

# PARASITE-MEDIATED COMPETITION AMONG RED-LEGGED PARTRIDGES AND OTHER LOWLAND GAMEBIRDS

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**Abstract:** Evidence suggests that the transmission of shared parasites from ring-necked pheasants (*Phasianus colchicus*), specifically the caecal nematode *Heterakis gallinarum*, may be 1 cause of the decline of the gray partridge (*Perdix perdix*) in the United Kingdom (UK) over the past 50 years. It may be a factor preventing the recovery of the remaining wild gray partridge populations. Trials were undertaken to investigate whether the red-legged partridge (*Alectoris rufa*) also is involved in this interaction, by exposing individuals of all 3 host species to infection on 7 gamebird estates. The low rate of parasite establishment in the red-legged partridge demonstrated that, as with the gray partridge, the parasite cannot persist in this host species. The lack of a relationship between *H. gallinarum* intensity and red-legged partridge condition indicated that, as with the ring-necked pheasant, this parasite does not seriously affect its host species. Hence, red-legged partridges play little or no role in the interaction mediated via *H. gallinarum* that occurs among UK lowland gamebirds, since they are unlikely to be either another source of deleterious infection to the gray partridge or adversely affected by the transmission of *H. gallinarum* from ring-necked pheasants. Ring-necked pheasants are thus implicated as being solely responsible for maintaining infections of *H. gallinarum* in other lowland gamebirds in the UK and any associated effects.

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**Key words:** *Alectoris rufa*, gray partridge, *Heterakis gallinarum*, nematode, parasite-mediated competition, *Perdix perdix*, *Phasianus colchicus*, red-legged partridge, ring-necked pheasant, United Kingdom.

Transmission of shared parasites among species can have profound effects on host community structure, particularly when the presence of reservoir hosts facilitates the infection of more susceptible host species (Holt and Lawton 1994, Hudson and Greenman 1998). Under such circumstances, exclusion of the susceptible host due to this indirect interaction (a form of apparent competition; Holt 1977, Chaneton and Bonsall 2000) is a distinct possibility. One wildlife system in which competition mediated via shared parasites is believed to play an important role is lowland gamebirds in the UK and their shared gastrointestinal nematodes.

Evidence indicates that apparent competition between the ring-necked pheasant (hereafter pheasant) and the gray partridge, mediated via the caecal nematode *Heterakis gallinarum* (Schrank), may be 1 cause of the recent decline in UK gray partridge numbers and may be hampering current efforts to reestablish and increase wild populations (Tompkins et al. 1999; 2000a,b; 2001). This hypothesis is supported by the docu-

mented increase in pheasants released for shooting that has occurred in the UK during recent decades (Tapper 1992), and a 2-host shared macroparasite model that predicts that the force of infection transmitted from the pheasant (acting as a reservoir host) can cause gray partridge exclusion (Tompkins et al. 2000b).

Another lowland gamebird in the UK that is released in large numbers for shooting is the red-legged partridge (Potts 1980). Like the pheasant, the red-legged partridge is a known host of *H. gallinarum* (Clapham 1935), and the number released for shooting has greatly increased in recent decades (Tapper 1992). The possibility thus exists that apparent competition with the red-legged partridge is an additional factor in the exclusion of wild gray partridges in the UK.

In our study, we conducted trials to investigate this possibility by maintaining red-legged partridges with gray partridges and pheasants on 7 sporting estates in Scotland. We investigated whether the red-legged partridge is a host in which the parasite persists (as it does in the pheasant) and thus may be another source of infection to the gray partridge through the common pool of infective stages or, alternatively, whether the parasite has harmful effects on the red-legged partridge (as it does on the gray partridge) and thus

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may be a species deleteriously affected by the transmission of parasites from pheasants.

## METHODS

During July and August 1999, we reared 70 birds of each species from day-old chicks on sterilized concrete to ensure that they were naive to parasite infection. At 8 weeks of age, we weighed the birds to the nearest 10 g, sexed them, and wing-tagged them for identification. We then placed 10 of each species into 5.4-m × 5.4-m holding pens on each of 7 gamebird estates in Scotland, and held them for 10 weeks to allow natural infection to occur. The pens were constructed of sections 1.8 m wide × 1.35 m high (90-cm wire mesh on top of 45-cm wooden board), with nylon mesh netting stretched over the top, and located at the following coordinates: 56°09'N, 03°57'W; 56°10'N, 03°56'W; 56°11'N, 02°48'W; 56°15'N, 02°53'W; 56°36'N, 02°30'W; 56°43'N, 02°56'W; 56°51'N, 02°36'W. Birds were held on different estates to ensure variation in parasite exposure and while in the pens were supplied with food (Poult Pellets; Spratt's Game Foods, Selkirk, Selkirkshire, UK) and water ad libitum.

At the end of the 10-wk exposure period, we euthanized all birds by dislocation of the neck, weighed their lean wet breast muscle mass to the nearest 0.01 g and adjusted for body size as an index of condition, and determined the intensity of *H. gallinarum* infection by sieving the gut contents. We also examined the trachea of each host for the gape-worm (*Syngamus trachea*). We measured the body length of all female *H. gallinarum* worms recovered to the nearest 0.025 mm. For further details regarding the estimation of host condition and parasite recovery and measurement, see Tompkins et al. (1999).

### Parasite Establishment and Fecundity

Previous work has demonstrated that *H. gallinarum* can persist in the pheasant, but not in the gray partridge, due to the success rate of *H. gallinarum* establishment being 9 times greater in pheasants than in gray partridges, and the fecundity of established worms being approximately 10 times greater in pheasants than in gray partridges (Tompkins et al. 2000b). In our study, since the 3 host species received the same exposure to parasites (they were in the same pens) and rates of *H. gallinarum* transmission to pheasants and partridges are similar (Tompkins et al. 2000b), *H. gallinarum* establishment in the red-legged partridge was investigated by comparing the worm burdens

of the exposed birds to those of the exposed pheasants and gray partridges by the application of generalized linear models (GLM) with explicitly defined negative binomial error distributions (Wilson et al. 1996, Wilson and Grenfell 1997).

Because *H. gallinarum* fecundity is correlated with worm size (Tompkins and Hudson 1999), parasite fecundity in the red-legged partridge was investigated by comparing the size of female worms recovered from this species with those recovered from the other 2 hosts, using standard GLM with normal error distributions.

### Impact on Host Condition

Lean wet breast muscle mass is highly correlated with the total protein content of gamebirds and, when adjusted for body size, is a good index of body condition (Brittas and Marcström 1982). Using a standard GLM with a normal error distribution, we analyzed red-legged partridge condition with respect to the prevalence/intensity of all parasites recorded, while controlling for estate. Significance levels were based on 1,000 permutations of the raw data to control for outliers (Manly 1997).

The demonstrated impact of *H. gallinarum* on the gray partridge (Tompkins et al. 2001) is detectable as a negative correlation in analyses such as the 1 proposed here (Tompkins et al. 1999, 2000a). No such correlation between pheasant condition and *H. gallinarum* intensity has been observed, and only a relatively minor impact has occurred on this bird species (Tompkins et al. 2001). To demonstrate that the level of parasite infection to which birds were exposed here compares to these other studies, gray partridge and pheasant body condition data also were analyzed as detailed above. We conducted all statistics in S-PLUS 2000 Professional (Mathsoft Engineering and Education, Cambridge, Massachusetts, USA).

## RESULTS

We examined 67 pheasants, 70 gray partridges, and 62 red-legged partridges after the 10-wk trial period. Although most nematodes recovered from the exposed birds were the caecal worm (*H. gallinarum*), individuals of all 3 host species were also infected with *S. trachea*, with a mean of 3.46 *S. trachea* observed in 13 of the pheasants, a mean of 5.00 in 5 of the gray partridges, and a mean of 2.67 in 3 of the red-legged partridges. A second gastrointestinal nematode, *Capillaria* spp., was recovered from the gut contents of 33 pheasants, 28 gray partridges, and 26 red-legged partridges.

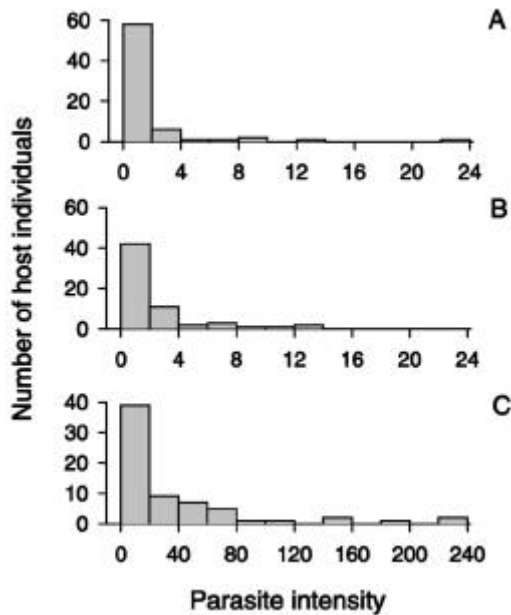


Fig. 1. Frequency distribution of *H. gallinarum* in (A) gray partridges ( $n = 70$  birds), (B) red-legged partridges ( $n = 62$  birds) and (C) ring-necked pheasants ( $n = 67$  birds), after 10 weeks exposure to ground contaminated with *H. gallinarum* eggs in the United Kingdom during Jul and Aug 1999. Parasite intensity followed an aggregated distribution that was not significantly different from a negative binomial, with an arithmetic mean of 1.19 and a negative exponent ( $k$ ) of 0.13 in gray partridges ( $P = 0.99$ ), a mean of 1.76 and a  $k$  of 0.55 in red-legged partridges ( $P = 0.75$ ), and a mean of 35.78 and a  $k$  of 0.62 in ring-necked pheasants ( $P = 0.54$ ).

However, we could not record intensity because the recovered worms were highly fragmented.

**Parasite Establishment and Fecundity**

After the 10-wk exposure period, both the red-legged partridges (deviance = 119.55;  $df = 1, 127$ ;  $P < 0.001$ ) and the gray partridges (deviance = 114.19;  $df = 1, 135$ ;  $P < 0.001$ ) were infected with significantly less *H. gallinarum* than were the pheasants (Fig. 1), while no significant difference occurred between the burdens of the 2 partridge species (deviance = 1.18;  $df = 1, 130$ ;  $P = 0.28$ ). The female *H. gallinarum* worms recovered from both the red-legged partridges (deviance = 8.19;  $df = 1, 23$ ;  $P = 0.004$ ) and the pheasants (deviance = 22.40;  $df = 1, 67$ ;  $P < 0.001$ ) were significantly longer than those recovered from the gray partridges (Fig. 2), while no significant difference occurred between the length of those recovered from the red-legged partridges and the pheasants (deviance = 1.36;  $df = 1, 68$ ;  $P = 0.24$ ).

**Impact on Host Condition**

The presence or absence of *Capillaria* spp. was not related to host condition for the gray partridge (slope of regression  $\beta = -1.57$ ,  $P = 0.26$ ), the pheasant ( $\beta = 6.43$ ,  $P = 0.23$ ), or the red-legged partridge ( $\beta = 5.58$ ,  $P = 0.12$ ). Likewise, the intensity of *S. trachea* in the exposed birds also was unrelated to gray partridge condition ( $\beta = -0.38$ ,  $P = 0.34$ ), pheasant condition ( $\beta = -1.14$ ,  $P = 0.27$ ), or red-legged partridge condition ( $\beta = -1.49$ ,  $P = 0.34$ ).

As with the previous studies, gray partridge condition at the end of the trial was negatively correlated with the intensity of *H. gallinarum* infection acquired during the exposure period ( $\beta = -2.03$ ,  $P < 0.001$ ; Fig. 3A). No relationship existed between the infection acquired and gray partridge body mass prior to the trial ( $\beta = -0.37$ ,  $P = 0.28$ ), indicating that *H. gallinarum* was the cause of the decrease in body condition and not vice versa. Also, as expected, no significant relationship existed between pheasant condition at the end of the trial and *H. gallinarum* intensity ( $\beta = 0.00$ ,  $P = 0.51$ ; Fig. 3C). Likewise, the host species—the red-legged partridge—showed no significant relationship

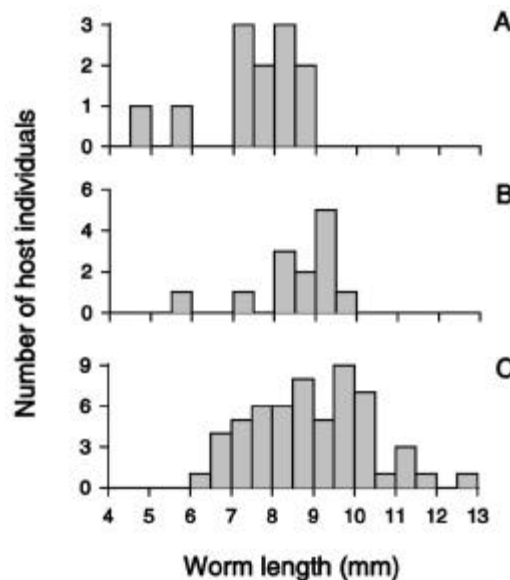


Fig. 2. Frequency distribution of mean body length of female *H. gallinarum* recovered from (A) gray partridges ( $n = 12$  birds), (B) red-legged partridges ( $n = 13$  birds), and (C) ring-necked pheasants ( $n = 57$  birds) in the United Kingdom during 1999. Worms recovered had a mean  $\pm$  SD length of  $7.42 \pm 1.17$  in gray partridges,  $8.57 \pm 1.12$  in red-legged partridges, and  $8.86 \pm 1.32$  in ring-necked pheasants.

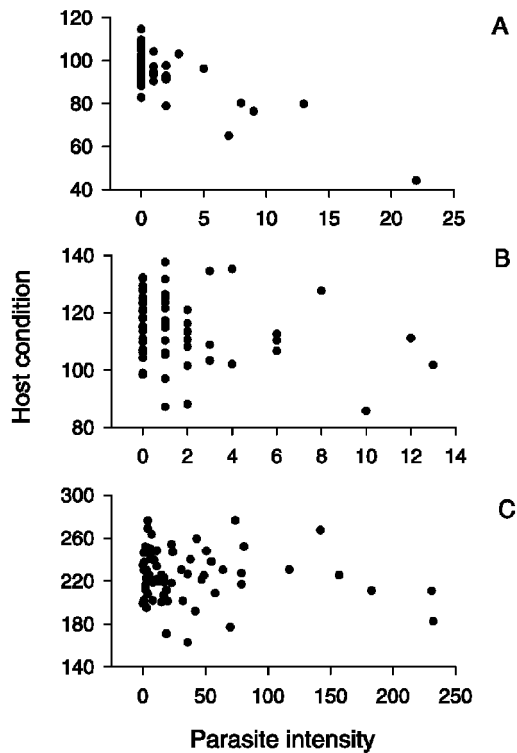


Fig. 3. Relationship between the intensity of *H. gallinarum* infection picked up by (A) gray partridges ( $n = 70$  birds), (B) red-legged partridges ( $n = 62$  birds), and (C) ring-necked pheasants ( $n = 67$  birds), and their condition after 10 weeks exposure to ground contaminated with *H. gallinarum* eggs in the United Kingdom during Jul and Aug 1999. Host condition was quantified as lean wet breast muscle mass (g) adjusted for body size.

between condition and *H. gallinarum* intensity ( $\beta = -0.76$ ,  $P = 0.13$ ; Fig. 3B).

## DISCUSSION

Our study suggests that the red-legged partridge is neither seriously affected by *H. gallinarum* infection nor acts as a reservoir host for the parasite, and is thus not involved in the parasite-mediated apparent competition that is believed to occur between the pheasant and the gray partridge in the UK.

That the red-legged partridge is not a reservoir host for *H. gallinarum* was demonstrated by the intensity of *H. gallinarum* infection after the trial being as low in the exposed red-legged partridges as it was in the exposed gray partridges (Fig. 1A,B). Since the 2 species were maintained in the same pens, and thus received the same level of

parasite exposure, the success rate of *H. gallinarum* establishment appears to be as low in the red-legged partridge as it is in the gray partridge. This is in contrast to the exposed pheasants in which the *H. gallinarum* intensities were far greater (Fig. 1C), reflecting the higher establishment rate that the parasite is known to have in this species (Tompkins et al. 2000b).

Although the success rate of *H. gallinarum* establishment appears to be low in the red-legged partridge, the fecundity of established worms compares with the pheasant, being greater than the gray partridge. This is demonstrated by the size of worms removed from exposed individuals at the end of the trial being similar between the pheasant and red-legged partridge but significantly smaller for the gray partridge (Fig. 2). Whether this high level of fecundity is sufficient to allow *H. gallinarum* to persist in the red-legged partridge, overcoming the apparently low establishment success rate and making this species a potential reservoir host for the parasite, was investigated by taking the expression for the basic reproductive rate ( $R_0$ ; the number of adult female parasites derived from each adult female parasite in a population of uninfected hosts) for *H. gallinarum* in the pheasant, developed in Tompkins et al. (2000b), and replacing the establishment rate in pheasants with the establishment rate in the gray partridge while maintaining worm fecundity at the pheasant level. This reduced  $R_0$  from 1.23 to 0.14, demonstrating that the parasite is unable to persist under such conditions (since an  $R_0$  of at least 1.00 is required for persistence). The red-legged partridge is thus unlikely to act as a reservoir host for *H. gallinarum* in the wild and, like the gray partridge, any infection observed is likely to be sourced from pheasants and not from other partridges.

The lack of serious effects of *H. gallinarum* on the red-legged partridge was demonstrated by the lack of a significant negative correlation between host condition after the exposure trial and the intensity of *H. gallinarum* infection picked up during the trial (Fig. 3B). Interpreting this as a lack of serious effects is justified since the level of infection to which the birds were exposed was sufficient to manifest the known impact of the parasite on the gray partridge as a significant negative correlation (Fig. 3A). There may be a negative impact on the red-legged partridge, if the nonsignificant trend between condition and *H. gallinarum* intensity observed indicates an actual effect. However, even if so, this would only

relate to a reduction in host breast muscle mass of 0.76 g per worm. This compares with the reduction of 2.03 g per worm observed in the exposed gray partridges, an impact which is consistent with all previous observational and experimental studies (Tompkins et al. 1999; 2000*a,b*; 2001).

Substituting the impact on the gray partridge in the 2-host macroparasite model developed in Tompkins et al. (2000*b*) with an impact equivalent to a decrease in body condition of 0.76 g per worm alters the predicted model outcome from 1 of partridge exclusion to 1 of pheasant and partridge coexistence. Thus, even if some deleterious effects of *H. gallinarum* occur on the red-legged partridge, they do not appear to be of sufficient magnitude to result in exclusion of this host species through apparent competition with the pheasant. It is possible that subtle effects of *H. gallinarum* (and also effects of *S. trachea* and *Capillaria* spp.) are being missed since only the 1 index of body condition was employed in our study. Other approaches that could be used to elucidate such effects include monitoring food consumption and/or gastrointestinal function (Tompkins et al. 2001), or researching numerous blood parameters, including hemoglobin levels, serum proteins, and white cell counts (Wilson and Wilson 1978). Subtle effects could have important consequences for host health, especially if they interact with other factors such as poor weather, low-quality habitat, or food limitation (Holmes 1995).

## MANAGEMENT IMPLICATIONS

Our results and evidence presented in previous papers support the view that the ring-necked pheasant is the ancestral host of *H. gallinarum* (Lund and Chute 1974). The mechanism that allows the parasite to persist in the pheasant but not in the gray or red-legged partridge, that of decreased establishment success and/or reduced fecundity of worms in alternative hosts, is similar to the mechanisms determining specificity in other gastrointestinal nematodes (Gemmill et al. 2000). This clearly supports the view that pheasants play a key role in maintaining infections of *H. gallinarum* in other lowland gamebirds in the UK, with the associated effects (at least in the gray partridge) having consequences at the community level.

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