



Territoriality and behavioural strategies at the natal host patch differ in two microsympatric *Nasonia* species

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Territoriality occurs in a wide variety of animal taxa. The defence of valuable resources, which in the case of territoriality are bound to a specific location, gives the defender priority of access to these resources. Males often defend areas in which the chance to meet females is high and territoriality frequently includes pheromonal marking. When closely related species co-occur within the same environment, different behavioural strategies frequently evolve to avoid reproductive interference. Males of the gregarious parasitoid wasp *Nasonia vitripennis* exhibit territorial behaviour on the host from which they emerge. However, descriptions of territorial behaviour have been for the most part anecdotal and quantitative standardized observations in an experimental set-up are lacking. In addition, studies of the behaviour of the other *Nasonia* species that frequently occur in microsympatry, that is, within the same host individual, have rarely been conducted. We investigated and compared territoriality in two species of *Nasonia* by extensive video recording of emerging wasps in a microcosm approach. We show that males of *N. vitripennis* meet the concept of territoriality whereas males of *Nasonia giraulti* do not. Although *N. giraulti* females are already mated when emerging from the host and males do not show territoriality, *N. giraulti* males mark the substrate with their abdominal sex pheromone as often as males of *N. vitripennis*. For *N. vitripennis* we further show that, although larger males were more often territorial, experience of being in the territorial position was particularly important for winning territoriality contests. Finally, we investigated differences in the pattern of emergence and dispersal between the two species and discuss how the different behavioural strategies may help them avoid reproductive interference.

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Many animals defend limited resources such as food, oviposition sites or mating partners against their competitors. This occurs in more, or less, aggressive contests in which one individual typically gains dominance while the other exhibits subordinate behaviour. In social groups, repeated contests frequently result in relatively stable dominance–subordination relationships between pairs of individuals and complex dominance hierarchies may develop (Kaufmann, 1983). The defence of resources that are bound to specific locations, for example oviposition sites, specific food patches, adequate breeding sites or locations frequently visited by females, is termed territoriality. The successful holder of a territory gains sole or priority of access to the resources that are present (Kaufmann, 1983; Maher & Lott, 1995). Defence of a resource, however, does not necessarily imply aggressive interactions. The

behaviours involved range from direct aggression to complex behavioural displays to mere advertisement by visual presence, acoustic signalling or scent marking (Baker, 1983). In males, chemical messengers used to scent mark the territory can function as attractants for females and indirect indicators of male quality (Johansson & Jones, 2007).

Territoriality exhibited by males at locations where encounters with females are likely to occur have been observed in a wide variety of animal taxa ranging from mammals (Clutton-Brock, 1989) and other vertebrates (Cuadrado, 2006; Eriksson & Wallin, 1986; Roithmair, 1994; Spence & Smith, 2005) to various arthropods (Christy, 1987; Edwards & Dimock, 1991; Fitzpatrick & Wellington, 1983; Suter & Keiley, 1984). In insects, males establish territories near or at oviposition sites, on routes to oviposition sites, near or at females' foraging sites, near or at nest entrances from which virgin females might emerge or directly at female pupae which are guarded until adult females eclose (Fitzpatrick & Wellington, 1983).

Territoriality at female emergence sites has also been described in parasitoid wasps, for example the ichneumonid wasp *Lytarmes*

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maculipennis (Godfray, 1994), several species of scelionid wasps (Waage, 1982; Wilson, 1961) and the pteromalid wasp *Nasonia vitripennis* (van den Assem, Gijswijt, & Nübel, 1980). Species of the last two examples are protandrous (i.e. males emerge earlier than females) and gregarious (more than one wasp develops within one host) or quasigregarious (only one wasp develops per host, but hosts are clumped). Protandry gives males the opportunity to set up territories before females emerge at the same host patch. Females can then be intercepted, courted and mated before they leave the natal host patch and seek oviposition sites (Godfray, 1994; Wiklund & Fagerström, 1977).

When two species that are reproductively isolated by postzygotic isolation mechanisms occur in sympatry they usually evolve prezygotic strategies to avoid reproductive interference and interspecific mating (Gröning & Hochkirch, 2008; Noor, 1999). In insects, such strategies often include mechanisms connected directly to mate recognition and mate choice, for example differences in courtship behaviour (van den Assem & Werren, 1994; Tomaru & Oguma, 1994) or discrimination between conspecific and heterospecific mating partners by chemical messengers (Singer, 1998; Wyatt, 2014). However, reproductive interference can also be avoided by developing differences in the temporal mating pattern or by shifting mating sites within the same habitat (Hardeland, 1972; Kuno, 1992).

A mating site shift has been suggested in the parasitoid wasp genus *Nasonia* (Drapeau & Werren, 1999; Giesbers et al., 2013; Leonard & Boake, 2006; Ruther, McCaw, Böcher, Pothmann, & Putz, 2014). The genus consists of four species which all parasitize pupae of cyclorrhaphous flies (Darling & Werren, 1990; Raychoudhury, Desjardins, et al., 2010; Whiting, 1967) but differ in various aspects of their mating behaviour. These include different degrees of interspecific mate discrimination during courtship as well as differences in the male sex pheromone composition and the mating sites (Buellesbach, Greim, Raychoudhury, & Schmitt, 2014; Diao et al., 2016; Drapeau & Werren, 1999; Giesbers et al., 2013; Leonard & Boake, 2006; Mair, Kmezcic, Huber, Pannebakker, & Ruther, 2017; Niehuis et al., 2013; Ruther et al., 2014). *Nasonia vitripennis* (*Nv*) is cosmopolitan and occurs in sympatry with each of the other three *Nasonia* species: *Nasonia longicornis* (*Nl*) in the western part and *Nasonia giraulti* (*Ng*) and *Nasonia oneida* (*No*) in the eastern part of North America (Darling & Werren, 1990; Raychoudhury, Desjardins, et al., 2010; Raychoudhury, Grillenberger, et al., 2010). All four species are gregarious and females of different species often multiparasitize the same host individual (Grillenberger, van de Zande, Bijlsma, Gadau, & Beukeboom, 2009). After hatching, larvae feed as ectoparasites on the fly pupa inside the fly puparium, pupate inside the host puparium and emerge after eclosion. As developmental times of *Ng*, *Nl* and *No* are only slightly longer than those of *Nv*, and fly pupae are usually parasitized over 2 or 3 consecutive days, individuals belonging to two different species may emerge simultaneously from the same host puparium (Bertossa, van Dijk, Beersma, & Beukeboom, 2010). Except for *No* and *Ng*, all four *Nasonia* species are reproductively isolated by postzygotic cytoplasmic incompatibility resulting from infections with different strains of the intracellular bacterium *Wolbachia* (Bordenstein, O'Hara, & Werren, 2001). As a result, no viable hybrids are produced when females consent to heterospecific mating (Breeuwer & Werren, 1990). In mating experiments, females of *Nv* and *No* exhibited strong discrimination against heterospecific males whereas females of *Nl* and *Ng* were less discriminatory (Buellesbach et al., 2014; Giesbers et al., 2013). While females of *Nv* mate after emergence from the host, almost all females of *Ng* mate inside the host puparium before emergence (Drapeau & Werren, 1999; Giesbers et al., 2013; Leonard & Boake, 2006). This so-

called within-host mating in *Ng* has been suggested to have developed as a mechanism to avoid reproductive interference with *Nv* (Drapeau & Werren, 1999).

Although males of all *Nasonia* species produce an abdominal sex pheromone which is highly attractive to virgin females (van den Assem, Jachmann, & Simbolotti, 1980; Ruther, Stahl, Steiner, Garbe, & Tolasch, 2007; Steiner & Ruther, 2009a), the composition of this pheromone differs between them. While the pheromone in *Ng*, *Nl* and *No* consists of (4*R*,5*S*)-5-hydroxy-4-decanolide and 4-methylquinazoline, the pheromone of *Nv* contains a third component, the epimer (4*R*,5*R*)-5-hydroxy-4-decanolide which allows females of *Nv* to differentiate between the pheromone of conspecific and heterospecific males (Diao et al., 2016; Niehuis et al., 2013; Ruther et al., 2014, 2007). After emergence, males of *Nv* stay at or near the host, are aggressive towards other males (van den Assem, Gijswijt, et al., 1980; King, Askew, & Sanger, 1969) and show marking activity which is increased after contact with females (van den Assem, Jachmann, et al., 1980; Barrass, 1969; Steiner & Ruther, 2009b). When *Nv* females emerge, they are courted, and mating follows. After mating, a behavioural switch happens in the females, which results in females no longer being attracted to the male sex pheromone (Ruther, Thal, Blaul, & Steiner, 2010; Ruther et al., 2007, 2014). Typically, females of *Nv* mate only once before switching to host-seeking behaviour and multiple mating is rare in nature (Grillenberger et al., 2008; King, Grimm, & Reno, 2000; Ruther et al., 2014).

The territorial behaviour of *Nv* males after emergence has been described by van den Assem, Gijswijt, et al. (1980) and King et al. (1969), but these descriptions are limited to anecdotal reports rather than quantitative observations in experimental set-ups. Males of *Nv* emerge prior to females (protandry) and the first emerging male usually succeeds in establishing a territory on the host puparium (van den Assem, 1996). The other males of the group have been described as establishing territories in the vicinity of the host, frequently challenging the territorial male on the host, trying to sneak in to gain copulation opportunities when females emerge (van den Assem, 1996; van den Assem, Jachmann, et al., 1980; van den Assem & Vernel, 1979) or wandering off to other hosts from which females are about to emerge (van den Assem, Gijswijt, et al., 1980; King et al., 1969; Shuker, Pen, Duncan, Reece, & West, 2005). However, no experiments have been conducted to corroborate these anecdotal descriptions by a quantitative analysis of behavioural data gained from a standardized experimental set-up. In addition, few studies have investigated behaviours after emergence in the other three *Nasonia* species. A first approach to comparing species-specific behaviours of the three *Nasonia* species after emergence in an experimental approach has been conducted by Leonard and Boake (2006). They found a negative relationship between within-host mating/dispersal rate and aggression of males on the host. In the same study, *Nv* and *Nl* showed pronounced aggression on the host and low within-host mating and dispersal rates whereas *Ng* showed no aggression and 100% within-host mating and male dispersal rate. However, more detailed observations of male and female behaviours after emergence are still lacking. Evidence that males of *Ng* leave the natal host patch after emergence raises further questions concerning the production of the abdominal sex pheromone in these males (Niehuis et al., 2013; Ruther et al., 2014). Pheromone biosynthesis is usually costly (Johansson & Jones, 2007; Zahavi, 1975) and in *Nasonia* it involves linoleic acid as a precursor which is also essential for the production of sperm (Blaul & Ruther, 2011; Brandstetter & Ruther, 2016; Wathes, Abayasekara, & Aitken, 2007). Considering these costs, it is likely that *Ng* males make use of the pheromone in one way or another. Because *Nv* and *Ng* exhibit the most pronounced behavioural differences in the *Nasonia* genus, they represent a good

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