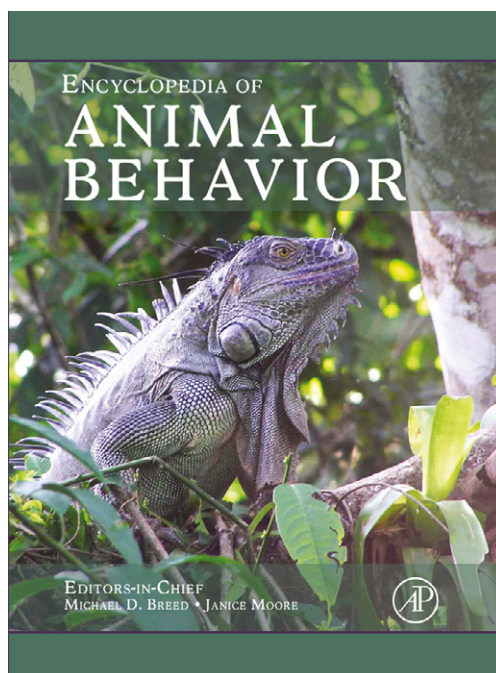


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## Nasonia Wasp Behavior Genetics

R. Watt, University of Edinburgh, Edinburgh, Scotland, UK

D. M. Shuker, University of St. Andrews, St. Andrews, Fife, Scotland, UK

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### Introduction

*Nasonia* is a genus of parasitoid wasp that attacks the pupae of many large fly species (across families such as the Muscidae, Sarcophagidae, and Calliphoridae; **Figure 1(a) and 1(b)**). As a parasitoid, *Nasonia* kill the pupae they attack, being as much predatory as they are parasitic (Godfray, 1994). In common with many other parasitoids, *Nasonia* can influence the population density of the host species they parasitize and may act as biological control agents. Also known as 'jewel wasps,' there are four species in the *Nasonia* genus. By far the best known is *Nasonia vitripennis*, which is distributed across the whole of the northern Palearctic region, being the only *Nasonia* species so far found in Europe and Asia. *N. vitripennis* co-occurs with the other three species in North America. *N. longicornis* is found predominantly in the west of North America, with *N. giraulti* and *N. oneida* occurring in the eastern United States. Recent data suggest that range margins may be changing however, and the very recent discovery of *N. oneida* suggests that further species may await discovery in both America and across Europe and Asia. The four species are reproductively isolated from each other both prezygotically by various behaviors associated with mating (discussed later) and also postzygotically due to nuclear–cytoplasmic incompatibilities associated with the endosymbiotic bacteria *Wolbachia*. Bidirectional cytoplasmic incompatibilities between different *Wolbachia* strains mean that F1 hybrids usually fail to develop, although antibiotic curing of the different wasp species of *Wolbachia* facilitates hybrid formation (albeit with some more 'conventional' loss of hybrid fitness). The ability to make these crosses has played an important role in the success of many *Nasonia* genetics projects, as differences between the species are usually more pronounced (and so easier to resolve) than differences among individuals within a species.

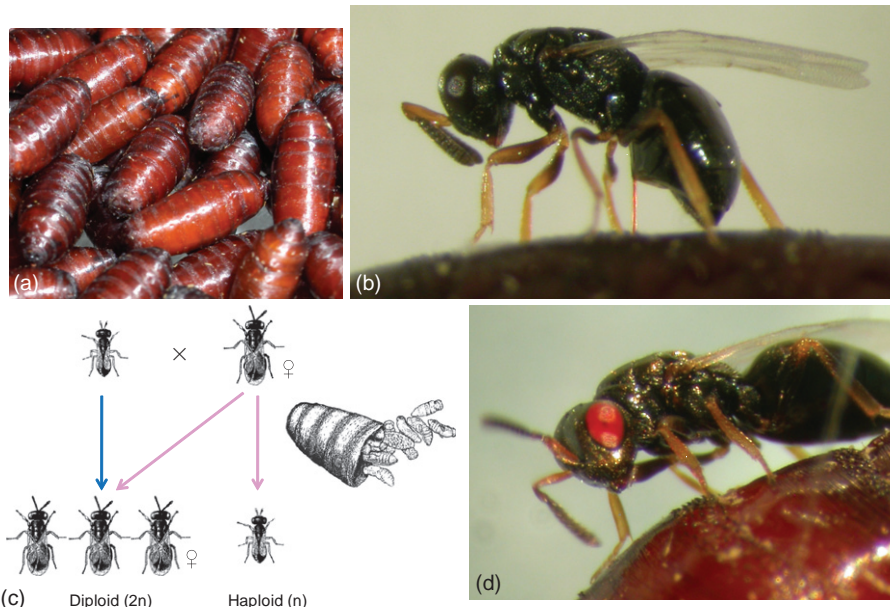
Another factor in the success of *Nasonia* genetic studies is haplodiploidy (**Figure 1(c)**). As with all Hymenoptera (bees, ants, and wasps), *Nasonia* are haplodiploid. This means that females are diploid with both maternal and paternal chromosomes, developing conventionally from fertilized eggs. Males on the other hand are haploid, developing parthenogenetically from unfertilized eggs. Males therefore only contain maternal chromosomes. Haplodiploidy combines many of the advantages of haploid genetic analysis (no effects of dominance for example), with an

organism with complex behavior and ecology. Moreover, haplodiploidy facilitates powerful quantitative genetic and crossing designs (**Figure 2**), which can be important given the low heritability of many behavioral traits.

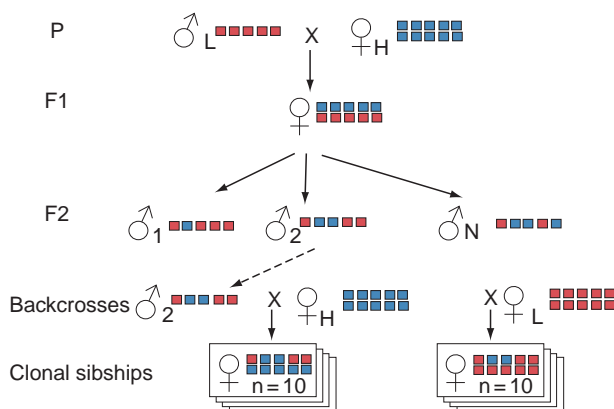
The study of the behavior and genetics of *Nasonia* wasps has a long history. As a genetic study organism, *Nasonia* played an important role in early studies of mutation (**Figure 1(d)**), but it is perhaps best known for its behavior, in particular its sex ratio behavior and for the presence of sex ratio distorting endosymbionts. More generally though, as a parasitoid wasp, *Nasonia* displays a broad array of behaviors, spanning host location and host choice, through to the reproductive allocation decisions that females need to make, and their elaborate courtship behavior. Our understanding of the genetic basis of many of these behaviors is only just beginning to take shape, but thanks to the *Nasonia* Genome Project the arrival of the full genome sequences of three of the four *Nasonia* species (*vitripennis*, *giraulti*, and *longicornis*) has resulted in a rich new source of genetic and genomic information. We will begin with an introduction to the field of insect behavior genetics and then review the behavior genetics of *Nasonia*, taking the life cycle of the wasp as our guide.

### Insect Behavior Genetics

Behavior genetics seeks to characterize the genes and genetic networks that control or influence an animal's behavior. As such, behavior geneticists have to integrate whole organism phenotypes (the behavior or behaviors of interest) with increasing levels of genotypic detail, including the action of individual molecules. Since behavior is, at its most basic, a motor response to some aspect of the environment, behavioral genes include those associated with the development and action of the nervous system, including the associated sensory systems, as well as aspects of physiology and cellular metabolism. Moreover, since behavior is a key intermediary between an organism and its environment, the ecological context of behavior is also crucial for understanding how genetics shapes behavioral variation and therefore influences evolution. All this means that behavior genetics is at the center of an integrated approach to understanding animal behavior, as envisaged by Tinbergen in his 'four questions.' Most obviously, genetics can tell us a lot about the mechanistic basis of behavior (what neural and physiological systems



**Figure 1** Some aspects of *Nasonia* biology. (a) Blowfly pupae are the host for this parasitoid wasp. (b) A female *Nasonia* laying eggs on a host: females choose hosts depending on the host species, its size, and whether or not other females have already parasitized the host. (c) As with all Hymenoptera, *Nasonia* are haplodiploid, with females being diploid ( $2n$ ), carrying chromosomes from both their mother (pink arrow) and father (blue arrow), while males are haploid ( $n$ ), carrying chromosomes only from their mother (pink arrow). Inset: *Nasonia* are gregarious, with multiple wasp pupae developing on one fly pupa, within the host puparium. (d) There are a number of visible mutant markers available, derived from early studies of mutation in *Nasonia*; shown here is the red-eye mutant *STDR*, often used in studies of sex ratio in *Nasonia*. Photographs by David Shuker and Stuart West. Line drawings from Whiting AR (1967) The biology of the parasitic wasp *Mormoniella vitripennis*. *Quarterly Review of Biology* 42: 333–406, used with permission from the University of Chicago Press.



**Figure 2** Haplodiploid genetics allow powerful breeding designs for genetic analysis. Here is illustrated a ‘clonal-sibship’ design for a QTL study. Parents from a ‘high’ and ‘low’ line (for a theoretical trait, such as body size) are first crossed. F1 daughters are collected as virgins and given hosts to parasitize, with the (all) male recombinant F2 offspring collected. These F2 males can then be backcrossed to high and low parental line females for the screening of the phenotypes of the recombinant male genotypes in both high and low genetic backgrounds (see Velthuis et al., 2005, for an example of this approach).

influence behavior), but genes can also tell us about how behavior develops, its evolutionary past (through the phylogenetic signal carried by genes), and its evolutionary present. Despite this integrative framework, behavior

geneticists tend to either focus on mechanistic, ‘bottom-up’ approaches to behavior, or on describing patterns of behavioral variation in populations, and from that inferring something about the genetics of behavior using quantitative genetic techniques in a more ‘top-down’ approach.

Insect behavior genetics, at least from a bottom-up perspective, has been dominated by study of the fruitfly *Drosophila melanogaster*. Considerable progress has been made in identifying and characterizing the genetic pathways influencing neural patterning (including famous genes such as *fruitless*), neurohormones and their receptors, neurotransmitters, and other important cellular signaling cascades. In terms of top-down approaches, while *Drosophila* has again been popular, many more species have been studied, not least because of the array of behaviors available across species and the evolutionary (as opposed to mechanistic) puzzles they represent. However, most species are without the access to the molecular resources available in *Drosophila* necessary to link molecular processes with the biological variation that evolution acts upon. One of the major challenges currently facing insect behavior genetics is to link bottom-up and top-down approaches, and species with both rich behavioral repertoires and well-characterized genetics may be important in the coming years in facilitating this link up. *Nasonia* represents one such species.

## Nasonia Behavior Genetics

### Oviposition Decisions

The *Nasonia* life cycle starts with oviposition (egg laying) by females on a host. The parasitoid lifestyle means that the hosts are other insects, in this case being the pupae of large-bodied Diptera. *Nasonia* are gregarious ectoparasitoids, meaning that several eggs are laid on a host and that after hatching the wasp larvae attach to the host and consume it from the outside in. Females drill through the puparium wall that surrounds the fly pupa proper, laying eggs in the airspace between the puparium and the fly pupa. When the eggs hatch, the first instar larvae attach themselves to the host, ingesting host fluids. The number of wasp larvae developing on a host depends on the species of host (less than 10 on a host like the house fly *Musca domestica*, to more than 60 on large calliphorid blowfly pupae) and also on aspects of host quality (size, the presence of other eggs, and whether or not an adult has already fed on the host – so-called host feeding). The feeding of the wasp larvae during their development destroys the host pupa.

Female *Nasonia* face several important reproductive decisions when they encounter a host. First, females may not actually lay eggs immediately, but instead drill through the puparium wall and into the pupa and then feed on the host fluids that escape. Nothing is known about the genetic basis of host feeding, but resource stress increases host feeding (either as a result of intense larval competition during development, or prolonged time away from food sources). Next, females have to decide if the host is suitable for oviposition. Females explore hosts prior to oviposition, presumably obtaining information via their antennae and other sensory apparatus, including the ovipositor if a drill hole from a previous female is located. Data from the four species suggest there are species differences in host preference (with *N. vitripennis* appearing the most general of the four), which presumably are genetic in origin. Moreover, recent work has identified a chromosome region associated with host preference using crosses between *N. vitripennis* and *N. giraulti*. *N. giraulti* has a much stronger preference for *Protocalliphora* hosts than *N. vitripennis*, and crosses identified a 16-Mb region of chromosome 4 associated with this preference. Recent gene expression studies have also revealed a complex transcriptome activated during oviposition. It is currently not known if rearing environment also influences female host preference later in life, as seen in some herbivorous insect species.

Once a female has decided whether or not to oviposit on a host, the next decision is how many eggs to lay. Experiments have shown that females use a variety of cues to determine clutch size (including the presence and number of other eggs, whether those eggs are from conspecifics or heterospecifics, and the presence of venom from another female), but the presence of a drill hole by

itself is not sufficient to influence clutch size. The genetic basis of clutch size has recently been explored with a quantitative trait locus (QTL) study in *N. vitripennis*. Unsurprisingly, the clutch size trait appears to be polygenic, with a clear QTL on chromosome 1, and further, weaker QTL on chromosomes 2, 4, and 5. The extent to which this variation is associated with genes identified by the gene expression study mentioned earlier (i.e., linking molecular patterns of variation with population level variation) remains to be explored.

One of the best-characterized behaviors in *Nasonia* is the sex ratio behavior of females. The population biology of the wasp (in particular, the small mating groups formed by offspring that share a patch of one or a few hosts) means that interactions among related offspring are common, including competition between related males (typically brothers) for mates. This localized competition for mates among sons favors females that limit this competition, leading to selection for female-biased sex ratios that vary with the number of females ('foundresses') laying eggs on a patch of hosts. William Hamilton suggested in 1967 that local mate competition (LMC) should influence female sex allocation, and much theory and experiment has followed, no more so than on *Nasonia*. Pioneering work by Jack Werren confirmed that LMC is an appropriate framework for understanding *Nasonia* sex ratios and confirmed the predicted patterns. Work since then has refined the general LMC models and identified how females estimate the likely level of LMC their offspring will face.

For all this theoretical and empirical work, much less is known about the genetic basis of sex ratio, but work is progressing. A series of heritability studies in the 1980s and 1990s showed that there is heritable variation in sex ratio in *N. vitripennis* (albeit quite low, around 10–15% or so), and that populations respond to artificial selection on sex ratio. More recently, a mutation accumulation study in *N. vitripennis* has been the first to show mutational variation in sex ratio in any species (shown by Pannebakker and colleagues to have a mutational heritability of about 0.001–0.002). That study again estimated the heritability of sex ratio (and again it was low) and then used our understanding of selection on sex ratios to estimate the strength of stabilizing selection on sex ratio. This selection against sex ratio mutants, combined with the rate of mutation revealed by the mutation accumulation study, allowed a prediction for the level of genetic variation expected in a population. This estimate suggested there should be more additive genetic variation (i.e., a higher heritability) than has so far been uncovered in studies of *Nasonia*, suggesting that other sources of selection may be acting against sex ratio mutants; in other words, sex ratio genes should be pleiotropic to some extent, thereby influencing other fitness-related traits.

This suggestion has been tested in the QTL study considered earlier. Not only did this study consider clutch

size, it also considered sex ratio. If sex ratio genes are pleiotropic and also act as clutch size genes, they should co-occur in QTL studies. The researchers found a significant QTL influencing sex ratio, but this time it was on chromosome 2. However, weaker sex ratio QTL were also found on chromosomes 3 and 5, with some overlap to the weaker clutch size QTL. While these data only suggest that perhaps some of the same genes influence clutch size and sex ratio, not least since each QTL encompasses a genome region containing potentially many hundreds of genes, promising chromosome locations for further study have nonetheless been identified.

Although it seems as though all four *Nasonia* species vary their sex ratios in line with LMC theory, sex ratios do differ between them as the extent of LMC experienced by broods also varies. This is mostly due to differences in 'within-host mating' (the extent to which eclosing adults mate inside the remains of the puparium before 'emerging' to the outside world). For example, *N. giraulti* has the highest rate of within-host mating, leading to the most extreme LMC and hence the most female-biased single foundress sex ratios. Again, these species differences are likely genetic in origin, and new results from interspecific crosses have indicated that genes in a region of chromosome 5 are associated with this species difference. An exciting possibility is that this region is associated with the same genes as the QTL identified in the intraspecific study in *N. vitripennis* considered earlier.

Eggs are not the only thing produced by females as part of oviposition. Prior to egg laying, females sting the host pupa releasing venom. Venoms of parasitic wasps can have many effects on the host, and in the case of *Nasonia*, it is known that developmental arrest of the fly pupa, suppression of the host immune system, and an increase of lipid levels in the hemolymph result from envenomation. Venom is therefore clearly important in preparing a host for larval consumption and shaping the larval environment. Work is still on going to identify the proteins involved in aspects of host transformation, but it has recently been shown that a protein between 67 and 70 kDa in size may be responsible for host developmental arrest and death. Moreover, bioinformatic approaches (both genomic and proteomic) as part of the *Nasonia* Genome Project have identified 79 genes associated with the venom, approximately half of which have not been ascribed venom function in other species.

### Larval Behavior

Compared to adult behavior, much less is known about larval behavior. Larvae undergo four instar molts before pupating. Circumstantial evidence from numerous studies has shown that larval density (assumed to be a correlate of larval competition) influences adult wasp size, fecundity, and energy reserves. As such, ovipositing females appear

to avoid laying eggs on hosts already containing many eggs that are likely to be highly competitive environments for their offspring. In *N. vitripennis*, male larvae develop faster, and there is evidence for asymmetric larval competition (whereby the two sexes represent unequal competitors for each other). However, the genetics of larval competition are completely unknown and represent a topic ripe for study, especially as theory predicts parent-offspring conflict over traits such as larval competition, which might lead to patterns of genomic imprinting influencing which genes are activated during larval development. Venom may also be an important mediator of larval behavior, influencing as it does how good a resource a host represents to the developing larvae (e.g., by debilitating host immune responses). The interactions between venom and larval behavior require further study however.

One interesting aspect of larval development has received more scrutiny however, namely, larval diapause. This developmental arrest of third instar larvae acts as an overwintering stage for larvae developing at the end of the temperate summer. Pioneering work by Saunders in the 1960s showed that this developmental switch is not controlled by the individual larvae however, but rather by the mother in response to changes in photoperiod (day length) and also to some extent to changes in temperature and host availability. Females therefore change some aspect of egg physiology to induce diapause, and resources now available from the *Nasonia* Genome Project mean that the molecular mechanisms controlling diapause induction are being teased apart, with the exciting prospect of a full molecular explanation of an important maternal effect.

### Adult Emergence and Mating

*N. vitripennis* is protandrous, with males emerging first from the host puparium in order to mate with females that will emerge soon after. As mentioned earlier, this is not true for all *Nasonia* species, with *N. giraulti* showing the greatest extent of within-host mating and *N. longicornis* showing intermediate behavior. The genetic basis for this species-specific difference is currently under scrutiny. This difference in within-host mating is also reflected in differences in mating site preference. In *N. vitripennis*, males prefer to wait outside emergence holes in the puparium for females to emerge, competing to hold these small mating territories unless high male density makes defense impractical. These mate site preferences seem less important for the other two species so far studied, perhaps due to the greater likelihood of within-host mating. Certainly, males in *N. vitripennis* mark their mating territory following successful mating with the recently identified pheromones (4*R*,5*R*)- and (4*R*,5*S*)-5-hydroxy-4-decanolide (HDL) and 4-methylquinazoline (4-MeQ); these pheromones are very attractive to virgin females, such that males typically

remain where they have been successful at obtaining mates. The species' differences in mating site are hypothesized to have evolved to reduce interspecific mating in areas of sympatry (i.e., East and West North America) and perhaps represent one of several mechanisms to facilitate prezygotic reproductive isolation.

### Courtship and Copulation Behavior

Courtship begins with the male finding a female, usually as she is emerging from the host puparium. Female contact pheromones are an important part of a male recognizing a female. Courtship in *Nasonia* is an intricate display that induces female receptivity. Once a male has located a female, he will mount her back and position himself above her head. Once in this position, the male will begin a series of 'head nods' which always start with the extrusion of the mouthparts. This behavior has been shown to coincide with the release of an as yet unidentified pheromone from mandibular glands that is important for female receptivity. After a species-specific series of head nods, the female will indicate her receptivity by lowering her antenna and extruding her genitalia, physical cues which then induce the male to back up and attempt copulation. Once copulation is complete, the male will return to his original position above the female's head and engage in a second bout of (postcopulatory) courtship. This second courtship sequence is usually shorter and is again terminated by the female lowering her antennae. This signal leads to the male dismounting and is associated with females becoming almost completely unreceptive, both to further males and their pheromones.

The genetic basis of courtship has been of great interest given its possible role in the reproductive isolation of the different species in North America. A within-species study in *N. vitripennis* identified low heritability of both courtship duration and copulation duration (significant in the latter case), although for both traits dam effects were significant, suggesting nonadditive genetic effects. Use of interspecific hybrids has confirmed a genetic basis for the differences in head-nod series, but they also revealed a so-called grandfather effect, such that the species of the maternal grandfather of the male performing the courtship influenced the behavior observed (it should be remembered that in haplodiploid species, males do not have fathers, only mothers, but they will have maternal grandfathers). Similarly, an intraspecific study in *N. vitripennis* suggested both heritable variation in courtship behavior and at least a weak grandfather effect within-species. The mechanistic basis for these transgenerational genetic effects is not known, but an obvious possibility is some form of genomic imprinting, such that paternal chromosomes manage to influence expression of a trait when passed through to grand-offspring. One of the most exciting discoveries of the *Nasonia* Genome Project has been a full DNA methylation toolkit, with all three families

of DNA methyl-transferase genes (*Dnmt-1*, *Dnmt-2*, and *Dnmt-3*) present. DNA methylation is one the best-known mechanisms of genomic imprinting, with methylated cytosine residues influencing how a gene is expressed (both up- and downregulation is possible). There is also now direct experimental evidence from *Nasonia* for DNA methylation (21 of 42 randomly chosen genes showed patterns consistent with DNA methylation), so genomic imprinting as a mechanism by which parents influence offspring behavior is a very real possibility.

Since female *Nasonia* are assumed to disperse from the natal patch almost immediately after mating, it has been thought that females will have little opportunity to remate and will thus remain monandrous in the wild. Evidence from population genetic studies of *Nasonia vitripennis* however suggests that multiply mated (polyandrous) females do exist in natural populations, albeit at a low frequency. Moreover, there is genetic variation in *N. vitripennis* for polyandry, and laboratory-maintained cultures of wasps do appear to evolve a greater degree of polyandry as a result of artificial selection arising from some as yet unidentified aspect of lab rearing. Interestingly, although female polyandry is heritable in *N. vitripennis* (i.e., there is significant additive genetic variation in remating), there is also evidence for nonadditive effects influencing female remating rate, even after controlling for common-environment effects. These residual nonadditive maternal effects could be genetic in origin, again raising the possibility that genomic imprinting may be influencing aspects of *Nasonia* mating behavior. Understanding the genetic basis of female receptivity is now being considered in terms of which genes are activated during and after mating, but one interesting fact has already emerged thanks to the *Nasonia* Genome Project. None of the *Nasonia* species appear to have either the sex peptide gene, or the sex peptide receptor. The sex peptide gene encodes one of a large array of male accessory gland proteins (ACPs) in *Drosophila*, and is associated with male effects on many aspects of female reproductive physiology after mating, including shutting down female receptivity. As such, sex peptide and other ACPs have been the targets of a great deal of interest in *Drosophila*, especially in terms of sexual conflict over the control of reproduction. However, the absence of sex peptide and its receptor in *Nasonia* suggests that different mechanisms may be involved, perhaps a key lesson for insect behavioral geneticists in the coming years.

There has been rather little work on sexual selection in *Nasonia*, barring some early attempts to explore 'rare-male effects' on female mate preferences, some descriptions of patterns of sperm precedence in multiply mated females (first male sperm precedence appears the most common pattern), and the descriptions of male territoriality mentioned above. However, female mate preferences in terms of conversus heterospecifics have received attention, and indeed females exhibit preferences for their own species

as expected. A QTL study using two strains of *N. longicornis* that varied in their willingness to mate with *N. vitripennis* identified three major QTL influencing female willingness to mate (Figure 3), but more remains to be done to explore the genetics of mate preference within and between *Nasonia* species.

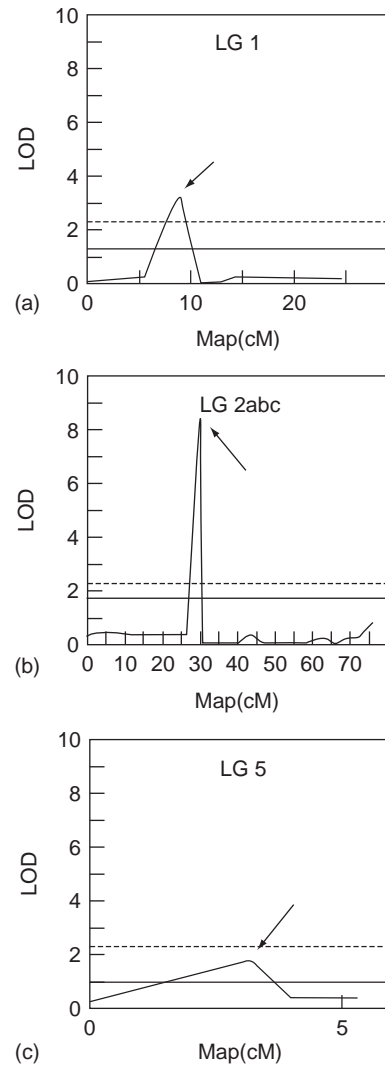
### Dispersal Behavior and Host Location

After mating, females disperse from the natal patch in order to look for new hosts. Little is known directly about this behavior, although population genetic studies of wild populations suggest that female dispersal is sufficient to limit population substructuring and levels of inbreeding to that occurring as a result of within-patch mating. In all species of *Nasonia*, females disperse from the natal patch. However, the extent to which males also disperse from the natal patch varies between the species. *N. vitripennis* males are brachypterous (short winged) and cannot fly. Any dispersal they undertake is done via walking away from the patch, and it is not known whether these males ever reach other patches and mate with females there. *N. giraulti* males on the other hand are fully winged and can disperse away from the host puparium (*N. longicornis* male wings are intermediate in size, and they have some ability to fly). QTL analysis by Gadau and colleagues of interspecific hybrids has shown that these differences between the species in wing morphology (including size and shape) are associated with 11 regions in the genome. That study also identified epistatic interactions between the QTL influencing wing size and also wing bristle density. Intriguingly, very recent work was suggested that regulatory sequences associated with the gene *doublesex*, better known for its well-conserved role in the sex-determination cascade of many organisms, including *Nasonia*, is the basis for one of the wing size QTL.

Once they start to disperse, host location is primarily determined by olfaction. Females have, through a series of olfaction tests, been shown to be attracted to rotting meat and specifically rotting meat on which maggots of the host species have fed, indicating that the larvae produce a chemical signal while feeding. Females appear to be able to remember smells associated with a host they have parasitized, which may help them to locate hosts at different patches. The genetic basis of these behaviors remains unexplored though.

### The Molecular Control of Behavior

We will end our consideration of the behavior genetics of *Nasonia* with a brief discussion of some of the latest



**Figure 3** Results of a quantitative trait loci (QTL) analysis for female mate discrimination in *Nasonia longicornis*. The arrows represent QTL for willingness to mate with *Nasonia vitripennis*. (a), (b), and (c) are the results for linkage groups 1, 2, and 5, respectively. LOD signifies the 'likelihood-of-odds' score, used to calculate the effect-size and significance of a putative QTL. The position along each linkage group is denoted on the X-axis in centimorgans (cM). The dotted horizontal lines represent genome-wide significance thresholds and the solid horizontal lines represent linkage-group-wide significance thresholds (both calculated via permutation tests;  $P < 0.05$ ). The QTL identified on linkage groups 1 and 2 have greater statistical support than the QTL found on linkage group 5 (this latter QTL was significant in an alternative genetic background: for further details of this study see Velthuis et al., 2005). Recent mapping work has coordinated the linkage groups from studies such as this to the five chromosomes of *Nasonia*. Adapted from Velthuis B-J, Yang W, van Opijnen T, and Werreh JH (2005) Genetics of female mate discrimination of heterospecific males in *Nasonia* (Hymenoptera, Pteromalidae). *Animal Behaviour* 69: 1107–1120, with permission from Elsevier.

findings from the *Nasonia* Genome Project in terms of the molecular control of behavior, to give a flavor of possible new avenues of research. Although *Nasonia*-specific pathways have yet to be elucidated, bioinformatic analysis of the *Nasonia* genome has revealed a number of important features.

First, from our review of *Nasonia* behavior earlier, olfaction is clearly an important aspect of behavior, especially in females. *Nasonia* has a large number of olfactory-binding proteins (OBPs), with ~90 annotated in the genome. In addition, *Nasonia* has a sizeable number of olfactory receptor proteins (around 300) and also gustatory receptor proteins (58 annotated genes). This overall repertoire is larger than both that of *Drosophila melanogaster* and the honeybee *Apis mellifera*, being more similar to that of the beetle *Tribolium castaneum*. Clearly, both smell and taste are important sensory modalities for *Nasonia* as it interacts with its environment and may be key to understanding many aspects of its behavior. Second, *Nasonia* has a suite of neurohormones and their associated G-protein-coupled receptors thought to control behavioral responses via their interaction with neural and cellular signaling pathways. In addition, the presence of neurotransmitter receptors such as cys-loop ligand-gated ion channels has been confirmed. While these findings are in some ways not especially surprising, they do provide a starting point for a more detailed molecular genetic analysis of the control of behavior in *Nasonia*. Finally, along with a number of other insects, *Nasonia* also boasts the recently discovered oxytocin/vasopressin-like protein inotocin and its receptor. Oxytocin and vasopressin are well-known molecules from vertebrates, with various cell signaling roles that are often associated with reproductive behaviors. Although the function of inotocin in insects is not yet known, it may well prove to be important in a number of *Nasonia* behaviors.

See also: *Drosophila* Behavior Genetics; Genes and Genomic Searches; Konrad Lorenz; Parasitoid Wasps: Neuroethology; Parasitoids; Sex Allocation, Sex Ratios and Reproduction.

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