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The more the merrier – experimental evidence for density-dependent feeding facilitation in the bird-specialised tick *Ixodes arboricola*

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ABSTRACT

Similar to many other parasites, the distribution of ticks among hosts is strongly skewed, with few hosts harbouring the majority of parasites. Because parasite-induced impairment of host health, parasite population growth and pathogen transmission are density-dependent, understanding why tick distributions are skewed is important for the population and evolutionary dynamics of both parasite and host. However, there is currently no knowledge concerning parasites that strongly depend on individual hosts. Here, we investigated the effects of tick density on feeding performance in the nidicolous tree-hole tick, *Ixodes arboricola*, which feeds on cavity-nesting birds and is the carrier of several tick-borne pathogens. Nidicolous ticks reside in or close to their hosts' nests and therefore depend strongly on individual hosts and their offspring. Increased feeding success at higher densities (facilitation) may therefore be detrimental to the ticks themselves. We investigated the effects of tick density on feeding performance of *I. arboricola* by infesting great tit nestlings with one to five adult ticks, which is within the natural range. There was no effect of tick density on initial attachment success, attachment after 48 h or engorgement weight, but tick recovery rates increased significantly with tick density. We also found a modest increase in nestling body mass with tick density, suggesting that birds over-compensate resource drainage by the ticks and, by doing this, anticipate the costs of a tick-rich environment. Our results indicate that nidicolous ticks perform better when feeding in aggregation. This may have important consequences for population dynamics and consequently pathogen transmission.

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1. Introduction

From microparasites such as viruses and parasitic protozoa, to macroparasites such as helminthes and ticks, aggregation on hosts is common, with relatively few host individuals harbouring the large majority of parasites (Shaw and Dobson, 1995; Woolhouse et al., 1997; Wilson et al., 1998; Poulin, 2007; Calabrese et al., 2011). The proximate explanation is that parasite aggregation is the result of heterogeneity either in exposure to parasites among individual hosts, which results from the uneven distribution of parasites in space and time relative to hosts, or in susceptibility to parasitism, arising from differences among hosts in behaviour or immune resistance (Poulin, 2013). It has also been suggested that aggregation is beneficial for parasites, and that traits promoting aggregation are favoured by selection. Such ultimate explanations of aggregation include facilitation of feeding and mating, and overwhelming host defences (Sonenshine, 1991; Kiszewski et al., 2001; Poulin, 2007). However, aggregating may also be detrimental for

parasite individuals by increasing intraspecific competition, pathogen prevalence, host resistance and mortality, and attraction of predators (Jaenike, 1990; Poulin, 2007). For parasites that have low mobility or transmission, or which strongly depend on individual hosts, selection can operate against traits that promote aggregation when it strongly reduces host survival.

It is largely unknown which underlying mechanisms determine whether aggregation leads to density-dependent facilitation, i.e. increased feeding success with increased parasite density on a host, or competition. Such knowledge is important because many parasites are directly detrimental to their hosts and/or are of potential significance as pathogen vectors for both humans and livestock (Clayton and Moore, 1997; Poulin, 2007). There are three aspects of aggregation that have important implications for the population and evolutionary dynamics of the parasite and its host. First, aggregation may lead to increased parasite population growth due to increased reproduction and interspecific competitive potential, but there may also be intraspecific competition for space or nutrients (Wilson et al., 1998; Poulin, 2007). Second, high parasite densities may have negative effects on hosts (even for bird-associated ticks; see e.g. Luttrell et al., 1996; Monks et al.,

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2006; Heylen and Matthysen, 2008, 2011a; Pfäffle et al., 2009) or lead to increased host resistance (Randolph, 1994; Jones et al., 2015) and thus aggregation can have strong effects on host and parasite fitness (Wilson et al., 1998). Finally, co-feeding, i.e. parasites feeding on the same host in time or space, can increase pathogen transmission, even in the absence of systemic infection (Randolph et al., 1996).

Ixodid ticks are haematophagous ectoparasites and important vectors of pathogens including bacteria (e.g. *Rickettsia* spp. and *Borrelia burgdorferi* sensu lato (s.l.)), viruses (e.g. tick-borne encephalitis virus) and protozoans (e.g. *Babesia* spp.) (Gray, 1991; Jongejan and Uilenberg, 2005). Their low intrinsic mobility, lack of adaptations to facilitate direct transmission from one host to the next and the need for blood during a single long-lasting period of several days per instar (larva, nymph and adult) make ticks highly dependent on individual hosts (Sonenshine, 1991). Therefore fitness loss due to host death would be substantial and, indeed, ixodid ticks generally have limited effects on their hosts (Sonenshine, 1991; but see e.g. Luttrell et al., 1996; Monks et al., 2006; Heylen and Matthysen, 2008, 2011a; Pfäffle et al., 2009). Yet, in nature relatively few individual hosts harbour the majority of ixodid ticks (Davidar et al., 1989; Harrison et al., 2012; Moshaverinia et al., 2012; Heylen et al., 2013a).

There are conflicting results from studies that investigated how tick density affects their feeding success. On the one hand, there may have been selection of traits that promote aggregation on the same host due to selective advantages such as increased feeding performance due to shared activities of salivary compounds that suppress host inflammatory responses and prevent haemostasis (Davidar et al., 1989; Wang et al., 2001; Ogden et al., 2002). Several studies on ticks have found increased tick feeding success at higher feeding densities, i.e. feeding facilitation (Sutherst et al., 1978; Davidar et al., 1989; Hazler and Ostfeld, 1995; Wang et al., 2001; Ogden et al., 2002). On the other hand, high densities of feeding ticks can result in a decrease in feeding success due to elevated awareness of the host or resource competition among ticks (Hazler and Ostfeld, 1995). Other studies found competition such that tick feeding success decreased due to increasing tick densities (Sutherst et al., 1979; Randolph, 1994; Levin and Fish, 1998; Bartosik and Buczek, 2012; Jones et al., 2015). The underlying mechanisms that determine whether tick aggregation on individual hosts leads to facilitation or competition among feeding ticks are not fully understood, but knowledge concerning the effects of aggregation on ticks and their hosts is essential to understand the population dynamics and the epidemiology of disease transmission by ticks.

To date, the effects of aggregation on feeding performance have been investigated in non-nidicolous ticks, but to the best of our knowledge no such data are available for nidicolous ticks (see references concerning non-nidicolous ticks in the previous paragraph). Non-nidicolous ticks can find a new, unrelated host relatively easily and are often exposed to genetically unrelated hosts during the different developmental stages in the tick's life cycle (Hoogstraal and Aeschlimann, 1982; Sonenshine, 1991; Hillyard, 1996). Therefore, if feeding aggregation leads to decreased host health, the effect on tick fitness is relatively limited. In contrast, nidicolous ticks remain hidden inside or near the hosts' nests or burrows and encounter only a limited variety of hosts (Sonenshine, 1991; Hillyard, 1996; Gray et al., 2014). If fitness of nidicolous ticks increases at the expense of host health, ticks may kill or drive away hosts and ultimately seal their own fate (Gray et al., 2014). Therefore, for nidicolous ticks, feeding aggregation may be largely detrimental.

The tick *Ixodes arboricola* Schulze and Schlottke 1930 is nidicolous and its entire life cycle is restricted to tree holes and human-made nest boxes (Walter et al., 1979; Heylen et al.,

2014). Thus, it chiefly infests cavity-nesting birds, with great and blue tits (*Parus major*, *Cyanistes caeruleus*) as the principal hosts (Walter et al., 1979; Hudde and Walter, 1988; Petney et al., 2011). Because intrinsic mobility is low and hosts show high site fidelity to single cavities (Gosler, 1993), the ticks' fitness depends on the survival and re-use of cavities by the same hosts and their offspring (Heylen and Matthysen, 2011a). This has been argued to be the reason *I. arboricola* has a lower engorgement weight, longer feeding duration and no effect on host health compared with the congeneric non-nidicolous tick *Ixodes ricinus* (Heylen and Matthysen, 2011a). In nature, ticks aggregate and the majority of *I. arboricola* ticks are found on a limited number of hosts and in a limited number of nests (Heylen and Matthysen, 2011b; Heylen et al., 2012, 2014; Van Oosten et al., 2014a). However, the effects of feeding aggregation on tick fitness remain unexplored. This knowledge is important to gain a better understanding of the population dynamics of this tick, which is the carrier of *Rickettsia* spp. and *B. burgdorferi* s.l. (Špitalská et al., 2011; Heylen et al., 2013b). Knowledge concerning the mechanisms underlying aggregation is also essential for predicting and possibly controlling parasites in general.

In the current study, we infested nestlings of the great tit with increasing densities, within the natural range, of adult female *I. arboricola*. The infestations were carried out with adult female ticks because this is the largest instar and most important in terms of tick reproduction. We investigated tick attachment and feeding success as well as nestling body mass in order to test whether increased tick feeding densities lead to facilitation or competition among feeding ticks.

2. Materials and methods

2.1. Study species

Ixodes arboricola is widely distributed across Europe (Liebisch, 1996; Petney et al., 2011). The tick goes through three active life stages (larva, nymph and adult) and during each stage, with the exception of adult males, takes a single blood meal either to moult (larvae and nymphs) or to reproduce (Sonenshine, 1991). Adult males do not take a blood meal and remain in the nest box where they copulate with unfed and engorged female ticks (Van Oosten et al., unpublished data). Adult female ticks feed primarily on nestling birds, and are most apparent during the breeding season (Heylen et al., 2014). To obtain a blood meal, ticks attach to a host inside the nest and remain attached for several days (Sonenshine, 1991). Detachment is often in the same nest box because its hosts show high nest fidelity (Gosler, 1993). As such, dispersal capabilities between cavities are limited and relatedness of ticks within cavities can be high (Van Oosten et al., 2014a). Because its entire life cycle is restricted to natural and human-made cavities, *I. arboricola* only infests hosts that make use of such cavities, primarily cavity-nesting birds (Walter et al., 1979; Petney et al., 2011; Heylen et al., 2014). While ticks are generally uncommon in Belgium (Van Oosten et al., 2014a), high local densities can be reached with up to 167 nymphs, 15 adult females and hundreds of larvae found in individual nest boxes, and up to 46 larvae, 22 nymphs and 5 adult female ticks on individual great tits (Heylen et al., 2014, unpublished data). Although there is seasonality in tick occurrences on hosts and in nest boxes, all three instars can be found throughout the year (Heylen et al., 2014). The natural prevalence of *I. arboricola* ticks infesting adult great tits has been estimated at 7.5% during the pre-breeding season (early March to early April) but much lower throughout the rest of the year (Heylen et al., 2014).

The great tit (family Paridae) is the most common secondary cavity-nesting bird in western Europe and uses available natural

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