

Field evidence for apparent competition mediated via the shared parasites of two gamebird species

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Abstract

Although apparent competition mediated via shared parasites is potentially an important force influencing community structure, there is limited evidence to demonstrate its occurrence in the field. Here we show that the intensity of infection by the caecal nematode *Heterakis gallinarum* picked up by naive grey partridges, both maintained in pens and released on six gamebird estates in the UK, is significantly correlated with the intensity of infection recorded in the previous year from pheasants on those estates. Furthermore, the worm burdens picked up appeared to be sufficient to negatively influence host condition. These results provide evidence that infection from pheasants determines the worm burdens of partridges in the field, supporting the hypothesis that parasite-mediated apparent competition with the pheasant may be a factor influencing the decline and subsequent recovery of wild grey partridges.

Keywords

Grey partridge, *Heterakis gallinarum*, host exclusion, indirect interactions, nematode, parasite-mediated competition, *Perdix perdix*, *Phasianus colchicus*, pheasant.

Ecology Letters (2000) 3: 10–14

INTRODUCTION

Theory suggests that competition between species, mediated via shared parasites, may be an important force influencing community structure (Holt & Lawton 1994; Greenman & Hudson 1999). Such interactions are a form of “apparent competition”, whereby the presence of one species decreases the fitness of another through the increased presence of a shared enemy (Holt 1977). However, while apparent competition mediated via shared parasitic organisms has been experimentally demonstrated under laboratory conditions (Bonsall & Hassell 1997, 1998), the limited evidence to support its occurrence in the field is often confounded by other factors (Hudson & Greenman 1998), and is far from conclusive (Settle & Wilson 1990; Grosholz 1992; Schall 1992; Schmitz & Nudds 1994; Hanley *et al.* 1995; Thomas *et al.* 1997). Moreover, a number of experimental manipulations conducted in the field have failed to demonstrate parasite-mediated apparent competition (Hanley *et al.* 1998; Rott *et al.* 1998). Further research into the ecological importance of such interactions is needed, since shared parasites have been implicated in population extinctions of several wildlife species (Tompkins & Wilson 1998).

While the decline of the UK grey partridge (*Perdix perdix*) over the past 50 years has been associated with the

intensification of agriculture and increased predation pressure (Potts 1986; Sotherton 1998), it has been postulated that apparent competition with pheasants (*Phasianus colchicus*) may also play a role (Wright *et al.* 1980; Kimmel 1988; Robertson 1996). Specifically, recent studies suggest that the pheasant is a reservoir host for the caecal nematode *Heterakis gallinarum*, infection by which may be highly detrimental to the partridge (Tompkins *et al.* 1999). However, while there is evidence that *H. gallinarum* cannot persist within partridge populations without the presence of alternative host species (D.M. Tompkins, unpublished manuscript), there is no evidence that infection from pheasants (which is believed to be the traditional host of this parasite; Lund & Chute 1974) determines the worm burdens of partridges in the wild.

In this study, trials were undertaken to determine if there is such a link, by both maintaining and releasing grey partridges on six sporting estates in the UK where both pheasants and grey partridges occur, and where the intensity of *H. gallinarum* infection in the pheasants was known from the previous year. Specifically, we tested the hypothesis that the intensity of parasite infection picked up by the partridges was related to the previous year pheasant burdens. We also investigated whether the worm burdens picked up were sufficient to influence partridge condition.

METHODS

During July and August 1998, 400 grey partridges were reared from day-old chicks on sterilized concrete to prevent natural infection and ensure that all birds were naive to parasite infection. At 7–8 weeks of age the birds were weighed to the nearest 10 g, sexed, wing-tagged for identification, and split into six equal groups for transport to the field-sites where they were placed into partridge release pens. A single pen was used on each estate, located in arable fields adjacent to wooded areas containing pheasant release pens. These are areas in which the habitat ranges of the two species naturally overlap (Cocchi *et al.* 1990). While in the pens the birds were maintained by local gamekeepers, and supplied with food (gamebird grower pellets), water and grit ad-lib. Two weeks after being transferred into the field, approximately 80% of the birds on each estate were released into the wild. The remainder were maintained in the pens for a further 8 weeks, at which point they were culled and the intensity of *H. gallinarum* infection and host body condition determined.

All caecal worms were removed from the gut of each bird by washing the caecal contents through a course sieve (1.4 mm) to remove host tissue, and a fine sieve (0.2 mm) to collect the worms. *Heterakis gallinarum* worms recovered were counted under a binocular microscope, and the presence or absence of another gastrointestinal worm, *Capillaria* sp., was noted. The trachea of each host was also examined for the presence of the gape-worm, *Syngamus trachea*. Host condition was estimated by measuring the breast muscle mass of each bird to the nearest 0.01 g, and adjusting for host body size (Tompkins *et al.* 1999). Coccidial infections were not monitored since previous work has failed to detect any relationship between these parasites and body condition for either pheasants or partridges (D.M. Tompkins, unpublished data). During November and December, released partridges were collected from estates when shot, and dealt with as above.

Since sample sizes were uneven (see below), the significance of correlations between parasite infections of pheasants and partridges, on a per estate basis, was based on 1000 permutations of the raw data (Manly 1997). The *H. gallinarum* intensity in pheasants on the six estates in 1997 was estimated from pheasants collected during April of that year (Draycott *et al.*, in press). Partridge condition was analysed, with respect to both parasite intensity and estate, by analysis of covariance. Significance levels were again based on 1000 permutations of the data, in this case to control for the effects of outliers. All analyses were conducted in S-Plus v4.5, 1998.

RESULTS

The penned birds on one estate were culled prior to the end of the experiment due to an outbreak of a mycoplasmal respiratory disease. No mortality occurred on the other five estates – a total of 55 penned birds were examined after the 10 week exposure period, of which 40% were infected with *H. gallinarum* and 47% were infected with *Capillaria* sp. The intensity of *H. gallinarum* infection picked up by the partridges was significantly correlated with the previous year pheasant burdens on the estates where they were maintained (Fig. 1; Kendall $\tau = 0.80$, $P = 0.025$). None of the partridges examined were infected with *S. trachea*.

While the presence or absence of *Capillaria* sp. infection had no discernible effect ($P = 0.40$), the condition of the penned partridges was significantly related to the intensity of *H. gallinarum* infection (Fig. 2a; regression coefficient = -2.46 , $P = 0.005$). There was no relationship between the infection acquired and partridge body mass prior to the trial (regression coefficient = 0.66 , $P = 0.41$), implying that *H. gallinarum* was the cause of the decrease in body condition and not vice versa. Estate also had a significant effect on partridge condition ($P = 0.02$). However, this effect does not appear to be independent of parasites since the differences among estates in condition were significantly correlated with the differences

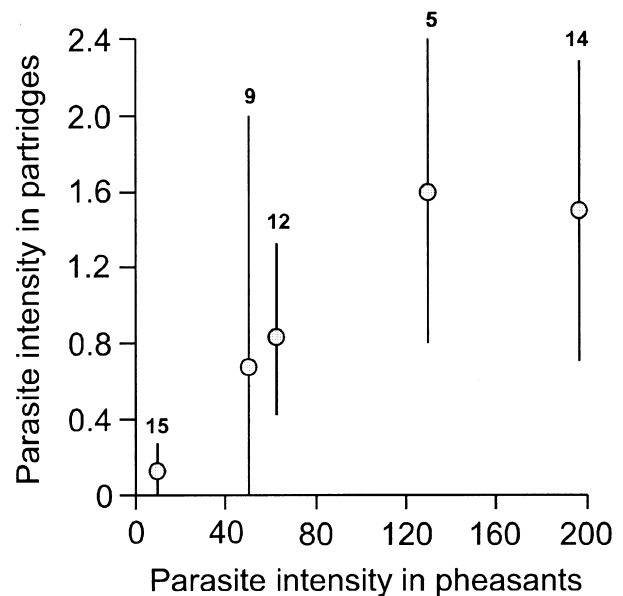


Figure 1 Relationship between the mean *Heterakis gallinarum* intensity picked up by partridges and the previous year pheasant burdens on five estates where they were maintained in pens for 10 weeks. Vertical lines indicate bootstrapped 95% confidence intervals, numbers indicate the sample size on each estate.

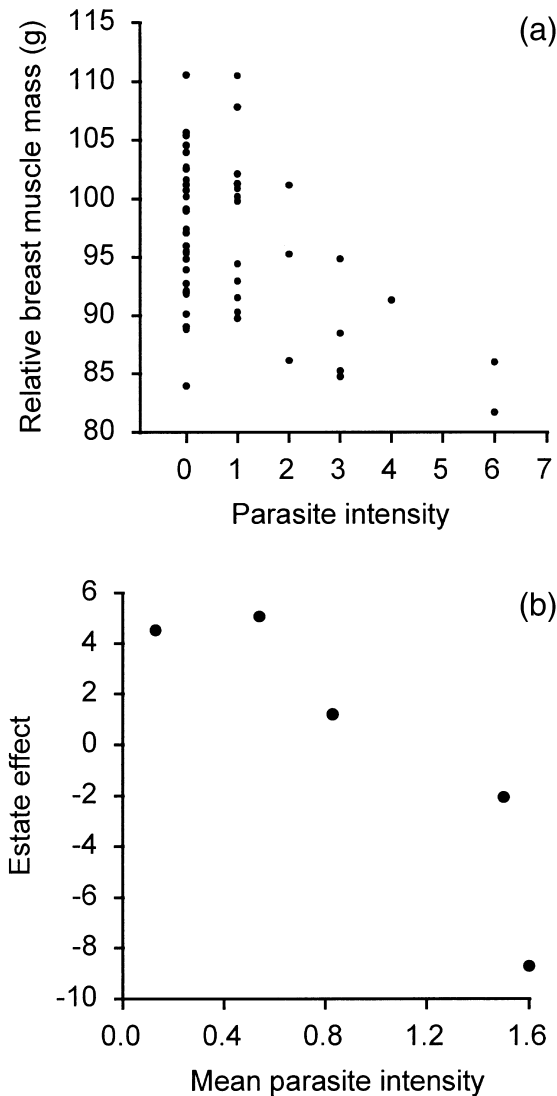


Figure 2 (a) Relationship between the intensity of *Heterakis gallinarum* infection picked up by penned partridges and their condition after the 10 week exposure period, as quantified by lean wet breast muscle mass adjusted for body size. (b) Between estate effect, from a general linear model of penned partridge condition *versus* parasite intensity and estate, *versus* the mean intensity of *H. gallinarum* infection picked up on each estate.

among estates in the magnitude of *H. gallinarum* infection picked up (Fig. 2b; Pearson $r = -0.90$, $P = 0.03$).

Of the birds released onto the six estates in September 1998, only nine were shot during November and December. This was an insufficient number to investigate parasite impact on survival, or to look at between estate differences in condition. However, as with the penned birds, the intensity of *H. gallinarum* infection picked up by these nine partridges was both correlated with the

previous year pheasant burdens on the estates where they were released (Fig. 3a; Kendall $\tau = 0.83$, $P = 0.02$), and significantly related to their condition (Fig. 3b; regression coefficient = -1.52 , $P = 0.01$).

DISCUSSION

This study provides supporting evidence for the role of apparent competition, mediated via shared parasites, between pheasants and grey partridges in the field. For partridges both penned and released on six UK estates, significant relationships between the intensity of *H. gallinarum* infection picked up and both the previous year pheasant burdens (positive relationship), and host condition after exposure (negative relationship) were observed. This supports the hypothesis that infection from pheasants determined the worm burdens of partridges in the field, reducing condition and probably their fitness. Since pheasants were present on all six estates and, more convincingly, since some of the partridges were maintained in pens with ad-lib food, the possibility that direct interactions with pheasants was confounding is discounted. This is of key importance to the case for apparent competition since, in addition to transmission of infection, pheasants are postulated to adversely impact the grey partridge via competition for habitat and aggressive behaviour (Kimmel 1988). However, the current study was not a definitive test, since host and parasite populations were not experimentally manipulated. Nevertheless, the fact that a similar pattern was observed for both penned and released birds is strongly supportive, and laboratory-based experiments do identify *H. gallinarum* as a cause, rather than an effect, of decreased body condition in grey partridges (D.M. Tompkins, unpublished data).

One point of concern with the hypothesis that *H. gallinarum* infection caused a decline in partridge condition, is that the parasite intensity observed in both the penned and the released birds was relatively low—while mean pheasant burdens ranged from 9 to 195 worms, the maximum *H. gallinarum* intensity in our exposed partridges was only 11 worms. Previous work has shown, however, that the success rate of *H. gallinarum* establishment in the grey partridge is only 6.5% (D.M. Tompkins, unpublished manuscript). As such, an observed burden of 11 worms indicates that that individual has probably been exposed to 170 infective larvae. This may also explain why an estate effect on host condition, that itself was correlated with *H. gallinarum* intensity, was also observed. The worms counted in individual partridges from each estate may not completely reflect the intensity of infection to which the birds have been exposed. Regardless of these complications, however, the parasite intensities on the six estates do appear to have been sufficient to influence

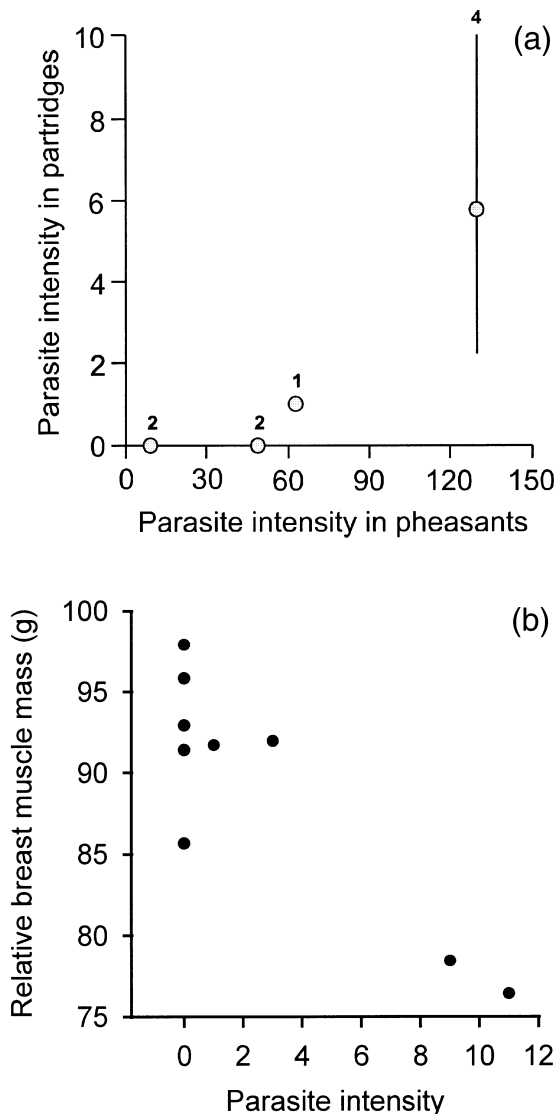


Figure 3 Relationship between the mean *Heterakis gallinarum* intensity picked up by partridges, and (a) the previous year pheasant burdens on four estates where they were released 2–3 months earlier, and (b) their condition, as quantified by lean wet breast muscle mass adjusted for body size. Vertical lines indicate bootstrapped 95% confidence intervals, numbers indicate the size of the shot sample on each estate. No released birds were shot on two other estates.

partridge condition. Hence, this study supports the hypothesis that the UK grey partridge decline may be partly due to parasite-mediated apparent competition with pheasants. Furthermore, it is possible that parasites are hampering current efforts to re-establish and increase wild partridge populations. Future research should aim to determine whether this parasite induced reduction in body condition translates into a reduction in the survival and

breeding success of grey partridges in the wild, through large scale experiments.

ACKNOWLEDGEMENTS

We wish to thank the Game Conservancy Trust, particularly Rufus Sage and Maureen Woodburn, for their help with the fieldwork, and Pauline Monteith for her assistance in the laboratory. We are also grateful to the landowners and gamekeepers, for all their help with the penned birds and for allowing access to their estates, and to Pete Robertson, Nicholas Aebischer, and two anonymous referees for comments on the manuscript. This study was funded by NERC grant GR3/10647.

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BIOSKETCH

Dan Tompkins' research programme is based on using host–parasite interactions to explore the ecological and evolutionary forces that determine biodiversity. His D.Phil. identified a mechanism by which variation in the resources provided by hosts can drive parasite specificity, and his postdoctoral research is investigating whether shared parasites can cause the extinction of wildlife populations.

Editor, S. Morand

Manuscript received 8 November 1999

Manuscript accepted 10 November 1999