Nasonia:

An ideal organism for research & teaching

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NASONIA

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Nasonia are excellent organisms for research and teaching. These parasitoid wasps (no, they cannot sting you and they are harmless to people) have been the subject of genetic, ecological, evolutionary and developmental research for over 40 years. Two general features that make these insects such excellent study organisms are (a) ease of handling and rearing, and (b) interesting and diverse biology. *Nasonia* are readily reared on commercially available fly pupae (the hosts). Virgin females and males are easily collected in the pupal stage (there is a 3 day time window for virgin collection). Adults are "user friendly" and can be handled without the need for anaesthetization. *Nasonia* has a short generation time (two weeks), but can be stored under refrigeration for periods of time, allowing for flexibility in experimental timing. A diapausing larval stage allows storage of strains for up to two years without maintenance. Both visible mutants and molecular markers are available for genetic mapping and instruction in genetics.

The system is excellent for basic studies in genetics, ecology, behavior, development and evolution. Three closely related species of *Nasonia* are present. The species are interfertile, allowing movement of chromosomal regions (and phenotypes) between the species for genetic and molecular genetic analyses of species differences in behavior, development, morphology and physiology. *Nasonia* is an excellent candidate for comparative genomic studies, as well. A key feature of *Nasonia* is haplodiploid sex determination; males are haploid and develop from unfertilized eggs and females are diploid and develop from fertilized eggs. This feature makes *Nasonia* a very useful organism for genetic research (advantages of this feature are described further below). Below I describe the basic biology of *Nasonia*, and discuss opportunities for research

Basic Biology

Nasonia are small parasitoid wasps (Hymenoptera: Pteromalidae) that sting and lay eggs in the pupae of various fly species, primarily blowflies and fleshflies. There are three closely related species in the genus, *N. vitripennis*, *N. longicornis*, and *N. giraulti*. *N. vitripennis* is found throughout the world; *N. giraulti* is found in eastern North America and *N. longicornis* is found in western North America. There are many intriguing aspects to *Nasonia* biology. Below I outline some of the basic features. A dated, but still excellent review of *Nasonia* biology is present in Whiting (1967, see Reference List).

Life Cycle: The basic life history described below is for *N. vitripennis*; the other two species have similar life-histories, and differences between the species will be mentioned.

When a female encounters a host puparium, she first examines the host, then drills through the host puparial wall with her ovipositor. She injects venom into the pupa, which will eventually kill the fly. The female then commences laying eggs upon the host, underneath the puparial wall. She typically lays from 20 to 50 eggs per *Sarcophaga bullata* pupa. The female may lay these eggs in one bout or may take a number of hours to complete oviposition. The female also uses excretions from her ovipositor to construct a feeding tube from the pupa to the puparial wall. From this she feeds on host hemolymph, which appears to be important in the production of additional eggs. At 25 C, eggs hatch around 36 hours after being laid. Developing larvae complete 3 instars and then pupate within the host around 9 days after laying (see Development Time Table). Pupal development takes approximately 3 days. Male and female pupae can easily be distinguished during this time. Adults eclose from pupation within the host, and then chew an exit hole. Emergence typically occurs by 14 days.

Mating occurs immediately upon emergence from the host. Courtship behavior is brief (typically taking 1-2 minutes) and involves stereotypic courtship displays. After mating, females disperse from the natal patch in search of new hosts.

Development takes slightly longer in *N. giraulti* and *N. longicornis*. *N. giraulti* females often mate within the host prior to emergence, in contrast to the other two species.

Genetics: In many respects, *Nasonia* is a superior organism for genetic research. The important features that make it so are (a) short generation time (b) large family sizes, (c) ease of handling (including virgin collection), (d) ability to inbreed and produce healthy inbred isogenic lines, (e) availability of visible and molecular markers (f) ease of complete genome screening for mutations in the haploid sex, (g) presence of three closely related and interfertile species, which provides a wealth of phenotypic and molecular marker differences, and (h) ability to produce hundreds of genetically identical (clonal) recombinant genotypes in the F3 generation (see description below). These features make *Nasonia* an excellent organism for basic studies in genetics, including developmental genetics, evolutionary genetics, molecular evolution and comparative genomic research. *Nasonia* is particularly suited for the study of complex genetic traits, due to advantages provided by haploid males and the ability to easily produce inbred lines and genetically identical recombinant individuals. Positional cloning is practical in *Nasonia*, due to the high recombination rate and abundance of molecular marker differences between the interfertile species.

Basic Genetics: All three species of *Nasonia* have 5 chromosomes, corresponding to 5 linkage groups. A visible mutant map of *Nasonia* exists; currently there are about 20 mutant strains available, most of which are eye color, body color, morphological and embryonic lethal mutations (Saul 1989). Screening for new mutations in *Nasonia* is straightforward, given that the complete genome can be screened for recessive mutations in the haploid sex. The generation and characterization of new mutations is definitely needed in *Nasonia*. A more complete visible mutant map will be useful in genetic and developmental genetic studies, and will also facilitate positional cloning studies. In addition, screening and mapping of *de novo* mutations in *Nasonia*

are practical projects for undergraduate researchers, who have the opportunity to discover new mutations in this system. There are also interesting opportunities for characterization of existing mutations in *Nasonia*. For example *dant*, (distal antennapedia) is a recessive homeiotic mutation that converts antennae to legs; it has not been extensively characterized, nor has it been determined whether this mutation is homologous to *antennapedia* in *Drosphila*.

In addition to a visible mutant map, a RAPD molecular map (Gadau et al 1999) and AFLP marker map (unpublished) have recently been generated. Production and mapping of molecular markers in *Nasonia* is surprisingly easy. This is because there is a high incidence of sequence differences between the species, and polymorphisms can be quickly mapped in haploid F2 males without the problems of dominance that can occur with many molecular markers. In addition, a set of hybrid recombinant inbred lines are coming available to use for even more rapid mapping of molecular markers.

Molecular Genetics & Comparative Genomics: The genome size of *Nasonia vitripennis* is approximately 250 Megabase (2X greater than *Drosophila melanogaster*); however, the recombination rate in *Nasonia* is approximately 4X greater than in *D. melanogaster*, resulting in an average recombination rate per kilobase approximately 2X greater (around 330 Kb/cm). This coupled with the ease of generating molecular markers suggests that positional cloning is practical in *Nasonia*. However, this has not yet been demonstrated. Currently a lambda phage library to *N. vitripennis* exists, but BAC libraries are not yet available.

There has been virtually no work done on topics such as gene regulation and expression in *Nasonia*, except for recent promising studies of early patterning mutants (described below under development). Some work has been conducted on repetitive DNA in Nasonia (Eickbush et al 1992) and a family of retrotransposable elements have been partially characterized in *Nasonia* (McAllister and Werren 1997).

Little is currently known about sequence differences within and between the *Nasonia* species. This is a research area with good potential. In addition, when a particular sequence difference has been identified, it can can be quickly mapped using recombinant F2 males or hybrid inbred lines. Therefore, *Nasonia* is a good candidate for comparative genomic studies in insects.

Evolutionary & Quantitaive Genetics: Given the existence of closely related and interfertile species, opportunities for evolutionary genetic studies are abundant. Strains have been collected from different populations in North America for all three species, and these are available for laboratories interested in population genetic research. Analysis of mitochondrial CO1 sequences suggests some population subdivision in *N. giraulti* and *N. longicornis*. Studies are currently underway to characterize some phenotypic differences (e.g. wing size and female mate preference) between the species. The tools for detailed evolutionary genetic studies are now in place, and this promises to be a growth area in the near future.

In *Nasonia*, epistatic gene interactions can more easily be investigated without the added complexity of dominance interactions, by using haploid males. The ability to produce isogenic inbred lines in *Nasonia* is a further advantage for quantitative genetic studies, since isogenic females can be placed in different environments to investigate genotype x environment interactions and norms of reaction. Finally, there is a feature fairly unique to *Nasonia*, which makes it very useful for quantitative and other genetic

studies. Crosses can be performed between strains (or species) with different phenotypes; virgin F1 females are then provided with hosts. Because of haplodiploid sex determination, these female produce recombinant haploid male progeny. Individual males are haploid and therefore produce identical haploid sperm. Therefore, recombinant haploid males can be crossed to inbred line females, and the resulting F3 females will all be genetically identical (clonal females), but with a recombinant genotype. This permits, in the F3 generation of a cross, the production of hundreds of genetically identical females for analysis. Genetically identical recombinant females can be placed in different environments to analyze genotype x environment effects. In addition, F2 males can mate with many dozens of females, allowing crossing of the same haplotype into many different genetic backgrounds, each then producing hundreds of females for phenotypic characterization. The F2 recombinant males can readily be genotyped (e.g. using molecular markers) without marker codominance problems, and the genotype of the F3 females is known by also genotyping the maternal inbred line. These features make *Nasonia* almost uniquely adapted (among higher eukaryotes) for the study of complex genetic traits.

An exciting feature of *Nasonia* speciation is the presence of *Wolbachia*, cytoplasmically inherited bacteria that cause sperm-egg incompatibilities. All three species of Nasonia typically harbor two strains of *Wolbachia*, and these induced a high level of reproductive incompatibility between the species. This topic has been the subject of considerable research (e.g Breeuwer and Werren 1990, Bordenstein and Werren 1998). In fact, it is antibiotically cured strains of *Nasonia* that are used in interspecies crosses. These allow introgression of genes between the species, once the bacteria have been eliminated.

Ecology & Behavior: *Nasonia* is an interesting organism for behavioral and ecological research. Its parasitoid life style allows investigations of questions relating to parasitoid-host dynamics, host preference, specialist versus generalist biology, et cetera. In terms of behavior, there are many interesting questions about courtship behavior, male aggression and territoriality, female dispersal, and sex ratio control. Presence of three closely related species with different biologies is useful, particularly because they are interfertile which allows movement of genes involved in these phenotypes between the species.

Courtship and Mating: Courtship involves stereotypic displays that differ between the species (van den Assem and Werren 1994) as well as the release of pheromones from the males mandibular region that plays an important role in female receptivity (van den Assem et al 1980). The genetic basis of courtship differences between the species is tractable for genetic analysis because of the ability to move genes between the species by hybridization and back-crossing of the fertile hybrids. Females of *N. giraulti* often mate within the host, whereas this is uncommon or absent in the other two species. Within-host mating clearly will have strong influences upon the population structure. Males show territorial behavior, defending host puparia that have female wasps within. Little work has been done on this interesting behavior. After mating, females disperse from the natal patch in search of new hosts. Dispersal behavior of females differs between strains and species. Males of *N. vitripennis* have vestigial wings and are incapable of flying. Males of *N. longicornis* have intermediate sized wings and *N. giraulti* males have large

wings similar in size to those of females. The latter two species are capable of flying, although they do not do so as readily as females.

Sex Ratios and Sex Ratio Distorters: Most matings occur locally within the natal patch, and sibling matings are not uncommon. Therefore, *Nasonia* is subject to local mate competition, and has been shown to alter sex ratio among progeny in response to the number of females in a group of hosts. When ovipositing, single females typically produce strongly female-biased sex ratios (80 -95% daughters), whereas when in groups they produce more equal ratios. Presumably, the haplodiploid sex determination provides a mechanism for control of the sex ratio among offspring, and reproductive anatomy of females suggest that they can control individual fertilization of eggs (Whiting 1967). In addition to the normal sex ratio control of the wasps, a suite of extrachromosomal sex ratio distorting factors exist in natural populations. These include *psr* (paternal sex ratio), a supernumerary chromosome that causes destruction of the paternal chromosomes following fertilization, resulting in conversion of males to females, *son-killer*, a bacterium that kills unfertilized (male) eggs of infected females, *msr* (maternal sex ratio), a cytoplasmic factor that causes nearly 100% fertilization of eggs. These factors are maintained in different lines of *Nasonia*, allowing for detailed biological study.

Host Preferences: The three species differ in their host preferences. *N. vitripennis* is a generalist and will parasitize a wide range of fly hosts, including blowflies, fleshflies and houseflies. The other two species appear to be specialists, and are found parasitizing *Protocalliphora*, blowflies that specialize as ectoparasites in birdnest. *N. giraulti* and *N. longicornis* prefer these hosts, although they will parasitize *S. bullata*. The behavioral, genetic basis of host preference differences has not been well studied.

Field Biology: *Nasonia* is a tractable, although occasionally smelly, system for field research. Wasps can be collected from bird nests and from the vicinity of carcasses (*N. vitripennis*). Baits using meat that has been fed upon by blowfly larvae placed in mesh bags can be efficiently used to sample natural populations. Field studies have uncovered a variety of the important features of this system, including sex ratio distorters, additional species, and strain differences in behavior and morphology. Strains collected from throughout North America are available to interested researchers, as is more detailed information on field sampling techniques.

Development: *Nasonia* is a good candidate for comparative studies of development. Mutations disrupting development can be rapidly screened for in haploid embryos, and maintained heterozygously in females. Genes affecting development can be quickly mapped using visible markers and the abundance of molecular marker differences present between the closely related species. These marker differences and a high recombination rate also make positional cloning a practical possibility within *Nasonia*. Recent work has uncovered several mutations affecting early pattern formation that appear to be homologous to homeiotic mutations in *Drosophila* (Pultz et al 2000), and also indicate that zygotic control of early development is more prevalent in *Nasonia* (Pultz et al 1999).

Additional work involves studies of morphological and developmental differences between the three closely related species. For example, males of the three species differ significantly in wing size and head shape. Genetic analysis of these features is tractable, including the eventual positional cloning of genes involved in these species differences.

Preliminary work indicates a relatively simple genetic basis to wing size differences (Weston et al 1999). Excellent opportunities exist for detailed studies of head development using the natural variation present in the three species.

Physiology & Morphology

There is a large early literature on physiology in *Nasonia*, including studies of diapause, and insect hormone effects on development. More recent studies have begun to investigate the physiological effects of venom on hosts (Rivers et al 1999). Physiological studies in Nasonia remain a wide open area for research.

Handling and Rearing

Nasonia is easy to work with. Below are some of the relevant features that make them convenient laboratory organisms.

Stock Maintenance: Stocks are easily maintained in *Nasonia* in plastic or glass vials or test tubes. Emerging females are collected into a new vial by placing the vial over the original vial with emerged wasps. Females are negatively geotaxic and move into the new vial. Hosts are then placed into the new vial (usually approximately 1 - 2 wasps per host). Fourteen days later (at 25° C) the next generation emerges. It's as simple as that. No special feeding or handling is necessary. Stocks can be slowed down by placing them at cooler temperatures, or speeded up (up to about 28° C). Cultures can be placed under refrigeration for a couple of weeks if necessary. This is best done at the yellow pupal stage and adult stage, but can be done at other life stages as well. Adult females can also be kept alive for several weeks at 25^0 C with a small amount of honey, and females can live for over a month if provided with fresh hosts.

Collecting Virgins: Virgin collection is very easy in *Nasonia*. Wasp pupae can be sexed in the pupal stage, which provides a three day time window for virgin collection. They are immobile in the pupal stage, and therefore can be collected without the need for anesthetization. Individuals are most easily sexed in the dark pupal stage, but with minimal training can be readily distinguished as yellow pupae. One looks for the presence of an ovipositor in the distal end of the abdomen. In *N. vitripennis*, males can also be distinguished by small wing pads.

Handling Adults: Adults are very "user friendly" and can be sorted and used in experiments without anesthetization. Although females can fly, they do not do so readily. However, they are positively geotactic. Therefore, to set up females individually on hosts, one need only dump a few females onto a surface and then place test-tubes over the crawling individuals. They will then conveniently climb into the tube. Add a host (or two) and plug the tube with cotton and you are done. Large numbers of individuals can be efficiently handled in this way.

Collecting Eggs: The easiest way to collect eggs is to allow females to lay eggs for a prescribed period of time on a host to which their access is restricted to one end. This is

accomplished by placing the host into a foam plug with a hole in one end, and placing this with the female into a test tube. After an oviposition period (the narrower the time, the more synchronized the eggs), hosts are removed, the puparial end is "popped off" with a probe, and eggs are collected with a fine brush. For maximum egg production, it is recommended that females be allowed to host feed for 2 – 3 days prior to placing them onto "plug hosts" for egg collection.

Diapause: Diapause larvae can be stored under refrigeration for up to two years, and then removed to room temperature, where they will complete development. Although two years is possible, for safety it is recommended that cultures be removed from diapause after around 1.5 years. Induction of diapause is accomplished by placing ovipositing females into short photoperiods (6L:18 D) and cool temperatures (e.g 15- 18^0 C). Better results are achieved by providing females with new hosts every several days under these conditions, and by allowing females to oviposit individually in test tubes. On occasion, a few generations are needed prior to diapause induction, and strains differ in diapause tendency.

Hosts: In working with *Nasonia*, you also need to have hosts. Fortunately, these are easy to obtain and also to rear, if you prefer. *Nasonia vitripennis* can be maintained on a number of different species, including *Sarcophaga bullata* (the fleshfly), various calliphorid flies including Calliphora vomitora, C. vicina, Phormia regina, and *Phaenicia sericata*, and on houseflies (*Musca domestica*). N. longicornis and giraulti can be cultured on blowflies and calliphorid flies (although their preferred hosts are *Protocalliphora* bird nest flies).

Hosts can be purchased from Ward's Natural Science, Carolina Biologicial and various other sources. Blowfly larvae (referred to as "spikes") are used as bait by fisherman, and can be purchased by bait stores in some areas. Potential sources include Baitman (1-800-729-7312 or 815-286-7312; http://www.baitman.com) or Wholesale Bait Co. (1-800-733-2380; http://www.wholesalebait.com). I do not know anything concerning species or quality of the material these companies provide. I am also willing to provide hosts to individuals conducting research on *Nasonia*. Arrangements can be made by contacting me. *Sarcophaga bullata* hosts can be easily reared, with sufficient numbers reared in one round to maintain wasps for several months.

Sarchophaga bullata pupae can be placed under refrigeration (4^0 C) for several months and remain suitable for parasitization. Host quality is checked by cracking open the puparium at the head region of a few hosts (to be discarded). Hosts are suitable up to the brownish eye stage, although are preferable when in the white-eye to yellow-eye stage. Once bristles begin to form on the body or the body begins to darken, the hosts are unsuitable.

Supplemental Information

Development Time in Nasonia vitripennis at 25°C

DAY	*STAGE (AND CHARACTERISTICS)*
0	Egg
1.5 – 2	First instar larva (active feeding)
2 – 3	Second instar larva (active feeding)
3 – 6	Third instar larva (active feeding)
6 – 7	(Cessation of feeding, resting stage, and defecation)
7 – 8	Prepupal stage (resting continues)
8 – 9	White pupa with gradual yellowing
9 – 10	Yellow pupa with eye color developing
10 – 11	Eye-color prominent; pigmentation of head and thorax
11 – 12	Fully pigmented head and thorax
12 – 13	Entirely pigmented body; males begin to eclose
13 – 14	Females eclose
14	Emergence from host puparium

Equipment & Supplies

Basic Equipment & Supplies List

Dissecting Microscope
Light Source (e.g. fiber optic illuminator)
Bench Liner
Paint Brushes
Bent & Straight Probes
Index Cards
Lab Markers
Test Tubes and Vials
Cotton plugs and foam plugs
Test tube racks
Large Vial Racks (empty scintillation vial boxes work well)
Lab Notebook
Hosts (e.g. *Sarcophaga bullata* pupae)

Potential Vendors for Supplies

Description	Supplier	Part Number
Clean Sheets Bench & Shelf Liners 18"	VWR	54110-320
Polypropylene Test Tube Racks	VWR	60983-007
Disposable Culture Tubes (Diapause/Shipping) - red	VWR	60818-434
Disposable Culture Tubes (Diapause/Shipping) - blue	VWR	60818-437
Disposable Culture Tubes (Diapause/Shipping) - green	VWR	60818-438
Cotton Balls	VWR	15431-630
Cotton Balls	General Medical	189153
12 x 75 mm Vials - clear	Fisher	14-958 C
12 x 75 mm Vials - white	Fisher	14-957-12A
12 x 75 mm Vials - yellow	Fisher	14-957-12B
12 x 75 mm Vials - green	Fisher	14-957-12C
12 x 75 mm Vials - orange	Fisher	14-957-12D
12 x 75 mm Vials - blue	Fisher	14-957-12E
Clear Polystyrene Drosophila Vials (25 x 95 mm)	Applied Scientific	AS-515
Clear Polystyrene Drosophila Vials (25 x 95 mm)	VWR	27500-000
Foam Plugs for Drosophila Vials (27 - 34 mm)	VWR	60882-189
Trays and Dividers for 25 x 95 mm Vials	VWR	27500-030

Nasonia vitripennis Linkage Map

(Redrawn and modified from Saul 1989)

		Linkage Group I	
% Recomb	Symbol	Name	Phenotype
	rep	red-eye pupae	slightly red eyed pupae
2*			
	rdh 1	reddish	dark red eyes
11	rev 421	reverend	legs of pupae extent towards ventral midline
3			
	ga 251	garnet	red eyes
1*			
	hb 441	hunchback	thoracic segments compressed
3			
	R	R-locus	many eye color mutants in region of no recombination, multiple loci. Includes stDR, oyDr, red 833 and others
4			
	cur 321	currant	red eyes
3*			
	cop 362	copper	frons copper-yellow
1*			
	cop 2	copper	frons copper-yellow
1*			
	stp 211	stumpy	abdomen shortened
2			
	ga 351	garnet	red eyes
2			
	gl XX	glass	eye facets poorly differentiated and number reduced
1			
	pu	purple	dorsal thorax purple and frons blue (absence of yellow sheen)
1*			
	ga 120 XX	garnet	red eyes
4*			
	cop 1	copper	frons copper-yellow
5			
	wa 362	white appendages	appendages white (entire body white in young pupae)
1*			
	stp 361	stumpy	abdomen shortened
1*			
	bk362 XX	black	black eyes
17			
	vg	vestigial	rudimentary wings

Linkage Group II

% Recomb	Symbol	Name	Phenotype
	bl 108	blue	frons blue
15			
	rdh 5	reddish	red eyes
<1			
	crw	crumpled wings	wings crumpled in adults, female sterile
<1*			position with respect to cl 131, bl 106 not yet determined
	cl 131 XX	cleft	ocellar region reduced w/ dorsal cleft between eyes number of antennal segments reduced
<1			
	bl 106	blue	frons blue
<1			
	se 121 XX	small eyes	eyes small, fewer facets than normal
<1			
	mh 493	mahogany	dark red eyes; rdh 810 is allelic
1			
	bl 109	blue	frons blue
25			
	unf 441 XX	unfolded	incomplete eclosion from pupal case in dorsal thorax; small mesothoracic wings

% Recomb	Symbol	**Linkage Group III** Name	Phenotype
	st5219	scarlet eyes	bright red eyes; stm allelic
10			
	tl 627	tile	rust-red eyes; pe 100 allelic
<1			
	bl 13	blue	frons blue
<1			
	bk 576	black	eyes slightly darker brown than wild type
3			
	bl 5101 XX	blue	frons blue
2			
	fx 331 XX	flexed	mesothorax duplicated; metathorax reduced; both pairs or wings of equal size, pupa flexed ventrally
9***			
	cop 411 XX	copper	frons yellow-copper
37			
	bk 424	black	black eyes
			*** note that recent results place st5219 and bl 13 onto LG IV approximately 10 map units from a lethal and 20 map units from or 123

% Recomb	Symbol	**Linkage Group IV** Name	Phenotype
	bgs 532 XX	blue grass	frons green with blue glints
10			
	st 473 XX	scarlet	bright red eyes
4			
	or 123	orange	light orange-red eyes
1			
	ws1	wing size	wing size locus, introgressed from *N. giraulti* into *N vitripennis* postion of ws1 with respect ot pu 416 and st 473 unknown
3			
	pu 416 XX	purple	frons deep blue or purple
1			
	vio 6	violet	frons deep blue or bleu-purple
			*** recent mapping studies put bl 13 <1 map unit from or 123 and ws1 and 20 map units from st5219. Results suggest that pu 416 may be bl 13 or allelic.

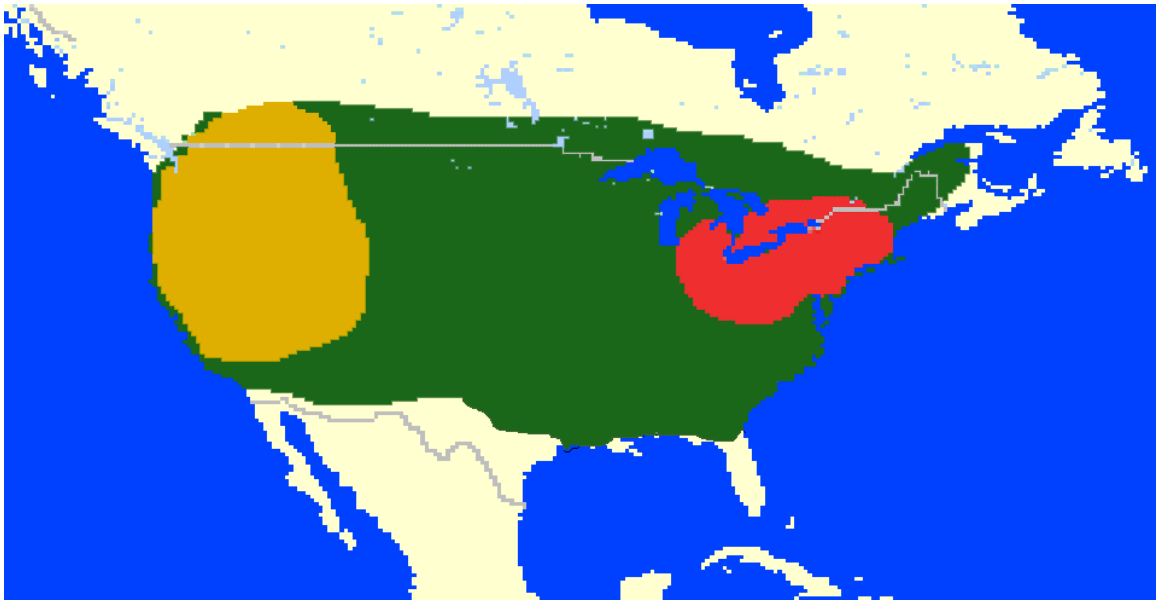
Linkage Group V

% Recomb	Symbol	Name	Phenotype
	ga 561	garnet	red eyes; tom's red is allelic
10			
	pel 311	pellucid	gray-white eyes
12*	mod 306	modifier	changes red and scarlet eyes to yellow and orange
7*			
	st 318	scarlet	bright red eyes
13			
	mm 251	mickey mouse	eyes protuberant, dorsal head defective
5			
	pm 541	plum	frons blue or reddish-blue
6			
	sw 561 XX	short wings	small mesothoracic wings; metathoracic wings project out from body

Special Comments

XX	strain no longer exists
*	recombination frequency not measured directly, estimated by distance to common loci
***	linkage of some markers on LGIII are questionable, and are actually on LGIV. Map will be revised when results are confirmed

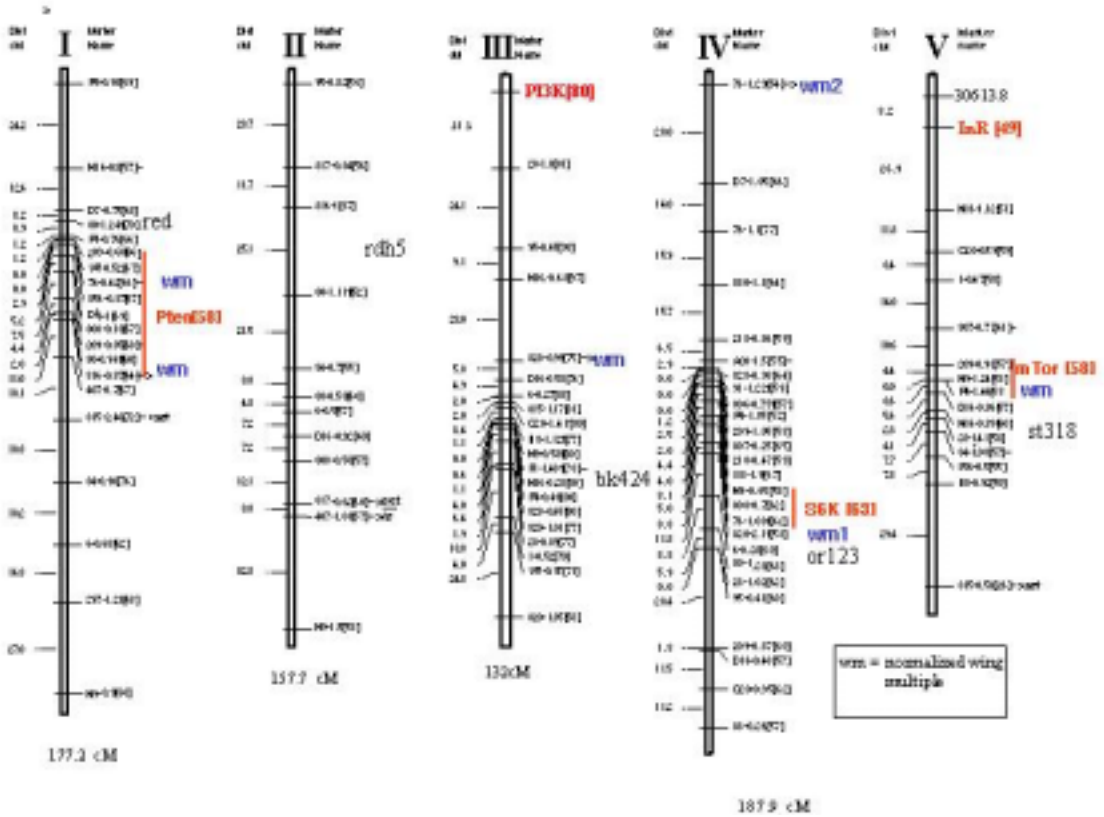
North American Range Map of Nasonia/



N. vitripennis - green, *N. giraulti* - red, *N. longicornis* - yellow

The map indicates approximate ranges of the three species. The limits of their range in the south and north are not known. N. vitripennis is a cosmopolitan species that is found throughout the world. The other species are found in North America.

Molecular Marker Linkage Map



Interspecific (Ng and Nv) Linkage Map indicating positions of RAPD markers, a set of insulin signaling pathway genes (pten, Tor, PI3k, S6K, mTor, and InR), and one visible mutant marker for each linkage group. Also indicated are major quantitative trait loci for wing size differences between the two species (wm). Latter results are from Gadau et al 2002.

Some Nasonia Literature

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