



## Information use in space and time: sex allocation behaviour in the parasitoid wasp *Nasonia vitripennis*

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Behavioural decisions require the appropriate use of relevant information about the environment. However, individuals may have imperfect information, imposing a constraint on adaptive behaviour. We explored how information use influences the sex allocation behaviour of the parasitoid wasp *Nasonia vitripennis* in response to local mate competition. Optimal sex ratios under local mate competition require females to estimate the number of other females that contribute eggs to a patch. Females rapidly changed their sex allocation in response to changes in the number of females in the environment, suggesting that they are not constrained by how quickly they can respond to new information. Furthermore, females also showed some response to olfactory cues that indicated oviposition by other females, suggesting that such indirect cues may be part of their information repertoire. Both the absolute and the relative size of the patch were important for sex ratio decisions, with sex ratios declining on larger patches in a way that suggests that large patches in effect become more than one patch, with females on larger patches allocating sex increasingly independently of other females. We conclude by highlighting variation among species in whether particular cues are used for sex allocation.

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The amount of information animals have available about their environment, and how they use it when making behavioural decisions, is central to understanding the adaptive significance of behaviour (Krebs & Kacelnik 1991; Giraldeau 1997; Dall et al. 2005; Pexton & Mayhew 2005). Variation in a given behaviour will include variation in how individuals obtain and use relevant information. Limitations on the availability of useful information may limit the responses open to individuals and constrain adaptive decision making (Outreman et al. 2001; Boomsma et al. 2003; Shuker & West 2004; Moore et al. 2005). However, it is often difficult to estimate how much of a constraint information actually represents, especially if the optimal responses to different environments are poorly characterized.

Sex allocation offers a good opportunity to explore constraints on adaptation, including those that arise

through information use (West & Sheldon 2002; Boomsma et al. 2003). This is because sex allocation is: (1) based on a simple trade-off, i.e. the production of either a son or a daughter; (2) easy to measure; (3) closely related to fitness; and (4) well characterized theoretically (Charnov 1982; Frank 1998; Hardy 2002). Particularly useful for this purpose is the case where related males compete for mates, leading to selection for female-biased sex ratios by a process that has been termed local mate competition (LMC; Hamilton 1967). The role of LMC in shaping sex allocation is now well established in many different taxa, from parasitic wasps through to protozoan parasites (reviewed in Godfray 1994; West et al. 2001, 2005; Hardy 2002). Information about the environment is clearly important since females have to estimate the degree of LMC that will be experienced by their sons (Stubblefield & Seger 1990; Flanagan et al. 1998; Shuker & West 2004; Shuker et al. 2005).

We explored information use in a species that experiences LMC, the parasitoid wasp *Nasonia vitripennis*. The sex ratio behaviour of this species has been the subject of considerable study (Shuker et al. 2005 and references

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therein). As predicted by LMC theory, females lay more female-biased sex ratios when the extent of LMC between their sons will be greater. This can occur for a number of reasons including when only one or a few females lay eggs on a patch (Werren 1983), females lay larger broods (Werren 1980; Flanagan et al. 1998), or when mating between males from different broods on a patch is not random (Nunney & Luck 1988; Shuker et al. 2005). Furthermore, this functional study of sex ratio manipulation has been complemented by studies that have examined the underlying proximate mechanisms (e.g. King & Skinner 1991; King et al. 1995; Shuker & West 2004) and genetic basis (e.g. Orzack et al. 1991; Orzack & Gladstone 1994) of sex ratio manipulation. None the less, there remains unexplained variation in offspring sex ratios that has led some to question the validity of LMC theory, and even the whole optimality approach to the study of behaviour itself (Orzack 1993, 2002).

We are carrying out a long-term project that uses sex ratio behaviour in *Nasonia* as a model system to determine what constrains perfect behaviour. A fundamental constraint is the extent to which females can assess the level of LMC both between and within patches (Shuker & West 2004; Shuker et al. 2005, 2006). Our aim in this study was to test the importance of several possible cues used by females. In our first two experiments we tested whether females produce less female-biased sex ratios in response to two cues that might suggest a higher likelihood that other females will lay eggs on a patch: (1) previous encounters with other females (Wylie 1976; Strand 1988; King & D'Souza 2004; and (2) olfactory cues from other females (Wylie 1976; Kochetova 1978; van Welzen & Waage 1987; Sabelis & Nagelkerke 1993). In our final two experiments we investigated how females adjust their offspring sex ratio in response to the interaction between the number of females laying eggs on a patch and patch size (Waage 1982). Patch size could have an effect if larger patches lead to: (1) females interacting less with one another, and so less accurately assessing the total number of foundresses on a patch (Wylie 1976; King et al. 1995; Shuker & West 2004); and (2) some population structuring and nonrandom mating within a patch (van den Assem et al. 1980; Hardy 1994; Shuker et al. 2005, 2006). Both of these would lead to a more female-biased sex ratio with increasing patch size. We considered these two effects using absolute and relative patch size.

## METHODS

### Study Organism

*Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae) is a gregarious parasitoid of large dipteran pupae (Whiting 1967). As the host species, we used *Calliphora vomitoria* (Diptera: Calliphoridae). Female *N. vitripennis* typically lay clutches of 20–40 eggs between the pupa and the puparium wall, and multiple females may oviposit on the same host within a 24–48-h period (superparasitism: Werren 1984; Shuker et al. 2005). In the laboratory at 25°C, adult males emerge after 13–14 days, followed by

females soon after (Leonard & Boake 2006). Males have reduced wings and are flightless, remaining on the patch to mate with emerging females. Females emerge and mate, and in the wild then disperse to find fresh hosts. For our experiments we used wild-type laboratory strains originally collected from Hoge Veluwe, the Netherlands by Professor Leo Beukeboom, and for experiment 3 we also used the red-eye mutant laboratory strain STDR, so that we could follow the oviposition behaviour of individual wild-type focal females. After they had mated, we pretreated females by giving them fresh hosts to feed on for 24 h, followed by filter paper wetted with honey solution for 24 h. This pretreatment allows protein and carbohydrate feeding and facilitates egg development and subsequent oviposition (Werren 1980; Rivero & West 2005).

### Latency of Cues

In experiment 1 we experimentally manipulated the time that females spent alone before oviposition to see how quickly they reverted to producing single-foundress sex ratios. We used wasps from the laboratory strain HV6 which we maintained throughout at 25°C. Females were allowed to emerge and then mate for 2 days in mass culture before we made 300 groups of five females for pretreatment. After pretreatment, we randomly allocated one female from each group to one of five treatments: (A) females ovipositing in their groups of five (multi-foundress female control); (B) females ovipositing alone immediately after being removed from their groups of five females; (C) females ovipositing alone 6 h after being removed; (D) females ovipositing alone 12 h after being removed; and (E) females ovipositing alone 24 h after being removed. The other four females from each group were not used in the experiment (apart from treatment A). We also individually isolated approximately 70 female pupae from the culture prior to emergence. On emergence, each of these females was given a randomly chosen male for 2 days, prior to pretreatment, thereby creating the sixth experimental treatment: (F) females ovipositing alone after having had no contact with other females for their adult life (single-foundress female control). All experimental females were given one host to parasitize for 6 h, after which all individuals were removed and the hosts incubated at 25°C. Washed tubes with fresh bungs were used throughout. We recorded the sex ratio (as proportion male) of all emerging offspring. In total, 69 females either did not oviposit or were putative virgins (producing males only), and these females were excluded from the analysis, leaving 333 experimental females, with sample sizes per treatment ranging from 51 to 64.

### Olfactory Cues

In experiment 2 we again used wasps from the laboratory strain HV6 maintained at 25°C. Females were allowed to emerge and then mate for 2 days in mass culture before being isolated for pretreatment. We then randomly allocated females to one of four treatments. The experiment was a fully factorial design with two sources of olfactory

cues: (1) presence or absence of female odour; and (2) presence or absence of parasitized host odour. To obtain the odours, we took new unused 75 × 25-mm tubes and treated them as follows: (A) left clean; (B) 10 mated female wasps were placed in the tubes for 48 h, without hosts; (C) 10 parasitized hosts were placed in the tubes for 48 h; and (D) 10 mated female wasps and 10 hosts were placed in the tubes for 48 h. We obtained parasitized hosts by putting 10 females with groups of 10 hosts for 48 h prior to placing them in the clean tubes. Female odours were therefore present in treatments B and D, and parasitized host odours were present in treatments C and D. All foam bungs and other glassware were clean before the experiment to remove other possible olfactory cues. We placed test females with two fresh hosts into the treated tubes and after 60 min we fitted one-way escape tubes to allow female dispersal, thus limiting self-superparasitism (Werren 1983; Godfray 1994, page 172). After 48 h we removed all females and incubated the hosts at 25°C. A few females ( $N = 31$ ) either did not oviposit or were putative virgins (producing males only) and these females were excluded from the analysis. The sample sizes for the four treatments ranged from 38 to 54 (total  $N = 188$  females). Offspring were allowed to emerge and the sex ratio recorded as before.

### Patch Size and Foundress Number

In two experiments we separated the effects of patch size and foundress number. In the first experiment (3A), we had two different numbers of foundresses and we varied the number of hosts they had available. In the second experiment (3B), we used three different numbers of foundresses with three different host:female (H:F) ratios to vary relative patch size.

For experiment 3A, we used wasps from strain HV287. We generated mated and pretreated females as before, and then created two foundress group sizes: (1) two foundresses, with a focal female placed with a red-eye mutant female, or (2) eight foundresses, with a focal female placed with seven red-eye females. Foundress groups were assigned to patch sizes of 1, 5, 10, 20, 40 or 60 fresh hosts. In this experiment we did not allow females to disperse from the patch, to encourage exploration of the whole patch, but we removed all wasps after 24 h to limit superparasitism. We scored the genotypes (wild-type or red-eye) and sex ratios of the emerging offspring as before. There were 10 replicate females per foundress number per host number for all but one treatment combination, in which there were nine females (total  $N = 119$  females).

For experiment 3B, we used wasps from strain HV6. As before we allowed females to emerge and mate in mass culture, before isolating them for pretreatment prior to the experimental manipulations. We used a fully factorial design with two factors: foundress number and relative patch size (H:F ratio). After pretreatment, we allocated females to one of three foundress number treatments: (1) single foundress; (2) three foundresses, in which a focal female was placed with two mated red-eye mutant females; and (3) eight foundresses, in which a focal female

was placed with seven mated red-eye mutant females. These foundress groups were then released on to patches of fresh hosts such that the H:F ratio was either 1:1, 4:1 or 8:1. After 1 h, one-way escape tubes were fitted to oviposition tubes, and we removed all females after 48 h. Emerging offspring were genotyped and sexed as before. The total number of females used in this experiment was 203, with sample sizes per treatment combination ranging from 15 to 40, apart from the eight foundress, 8:1 H:F ratio combination, in which only two females oviposited.

### Statistical Analysis

The data were analysed with generalized linear models, with binomial errors and a logit link function in S-Plus 6 and 7 (Insightful Corporation, Seattle, WA, U.S.A.), following Crawley (2002) and Wilson & Hardy (2002). Models were simplified by removing terms sequentially and testing whether the change in deviance was significant. The significance of each main effect was tested after fitting all the other significant main effects first. After inspection of the data, higher order main effects (quadratic and cubic effects) were tested as appropriate (see Patch Size and Foundress Number). Generally the data were slightly overdispersed (the dispersion parameters for experiments were between 2 and 4) and so the significance of main effects and interactions was tested with  $F$  tests (Crawley 2002).

## RESULTS

### Latency of Cues

Being kept with other females prior to oviposition had no effect on the sex ratio produced by females, regardless of how recent this exposure was (Fig. 1). There was a highly significant effect of treatment on sex ratio, with females kept in groups of five producing a less female-biased sex ratio than all the other treatments ( $F_{5,327} = 123.58$ ,  $P < 0.0001$ ,  $R^2 = 0.68$ ). However, females ovipositing alone produced similar sex ratios, regardless of how long they had been alone before oviposition (collapsing treatments B–F:  $F_{4,327} = 1.22$ ,  $P = 0.30$ ).

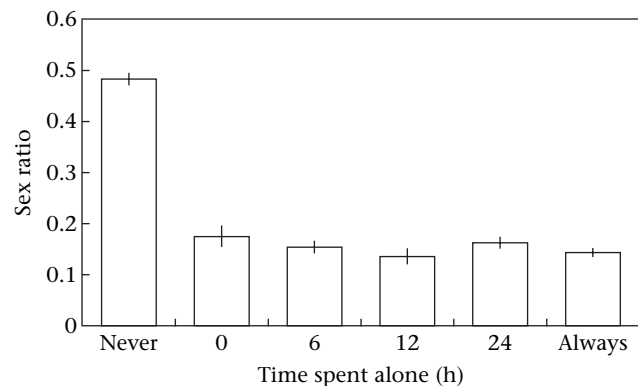


Figure 1. Sex ratio (proportion male) produced by females in relation to the time the females spent alone before oviposition. Error bars are binomial standard errors.

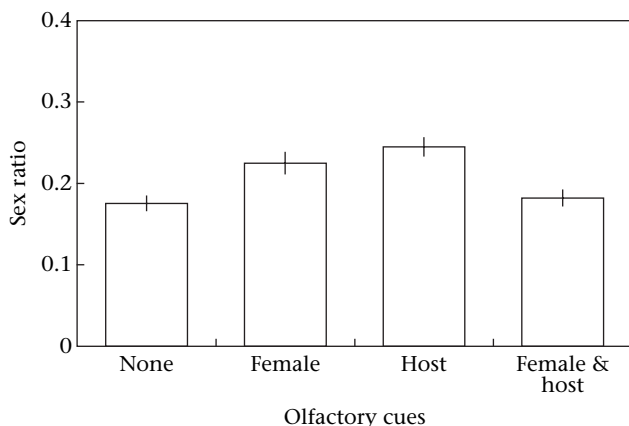
## Olfactory Cues

Across the four treatments, the overall sex ratio was 0.207. There was no significant effect of female odour on sex ratio ( $F_{1,185} = 0.01$ ,  $P = 0.94$ ) and also no significant effect of parasitized host odour ( $F_{1,185} = 0.84$ ,  $P = 0.36$ ). However, the interaction between these two factors was highly significant ( $F_{1,184} = 12.16$ ,  $P = 0.0006$ ; Fig. 2). The data suggest a slight increase in sex ratio when either the female or parasitized host odours were present by themselves, when compared to the clean tubes, but there was no such increase when the two odours were present together.

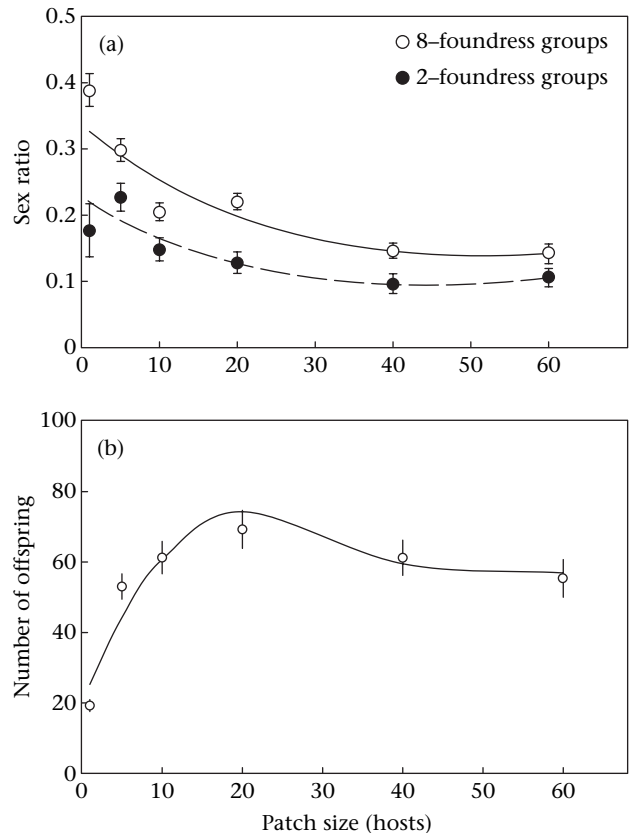
## Patch Size and Foundress Number

Both relative and absolute patch size, and foundress number, influenced sex ratio. In experiment 3A both foundress number and number of hosts were significant (Fig. 3a), with females with seven cofoundresses producing higher sex ratios ( $F_{1,115} = 24.52$ ,  $P < 0.0001$ ,  $R^2 = 0.14$ ), and sex ratios declining with increasing patch size ( $F_{1,115} = 17.07$ ,  $P < 0.0001$ ,  $R^2 = 0.10$ ). There was also a significant quadratic effect of patch size ( $F_{1,115} = 6.80$ ,  $P = 0.01$ ,  $R^2 = 0.04$ ), with larger patches yielding negligible shifts in sex ratio. There were no significant interactions between these variables (all interactions removed from the minimal adequate model:  $P > 0.55$ ) and the number of offspring produced by focal females was also not associated with sex ratio ( $F_{1,114} = 2.30$ ,  $P = 0.13$ ). Females produced more offspring on larger patches (Fig. 3b), although both quadratic and cubic terms were significant, suggesting that offspring production peaked at a patch size of around 20 hosts (linear, quadratic and cubic terms all  $F_{1,115} > 12.30$ ,  $P < 0.001$ , model  $R^2 = 0.37$ ).

In experiment 3B, sex ratio increased with an increasing number of cofoundresses ( $F_{1,200} = 27.86$ ,  $P < 0.0001$ ,  $R^2 = 0.11$ ) and decreased with increasing relative patch size ( $F_{1,200} = 13.09$ ,  $P = 0.0004$ ,  $R^2 = 0.05$ ; Fig. 4). There was also a weak interaction between these two factors ( $F_{1,199} = 4.12$ ,  $P = 0.044$ ,  $R^2 = 0.02$ ), such that relative



**Figure 2.** Sex ratio (proportion male) produced by females exposed to various olfactory cues. Error bars are standard errors.

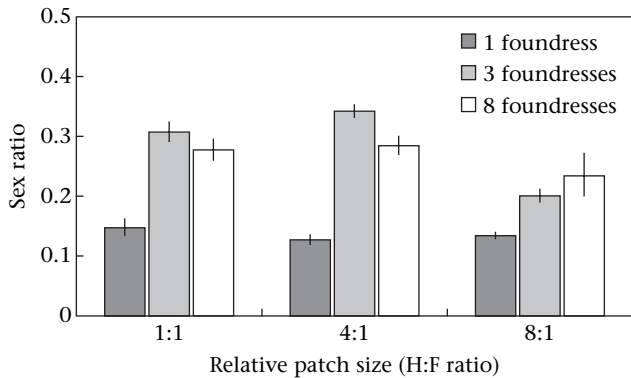


**Figure 3.** (a) Sex ratio (proportion male) and (b) number of offspring produced in response to foundress number and patch size. (a) The regression lines are (solid line, eight foundresses) sex ratio =  $\text{antilogit}[0.68022 - 0.04445(\text{number of hosts}) + 0.00043(\text{number of hosts})^2]$  and (dashed line, two foundresses) sex ratio =  $\text{antilogit}[1.22362 - 0.04551(\text{number of hosts}) + 0.00050(\text{number of hosts})^2]$ . Error bars are binomial standard errors. (b) The regression line is number of offspring =  $19.6062 + 5.8295(\text{number of hosts}) - 0.1888(\text{number of hosts})^2 + 0.0017(\text{number of hosts})^3$ . Error bars are standard errors.

patch size had little effect on single foundresses whereas it did influence multifoundress groups (Fig. 4). We can more clearly look at the effect of females interacting with each other if we consider the two multifoundress treatments. In this case, relative patch size significantly influenced sex ratio ( $F_{1,112} = 11.02$ ,  $P = 0.001$ ,  $R^2 = 0.09$ ), but foundress number did not ( $F_{1,111} = 2.08$ ,  $P = 0.15$ ). There was also no interaction between relative clutch size and foundress number ( $F_{1,110} = 1.98$ ,  $P = 0.16$ ).

## DISCUSSION

In our first experiment when females laid eggs on a patch alone they produced a highly female-biased sex ratio, regardless of whether they had been previously confined with multiple females (Fig. 1). This suggests that previous experience of a low-LMC environment does not constrain female ability to produce a sex ratio appropriate for a high-LMC patch. As such these results confirm earlier work by



**Figure 4.** Sex ratio (proportion male) produced by females in response to relative patch size and foundress number. Relative patch size measures number of hosts (H) per female (F) on a patch. Error bars are binomial standard errors.

Wylie (1976) and extend recent work by King & D'Souza (2004) who showed that females can respond within 24 h of an environmental change; our results show that this can happen even more quickly. This contrasts with the results that King (2002) obtained with the parasitoid wasp *Spalangia endius*. In this species, females took at least 24 h to respond to a change in the environment (again, the presence or absence of a cofoundress), as did female *Muscidifurax raptor*, although in this latter species the latency of the cue from a cofoundress also depended on how long females were kept together (King & Seidl 1993). The latency of LMC cues has also been explored in another solitary parasitoid species, *Telenomus heliothidis*, in which females take up to 7 days after experience of cofoundresses to produce a sex ratio typical of a lone foundress (Strand 1988). In addition, nonpollinating fig wasps may adjust their sex allocation behaviour in response to the average encounter rate with other females (West & Herre 1998). These results beg the question of why different species have different latencies of responses to cues. Progress will require further mechanistic work in a range of species, in particular for those that vary in how often they experience cofoundresses (i.e. further ecological details are needed). A useful extension would be to allow females to oviposit in the presence of different numbers of females and see whether this influenced behaviour on the next patch visited.

We have recently shown that females make use of the timing of oviposition events by other females on a patch when allocating sex in a way predicted by asymmetrical LMC models (Shuker et al. 2005, 2006). That work did not identify what cues were used by females, although it is likely that females can obtain information about the age of eggs and/or larvae present on a host by probing previous oviposition holes: females use such information when deciding whether to superparasitize a host (Werren 1984; King & Skinner 1991). In the present study we tested whether olfactory cues left in the environment from either females or parasitized hosts are also used. While the use of olfactory cues for host location has been well recorded in parasitoids (Godfray 1994), much less is known about the use of olfactory cues, including

pheromones, in other contexts in parasitoids (Fauvergue et al. 1995; Pompanon et al. 1997; Desouhant et al. 2005). Our results suggest that females do show some response to the past presence of females via an indirect olfactory cue or cues, but this effect was apparent only in terms of an interaction between female and host cues. Previous work with parasitoids has found evidence that olfactory cues left by other females lead to sex ratio adjustment in *Trissolcus grandis* (Kochetova 1978) and *Telenomus remus* (van Welzen & Waage 1987) but not in *N. vitripennis* (Wylie 1976) or *Spalangia cameroni* (King 1989). A role for similar cues was suggested in the mite *Phytoseiulus persimilis*, where females lay a less-biased sex ratio on a patch if it was previously visited by another female (Sabelis & Nagelkerke 1993). However, the cue in these experiments could have been the eggs laid by the previous female, as occurs with *N. vitripennis* (Werren 1980; Shuker & West 2004; Shuker et al. 2005). At present it is not clear whether this variation across species represents variation in the availability or costs and benefits of cues or just different methodologies.

Our patch size results make it clear that the effects of patch size (or more generally the spatial distribution of hosts) need to be included in LMC models when testing the precision of adaptation. For instance, giving females two or 10 hosts will lead to different sex ratios among larger foundress groups (Fig. 3a). Perhaps more importantly, our results also suggest that large patches can lead to 'within-patch' structuring, increasing the level of LMC at an extremely local scale (perhaps a few closely associated hosts). If patch size influences LMC primarily by diluting interactions between females, then any such effect should take longer to occur with larger numbers of foundresses. In experiment 3A, therefore, there should have been an interaction between foundress number and absolute patch size, with foundress number becoming less important as patch size increases. However, if patch size directly influences the sex ratio by creating fine-scale structure, then we might only expect to see a patch size main effect and a foundress number main effect: this is what we observed. Similarly, in experiment 3B, we might have expected an interaction between the two multifoundress treatments. Instead, we saw only a significant effect of relative patch size. Frank (1985) suggested that within-patch structuring might arise with fig wasps, i.e. within a single fruit. Results from the fig wasp *Liporrhopalum tentacularis* suggest that females do indeed take this fine-scale spatial structure into account when allocating sex (Zavodna et al. 2005). In addition, for parasitoids that lay eggs on multiple hosts per patch, any spatial structuring across a patch will be increased by any temporal structuring if females lay eggs asynchronously, increasing LMC and again leading to more female-biased sex ratios (Nunney & Luck 1988; Shuker et al. 2005, 2006).

A major task for the future is to follow the oviposition behaviour of individual females over space and time to allow us to 'map' LMC responses across large patches. However, we also need more data on how males and females move around patches when mating, to parameterize models and make predictions about the level of LMC across large patches (Shuker et al. 2005). More generally, this work has implications for interpreting sex ratios

and testing theory in the field, in both *Nasonia* and other LMC species. We need to be clear about what constitutes a patch in terms of LMC and to what extent females can obtain the information relevant to this spatial scale; this may well vary across species and explain the different patterns of information use across species (see above). At one end of the population structure continuum males may move between patches to some extent, reducing population structure and the level of LMC ('partial LMC': Hamilton 1979; Nunney & Luck 1988; Werren & Simbolotti 1989; Hardy 1994; West & Herre 1998). Our work has highlighted the opposite end of the spectrum: patches may be more structured than we imagine, not less.

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