast, males did not vary residence time in response to difference in prey density.
Thus, patch quality in respect to prey availability cannot explain male behaviour. It may be more
advantageous for males to leave patches with high prey availability to search for females as their
overall fitness increased by mating with more females (e.g. Bateman, 1948). For males, spending
time searching for prey and remaining in patches where prey exist in the absence of females will
lessen their chance of locating mates, and decrease their fitness. Recently, Nakashima and Hirose
(1999b) demonstrated that O. sauteri males use a trail sex pheromone left on the plant surface by
females as a cue for searching mates, and that the pheromone is effective for mate finding. Males
probably search the patches containing the pheromone and thus show foraging responses independent of patch quality for prey.

Daily number of prey consumed by females was greater than for males, perhaps because females are larger than males and also require additional energy to produce eggs. Differences between sexes in patch residence times in prey-rich patches might be due partly to higher female prey requirements and increased handling time, however the difference in handling time could not explain the sex-specific patch responsiveness. The difference in number of prey eaten per day between the sexes was about three and the time spent feeding on a single thrips larva is approximately 5 min (Y. Nakashima, unpubl.). Thus, the difference in patch residence time between sexes in prey-rich patches due to feeding time can be, at most, 15 min during the experiment period (10 h).

Different sex-specific responses to patch quality were reported by Inoue and Matsura (1983), who found that mantid females (*Paratenodera angustipennis* de Saussure) changed foraging tactics from ambushing to active searching when prey capture rates decreased but that males did not change their tactics according to prey density. Likewise, Hemptinne et al. (1996) demonstrated that coccinellid females (*Adalia bipunctata* (L.)) modified searching patterns in response to aphid density. More time was spent in area-restricted searches and less time in extensive searches at higher prey density. In contrast, males did not alter searching patterns in response to changes in prey density.

Dispersal patterns in patches with different prey availability differed between the sexes. Most of the females released in prey-rich patches did not disperse whereas most of the females released in prey-deficient patches dispersed to prey-rich patches. Depending on patch prey availability, this pattern of female movements could increase fitness. In contrast, male dispersal between patches did not depend on prey availability in the patches where they were released. Most
of the males dispersed to other patches regardless of initial prey availability. This search strategy may be designed to maximise encounter with mates rather than with food as Honek (1985) suggested that *Coccinella septempunctata* L. males fly more frequently between plants than do females in the field and concluded that males spend more time searching for females than for prey.

**Patch quality and oviposition decisions.** Females of *O. sauteri* oviposited at higher rates in prey-rich patches than in prey-deficient patches, no matter where they were released. Females released in prey-rich patches did not lay eggs in prey-deficient patches because females did not disperse to patches without prey. Although females released in prey-deficient patches did oviposit a few eggs there, the number of the eggs deposited in prey-deficient patches was significantly smaller than the number deposited in prey-rich patches. The oviposition in prey-deficient patches may occur before females perceived patch quality because these females had been provided sufficient prey before the experiment. This oviposition site selection could be adaptive because oviposition in a prey-rich patch increases offspring survival and prey consumption in a prey-rich patch leads to increased oviposition rates (Nakashima & Hirose, 1999a).

The presence of thrips and their associated chemical cues may induce oviposition of females in patches with prey. Chemical cues that stimulate oviposition in coccinellids have been demonstrated in *C. septempunctata* (Evans & Dixon, 1986) and *Cryptolaemus montrouzieri* Mulsant (Merlin et al., 1996). Proximal factors promoting oviposition site selection in *O. sauteri* and other hemipteran insects are not known so far and remain to be determined.

**Oviposition decisions and prior experience.** *Orius sauteri* females released in prey-deficient patches laid eggs in prey-rich patches at higher rates than females released in prey-rich patches, supporting a prediction of a dynamic state variable model (Mangel, 1987). The model, in which
an insect parasitoid-host system is considered, predicts that the low probability of encounter with resource/hosts (in this case, prey) to oviposit leads to greater frequency of large clutches compared with the high probability of encounter.

Our result shows that prior experience with low-quality patches (i.e. low probability of encounter with prey) affects female oviposition rates in subsequent high-quality patches. Females released in prey-deficient patches searched for about 2 h, and experienced poor environments before moving to prey-rich patches. After the move, prey availability (or encounter rates) increased greatly. In contrast, for females released in prey-rich patches that provided highly favourable foraging environments, prey encounter rates in the patches were unlikely to change during the experiment due to the abundant supply of prey in those patches. Clearly, prior experience of patch quality influenced their oviposition decisions. The experiences provided by a poor environment will increase the value of any prey-rich patch that is subsequently encountered, leading females to oviposit more at this time.

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Figure legends

Figure 1. Schematic representation of experimental arena used to detect different responses of *O. sauteri* female and male adults to patch quality and their oviposition site selection. Experiments were conducted on four whole plants of kidney bean that were grown in 10-cm pots. These plants were placed as shown above, allowing *Orius* to move freely among plants by walking on the leaves. Each arena consisted of two plants with prey and two plants without prey. The plants with prey had 60 second-instar larvae of *T. palmi* on the leaves.

Figure 2. Patch residence time of *O. sauteri* adults in response to patch quality. Vertical lines above bars indicate 1 SE. Two-way ANOVA showed that the effects of sex, prey availability, and sex × prey availability interaction on patch residence time were highly significant.

Figure 3. Oviposition site preference of *O. sauteri* females released in patches with (left) and without (right) prey. Vertical lines above bars indicate 1 SE. Female oviposition rates were significantly higher in patches with prey, regardless of prey availability in patches where females were released (Wilcoxon’s signed rank test, *P* < 0.05).

Figure 4. Oviposition rates of *O. sauteri* females in patches with prey when they were initially released in patches with (square) or without (circle) prey. Two females released in patches without prey were excluded from the analysis because they did not move from released patches to patches with prey (see Table 2). Vertical lines above bars indicate 1 SE. Oviposition rates of females released in patches with prey were significantly higher than those of females released in patches without prey (Mann-Whitney *U* test, *P* < 0.05).

Figure 5. Survival rates of *O. sauteri* nymphs at different prey densities per vial. Vertical lines above bars indicate 1 SE. Bars with different letters differ significantly from each other (Fisher’s exact probability test with the sequential Bonferroni method, *P* < 0.05).
Table 1. Movement of *O. sauteri* adults from released patches containing either prey (60 thrips) or no prey. Numbers of individuals are shown in parentheses.

<table>
<thead>
<tr>
<th>Sex</th>
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Movement patterns of *O. sauteri* adults to patches with prey or patches without prey differed significantly between sexes (Fisher’s exact probability test, for patches with prey, $P < 0.01$; for patches without prey, $P < 0.01$).
Fig. 2

Y. Nakashima
Number of eggs laid per hour

Fig. 3

Y. Nakashima
Number of eggs laid per hour

Released in patches with prey
Released in patches without prey

Fig. 4
Y. Nakashima
Fig. 5

Y. Nakashima

Per cent survival vs. Prey density