



## Social interactions modulate the virulence of avian malaria infection

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### ABSTRACT

There is an increasing understanding of the context-dependent nature of parasite virulence. Variation in parasite virulence can occur when infected individuals compete with conspecifics that vary in infection status; virulence may be higher when competing with uninfected competitors. In vertebrates with social hierarchies, we propose that these competition-mediated costs of infection may also vary with social status. Dominant individuals have greater competitive ability than competing subordinates, and consequently may pay a lower prevalence-mediated cost of infection. In this study we investigated whether costs of malarial infection were affected by the occurrence of the parasite in competitors and social status in domestic canaries (*Serinus canaria*). We predicted that infected subordinates competing with non-infected dominants would pay higher costs than infected subordinates competing with infected dominants. We also predicted that these occurrence-mediated costs of infection would be ameliorated in infected dominant birds. We found that social status and the occurrence of parasites in competitors significantly interacted to change haematocrit in infected birds. Namely, subordinate and dominant infected birds differed in haematocrit depending on the infection status of their competitors. However, in contrast to our prediction, dominants fared better with infected subordinates, whereas subordinates fared better with uninfected dominants. Moreover, we found additional effects of parasite occurrence on mortality in canaries. Ultimately, we provide evidence for costs of parasitism mediated by social rank and the occurrence of parasites in competitors in a vertebrate species. This has important implications for our understanding of the evolutionary processes that shape parasite virulence and group living.

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### 1. Introduction

The ubiquity of parasites ensures that the ability to minimise costs of infection is one of the major factors affecting an organism's fitness. Hosts vary in the degree of damage suffered when exposed to a similar parasitic challenge, and assessing the factors which determine these differences in parasite-mediated morbidity and mortality (generally called parasite virulence) is of fundamental interest to evolutionary biologists (Alizon et al., 2009). Parasite virulence is affected both by host genotype, parasite genotype and their interaction (Grech et al., 2006; Lefevre et al., 2007). As well as genetic differences, environmental conditions can alter parasite virulence (e.g. Jokela et al., 1999; Ferguson and Read, 2002; Bedhomme et al., 2004; Tseng, 2006), and individual differences in physiological condition (e.g. levels of host physiological stress) can alter the magnitude of the cost of infection (Brown et al., 2000).

One factor influencing parasite virulence, which has been experimentally demonstrated, is additive costs of parasitism through modification of host competitive ability (Hochberg, 1998). Here, the effects of a parasitic infection are not only determined by parasitism of the focal host but also by parasitism of the host's conspecific competitors. Bedhomme et al. (2005) showed that when larvae of the mosquito *Aedes aegypti* were infected with the microsporidian parasite *Vavraia culicis* they had a longer developmental time, a demonstrable fitness cost in this species. However, this cost of parasitism was also dependent on the infection status of conspecifics: the developmental time was always longer for infected larvae competing with non-infected larvae, than for infected larvae competing with other infected individuals. This suggests that although competition between individuals is normally costly, the strength of this cost is determined by both individual parasitic intensity and the prevalence of parasitism in conspecific competitors. This idea has been confirmed in one plant species (Pagan et al., 2009) and two animal species (Bedhomme et al., 2005; Koprivnikar et al., 2008); however, the hypothesis is also likely to apply to many group-living organisms.

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Unlike plants or mosquito larvae, many vertebrates including birds live in social groups and have a large behavioural repertoire. As such, interactions among individuals are likely to be very complex. In many group-living birds, social hierarchies are established between dominant and subordinate individuals. In these cases, competition between individuals is often mediated by social rank. For example, in canaries it has previously been shown that dominant birds have a greater access to food than subordinates and subordinate birds avoid interactions with dominants at food sites (Parisot et al., 2004). For such social animals, not only may parasite virulence depend on the infection status of competitors, but also on their level of competitive ability (determined by social rank). We expect that the outcome of intraspecific competition may be influenced more by conspecific infection status for subordinate than dominant birds. Thus, we predict the competition-mediated increase in morbidity and mortality with infection to be more severe for subordinate than for dominant birds.

The goal of this study was to assess the interactive effects between infection, social status and the occurrence of a parasite in social competitors on morbidity and mortality, using domestic canaries (*Serinus canaria*) as hosts and *Plasmodium relictum* (lineage SGS1) an avian malarial parasite. We predicted significant three-way interactions among social status, occurrence of parasite in competitors, and infection status on mortality rate, and physiological changes thought to reflect parasite virulence. Our major specific prediction was that infected subordinate birds competing with uninfected dominant birds would suffer greater morbidity than infected subordinate birds competing with infected dominant birds. However, for infected dominant birds this difference in morbidity mediated by the infection status of competing subordinates would be ameliorated (or reduced) by their greater competitive ability.

## 2. Materials and methods

Ninety-six adult male canaries were used during the experiment, sourced for us by a local provider and breeder. All of the canaries were adults and prior to commencement each bird was molecularly sexed following a standard PCR technique (Fridolfsson and Ellegren, 1999). We only used male canaries in the experiment as we did not wish to confound the experiment with differences between sexes, or by interactions within- and between pairs of birds. After confirming the sex of each bird, we divided them between 16 aviaries (2.5 × 1.5 × 2.2 m), six birds per aviary. Each bird was weighed and had its tarsus length measured prior to re-housing in a new flock.

### 2.1. Husbandry and competition

Before commencing the manipulation of competition, all cages were provided with food ad libitum (a commercial seed mix, lettuce and apple) for 7 days. Since we were interested in competition between birds and previous studies have shown that the provision of limited food results in an increase in competition (Bedhomme et al., 2005; Hawley et al., 2006), following the 7 days of acclimation, the birds were provided each day with 12 g of seeds per bird per day, provided in one circular feeding dish per cage. A pilot trial showed that 12 g of seeds is the maximum amount a single bird would eat per day (Larcombe et al., unpublished data). This amount of seed was thus sufficient to nourish each bird, but to encourage competition between birds (Larcombe, personal observation). During the course of the experiment, the cages were monitored daily and if a bird died the amount of seed was reduced accordingly.

### 2.2. Behavioural observations

Behavioural observations were performed to assess the social status of each bird before the experimental infection (after being housed in the experimental flocks), and to monitor any changes in social status related to the treatments. The first phase of observations was carried out 4 days after the start of the limited seed provision and 11 days after being placed in their flocks, by which time birds had established dominant and subordinate roles. We performed behavioural observations for three consecutive days. Each morning at 09:00 h we removed the remaining seed from the previous day and left cages for 30 min without seed. Following the 30 min food deprivation, we placed a seed feeder that allowed only a single bird to feed at a time in each cage. We also placed a video camera in each cage and filmed the interactions among birds at the feeder for 20 min, starting when the feeder was first introduced. Birds were marked with non-toxic coloured pen on the back of the head or wings for identification on the video tapes.

To score the bird's behaviour, when the video was viewed, the 20 min time period was divided into two 10 min blocks. Birds were scored for the presence or absence of certain behaviours in each block. The frequency of the following behaviours in the experimental trials were counted: primary access (PA) to the feeder, where a bird successfully fed directly from the hole in the feeder; secondary access (SA), when a bird was motivated to feed and appeared at the feeder, either attempting to feed or pecking at discarded seeds, but did not achieve primary access; aggression (AGG), where a bird aggressively postured towards another, typically by lowering its head and fanning and trembling its wings or by pecking out at the other bird, sometimes escalating into a physical fight. All of these behavioural measures represent dominance (primary access and aggression) or subordination (secondary feeding).

It is clear that social hierarchies, even within those assumed to be linear, are often very complex. Here, we wished to compare "dominant" and "subordinate" birds in their reactions to infection. As such birds were required to be labelled prior to infection. Birds were classified within a flock into two categories, based on social status: three dominant birds and three subordinate birds. Although this assumes that the third ranked bird in a cage is a third dominant, as opposed to a fourth subordinate, we believe this was justified. Classification was based on the mean number of primary accessions to the seed across the first 3 days of behavioural observations. Social status classification was based on primary access as we felt this best reflected "dominance" per se, that is the ability to monopolise the food resource. After infection, to check that our classifications were sound a ratio of primary to secondary access was created for the same 3 days as (PA day 1 + PA day 2 + PA day 3 + 1)/(SA day 1 + SA day 2 + SA day 3 + 1). In this case a ratio of  $\geq 1$  suggested a bird was dominant (spent more time primary feeding than secondary feeding), with the opposite true for a ratio of  $< 1$ . The mean number of  $\geq 1$  birds per cage was  $2.5 \pm 0.29$ . Thus we believe our initial categorisation of three dominant versus three subordinate birds was sound. It is also important to note that daily primary access was highly positively correlated with daily aggression (Spearman's  $\rho > 0.716$ ,  $P < 0.0001$  in all cases). Additionally, our behavioural scores were repeatable across the consecutive days measured (PA: Spearman's  $\rho > 0.582$ ,  $P < 0.0001$  in all cases. AGG: Spearman's  $\rho > 0.457$ ,  $P < 0.0001$  in all cases). We believe we have accurately described each bird as having a distinct, repeatable behavioural pattern. Measures such as frequency of aggression or submission have previously been used in avian behavioural studies (e.g. Torda et al., 2004; Müller et al., 2012), and it is important in classifying animals as having stable behavioural types that these must be repeatable across time (Sih and Bell, 2008). Cronbach's alpha, an internal consistency statistic that has previously been used to assess the stability of animal

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