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ORIGINAL ARTICLES

The diet and disease susceptibility of grey partridges *Perdix perdix* on arable farmland in East Anglia, England

Stephen J. Browne, Nicholas J. Aebischer, Stephen J. Moreby & Luke Teague

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A three-year field-based study of 85 radio-tagged female wild grey partridges Perdix perdix was undertaken during 2001-2003 in East Anglia, England, to investigate possible links between chick diet and parasite-induced disease. The females produced 30 broods, whose diet measured by faecal analysis was typical of that previously reported. Chicks in some broods, however, consumed large numbers of known parasite vectors, particularly ants. Survival to the age of six weeks of chicks in a brood declined, on average, as the percentage of ants in the diet increased. Additionally 79 wild partridges found dead or in poor condition were submitted for necropsy to assess internal parasite burdens. Of these, 22 (28%) contained parasitic infections, although only 12 (15%) had levels of parasites that may have resulted in death. Internal parasites were found in only 7% of a subsample of 46 birds that died accidentally or were shot, and this was likely to be representative of the background level of infection. In a separate laboratory study of nutrition, no parasites were recorded in 180 six-week-old chicks that had eaten > 16,000 potential parasite vectors during the first three weeks after hatching. Either parasite levels were very low among host invertebrates or other factors contributed to increase disease susceptibility. Our results suggest that poor wild brood survival was indicative of low habitat and food quality rather than of a high rate of parasite infection. Management to conserve and increase wild grey partridge numbers should concentrate on improving foraging habitat quality, i.e. increasing the abundance of nutritious invertebrate chick-food, rather than directing efforts at reducing the small-scale effects of disease.

Key words: breeding success, diet, disease, grey partridge, growth rates, parasites, Perdix perdix

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In Britain, the grey partridge *Perdix perdix* has shown a serious decline in both range and abundance since the 1950s (Potts 1986, Gibbons et al. 1993, Baillie et al. 2002). The decline in abundance has been estimated at 89% during the period 1968-1999 (Baillie et al. 2002), and the species has undergone a range contraction of 19% between 1968-1972 and 1988-1991 (Gibbons et al. 1993). These declines, which are similar to a number of other bird species that occur primarily on farmland, have resulted in the species being classified as a 'Red List' bird species of conservation concern (Gregory et al. 2002) and a UK Biodiversity Action Plan species (Anon 1996).

The principal cause of the decline of the grey partridge has been the post-war modernisation of agriculture, particularly since the 1950s (Potts 1980, 1986, Aebischer & Potts 1998). The increased use of pesticides has reduced food availability for chicks, which has reduced breeding success. Field enlargement through the removal of hedgerows has reduced the availability of nesting sites. Additionally, a post-war reduction in the number of gamekeepers has allowed predation losses to increase.

The grey partridge was once the most common gamebird in the UK and was the principal quarry bird species (Tapper 1992). With its changing fortunes, many shooting estates have become more dependent on the redlegged partridge *Alectoris rufa* and pheasant *Phasianus colchicus*. The resultant lack of dedicated grey partridge management, the increased dependence on reared rather than wild game and in some cases overshooting has hastened the species' decline in certain areas (Potts 1986). However, in East Anglia traditional grey partridge management has persisted and the region is one of the last strongholds for grey partridges in Britain (Tapper 1992).

In the mid and late 1990s the grey partridges on a number of estates in East Anglia suffered successive years of poor breeding success and the relatively stable numbers went into decline (Anon 1998, Anon 1999). Whilst the precise causal factors for this reduced breeding success were unknown, it coincided with increased reporting of parasite-induced disease amongst wild partridge stocks. Adult grey partridges eat a varied diet consisting of plant material and seeds for much of the year, with the addition of invertebrates during the summer (Middleton & Chitty 1937). Newly-hatched grey partridge chicks eat predominantly invertebrates until they are 10 days old, after which they consume increasing amounts of plant material and seeds (Green 1984). Consequently it was hypothesised that invertebrate food availability had become so low that grey partridge chicks were forced to eat invertebrates that were potential vectors of internal parasites, thereby leading to the spread of disease.

In order to establish whether diet and disease susceptibility had altered in recent years, The Game Conservancy Trust undertook a three-year field-based study of wild grey partridges during 2001-2003 in East Anglia. A separate laboratory study of chick nutrition, in which reared grey partridge chicks were fed a range of invertebrate groups, provided important complementary information on whether consumption of certain invertebrates alone led to parasitic infection, or if other factors were more important. The project sought to establish whether 1) East Anglian grey partridges suffered from sufficiently high levels of parasites to cause death; 2) the chicks were consuming invertebrate vectors of parasites; 3) there was a link between chick diet and chick survival; 4) the consumption of parasite vectors was the sole cause of parasitic infection, and if so, which vector groups were most likely to transmit disease.

Material and methods

Field-based study

At three study sites in Norfolk, England, 85 wild female grey partridges were caught during early spring 2001-2003. One site, Hilborough (52°34'N, 0°39'E), took part in 2001-2003, another, West Barsham (52°51'N, 0°51'E), took part in 2001 only and the third site, Holkham (52°55'N, 0°51'E), took part in 2002-2003. Each study site contained a range of arable crops (winter- and spring-sown wheat *Triticum aestivum* and barley *Hordeum vulgare*, sugarbeet *Beta vulgaris*, potatoes *Solanum tuberosum*, carrots *Daucus carota* and parsnips *Pastinaca sativa*), representative of the region. On each one, partridge management included the provision of suitable nesting and feeding habitats and the limitation of nest predator numbers, principally red foxes *Vulpes vulpes*, mustelids and corvids (Potts 1986, Aebischer 1997).

In total at the three study sites, 85 female grey partridges were caught at night whilst at roost, using a highpowered lamp and hand-held net, in March and early April. Each captured bird was fitted with a necklace radio transmitter of about 6 g, which corresponds to < 2%of the body mass (395-510 g) of the partridges caught, with a life span of at least 26 weeks and a range of approximately 2 km. Each bird was relocated at 2-3 day intervals after capture throughout the breeding season. Nesting birds were left undisturbed, and after chicks had left the nest, the nest contents were examined to determine the clutch and brood size at hatching. After hatching and at 2-3 day intervals, nocturnal roost sites of the tagged birds were located at nightfall and checked the following morning. All faecal material was collected and the amount present recorded. Chick faeces were preserved in 90% industrial alcohol for identification of dietary components and a measured sample of about 1 g of adult faecal material was preserved in 10% formalin solution for worm egg counts.

Six weeks after hatching, the chicks in each brood were counted repeatedly until successive counts agreed. No attempt was made to assess brood size earlier in order to avoid unnatural chick losses. Complete brood losses became apparent when no chick faeces were found at roost sites, whereupon the females were relocated to confirm the absence of chicks.

Each sample of chick faeces was broken up in water and washed through a 0.2-mm mesh sieve. Food fragments were identified under microscopic examination. Arthropod structures were counted and the minimum number of individuals required to account for the number of fragments was evaluated, to estimate the number of individuals eaten (Moreby 1988). For the purpose of data presentation and analysis, the invertebrate data were grouped into eight categories: caterpillars (larvae of sawflies Symphyta, moths Lepidoptera and lacewings Neuroptera), ground and soldier beetles (Carabidae, Cantharidae), leaf beetles and weevils (Chrysomelidae, Curculionidae), ants (Formicidae), aphids (Aphididae), bugs and hoppers (non-aphid Hemiptera) and other invertebrates (spiders Araneae, harvestmen Opiliones, nonsawfly Hymenoptera, flies Diptera, earwigs Dermaptera, grasshoppers Orthoptera, snails Mollusca and unidentifiable components). This approach reliably reflected the composition of hard-bodied invertebrates and caterpillars, but underestimated that of Hemiptera (Green 1984).

For worm egg counts, a 3-g sample of faeces was added to 42 ml of cold tap water in a 120-ml glass bottle containing four glass beads and was shaken vigorously to break up the material. The resultant mixture was washed through a 0.15-mm mesh sieve. The strained fluid was caught and centrifuged at 1,500 rpm for two minutes. The supernatant was removed and the remaining plug was broken up and mixed with a saturated sodium chloride solution, made up of 317 g of NaCl in 881 ml of water, with a specific gravity of 1.198. This was thoroughly mixed and a sample of the solution was drawn off with a Pasteur pipette from the middle of the

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sample. The sample was placed in two pre-wetted chambers of a McMaster slide. The eggs present were identified and counted. The figure obtained was multiplied by 50 to obtain the number of eggs per gram.

All wild grey partridges (tagged or untagged), irrespective of age, that were found dead or seen in poor condition were taken immediately for necropsy at a poultry veterinary laboratory. A full examination of the entire carcass and internal organs was undertaken to establish the cause of death. The veterinarians undertook a gross examination of the entire digestive tract and trachea, and microscopically examined sections of the digestive tract to look for the presence of parasitic worms and worm eggs. Where possible the parasites and their eggs were identified to species level. However, in many cases degradation of the parasitic worms by digestive enzymes made this impossible and identification only to the level of family was possible. Additionally, bacterial cultures were grown from samples taken from the liver and the digestive tract.

Laboratory nutrition study

Twenty batches of 12 one-day-old grey partridge chicks were obtained from a commercial game farm and kept in captivity on a sterile substrate. All batches were fed a commercially available, drug-free diet of chick starter crumbs (25% protein) for the first four weeks with the addition of gamebird mini-grower pellets (20% protein) thereafter. For the first three weeks, the diets of 15 batches were augmented with various invertebrates known to be eaten by wild chicks (Potts 1986). Five batches received adult ants (principally Lasius flavus), five were given a variety of small (diameter < 5 mm) snails and five were fed small ground beetles of the family Carabidae. These taxa are known to be potential vectors of internal partridge parasites (Jordan & Pattison 1996). The remaining five chick batches were kept on the standard diet as controls. The diet was allocated to each batch of chicks at random. The invertebrates were all collected by hand in early June 2003 from an area on one of the study sites frequented by wild partridge broods, where disease was considered to have been prevalent in the past. The ants were separated from nest material by placing them in a heated and illuminated box connected by a small tube to a cool dark box, into which the ants relocated. The majority of the invertebrates were fed alive to the chicks, although some of the larger beetles were cut into smaller pieces. The joints in the pens containing each chick batch were sealed and bio-security measures were employed to prevent cross-contamination. In total, the experiment involved the collection and feeding of over 3,000 beetles, 3,000 snails and over

10,000 ants. The chicks were observed and their faecal material examined microscopically to confirm that the invertebrates had been consumed. In most cases all invertebrates were consumed within seconds of being introduced to the chicks. Daily food consumption was measured (to 0.1 g) as the difference between food (chick crumb) provided one day and the amount remaining the next day. To assess growth rates, wing length (measured to 1.0 mm), body mass (measured to 0.1 g) and tarsal length (measured to 0.1 mm) were measured weekly for each chick. Measurements of food consumption started on day 2 of the experiment and finished on day 40. All 51 chicks that died during the first six weeks and all 189 surviving chicks were subjected to necropsy to assess internal condition, including a count of the number and species of internal parasitic worms.

Statistical analysis

The results from the faecal worm egg counts and necropsies of wild birds were tabulated in terms of the total number of birds with parasites present. Clutch size and brood size at hatching for the three sites were compared using analysis of variance (ANOVA) with the factors year, site and their interaction. Differences in brood diet between the three study sites over the three years were assessed using compositional analysis (Aitchison 1986), based on producing logratios of the proportion of invertebrates within specific groups (see Aebischer et al. 1993 for full details). The logratios were analysed using a multivariate analysis of variance (MANOVA), with tests based on the Wilk's Lambda statistic. The association between brood survival and brood diet was investigated using logistic regression to relate the proportion of hatched chicks still alive at 42 days to the mean proportion of ants, the mean proportion of 'good' partridge food (caterpillars, leaf beetles and weevils; Aebischer 1997) and the ratio of ants to 'good' food in the brood's diet, which gave an indication of diet quality.

For the laboratory study, chick survival rate was measured for each batch of chicks by dividing the number of chicks surviving to six weeks by 12, the original number of day-old chicks in the batch. Average chick survival rates were compared between diets using logistic regression. Average growth rates of the experimentally reared chicks were compared between diets using a twostep analysis. The first step was, for each batch, to carry out an analysis of covariance (ANCOVA) taking wing length, tarsus length and body mass (log transformed) in turn as independent variables, chick as a factor and age (log-transformed) as a covariate. The slope of age provided a pen-specific growth rate for each body measurement. The next step compared average growth rates between diets using ANOVA. The average daily food consumption per chick was compared between diets using ANCOVA with pen and treatment as factors and age as the covariate, weighted by the number of chicks alive in each pen. This analysis was carried out initially on the data collected throughout the entire study period, then repeated for the first 21 days, corresponding to the time when supplementary food was provided. The outcome was identical, so results are presented for the initial analysis only.

Where appropriate all analyses included interactions between factors, which, if non-significant, were removed from the model prior to testing the main effects. All analyses were undertaken using either SYSTAT (version 10) or GENSTAT 6 (Genstat Committee 2002). Means are expressed \pm SE.

Results

Field-based study

Adult survival and breeding success

A total of 85 female grey partridges were tagged: 46 at Hilborough in 2001-2003, 14 at West Barsham in 2001, and 25 at Holkham in 2002-2003. Of the 85 originally tagged birds, four (5%) lost their tags and 58 (68%) survived to the start of the breeding season. Of those that died, seven (8%) were predated, six (7%) died through disease or illness, one (1%) was hit by a car, and nine (10%) died as a result of other or unknown circumstances. At all sites, of the 58 females that survived into the breeding season, 54 (93%) produced clutches of eggs, of which 34 (63%) produced young. Overall 13 (24%) clutches were predated, five (9%) were abandoned, one (2%) was infertile and one (2%) was destroyed during set-aside cultivation.

There was no significant interaction between year and site when considering the size of 44 grey partridge clutches and 32 broods recorded between 2001-2003 at the three study sites (clutches: $F_{3,38} = 0.41$, P = 0.747; broods: $F_{3,26} = 0.44$, P = 0.726). Clutch and brood size did not vary significantly between year (clutches: $F_{1,38} = 1.61$, P = 0.212; broods: $F_{1,26} = 0.01$, P = 0.921) or study site (clutches: $F_{1,38} = 1.01$, P = 0.321; broods: $F_{1,26} = 0.77$, P = 0.388).

Accordingly the data for each of the years and study sites were combined. The average clutch size was 14.9 ± 0.4 (range: 10-23) and the average brood size 13.5 ± 0.6 (range: 7-22). Six weeks after hatching only 20 broods remained, with an average brood size of 7.0 ± 1.1 young per brood (range: 1-17).

Table 1. Frequency of broods that had parents with low (< 100) or high (> 100) numbers of parasitic worm eggs in their faeces at three sites in Norfolk in 2001-2003, based on the maximum egg count in faecal samples from each brood. In some cases both types of parasitic worms were present.

				worms dia spp.	Threadworms <i>Capillaria</i> spp.	
Study Site	Year	Number of broods	< 100	> 100	< 100	>100
Hilborough	2001	2	1	0	0	1
Hilborough	2002	6	4	0	0	1
Hilborough	2003	9	7	2	1	0
W Barsham	2001	3	1	0	1	0
Holkham	2002	1	1	0	0	0
Holkham	2003	6	2	1	1	0
Overall		27	16 (59%)	3 (11%)	3 (11%)	2 (7%)

Parasite burdens of wild grey partridges

We examined 59 samples of faecal material from adults associated with 27 broods for parasite eggs (Table 1). For 81% of broods, the number of eggs that were recorded were low (<100).

A total of 79 partridges were submitted for necropsy, and their parasitic worms counted (Table 2). Of these partridges, 46 were found dead in circumstances where disease was not considered to have been the cause of death (e.g. shot, predated or hit by a car). Of these only three (7%) were subsequently found to have parasites, none at levels high enough to cause illness. By comparison, 19 out of 33 birds that were ill or were thought to have died as a result of disease carried parasites (χ^2_1 = 40.59, P < 0.001). In the latter group, parasites were associated with other conditions in four cases (e.g. bumble foot and an eye infection) and only 12 (36%) had their illness or death attributed directly to parasitic infection. Of the 33 ill birds, 14 (42%) had tapeworms (Cestoda), three (9%) the gapeworm *Syngamus trachea*, seven (21%) threadworms *Capillaria* spp. and seven (21%) the nematode *Trichostrongylus tenuis*.

Grey partridge chick diet

Faecal samples were collected from 30 broods: 19 at Hilborough, two at West Barsham and nine at Holkham. Initially the analysis revealed that there was a significant interaction between year and site when considering the composition of the diet consumed by the partridge broods ($\Lambda = 0.283$, $F_{7,17} = 6.15$, P = 0.001). This variation was due to the number of aphids consumed at the different sites, which at Hilborough in 2001, 2002 and 2003 averaged 8.8 ± 8.1%, 3.5 ± 1.7% and 20.3 ± 4.4%, respectively. At West Barsham in 2001 the percentage of aphids eaten was 30.0 ± 1.1% and at Holkham in 2002 and 2003 it was 0% and 18.1 ± 4.2%, respectively. With aphids removed there was no significant difference in the diet composition of the grey partridge broods with respect to either year ($\Lambda = 0.498$, $F_{12,42} =$

Table 2. Incidence of parasitic worms amongst wild adult and young grey partridges that were submitted for necropsy from three sites (A: Hilborough; B: West Barsham; C: Holkham) in Norfolk in 2001-2003. In some cases more than one type of parasitic worm was present.

Study site	Year	Туре	N	Parasites present	Tapeworms (Cestoda)	Gapeworms Syngamus trachea	Threadworms Capillaria spp.	<i>T. tenuis</i> (Nematoda)	Roundworms Ascaridia spp.
А	2001	Healthy	4	1	0	0	0	0	1
А	2001	I11	13	9	6	1	4	4	0
А	2002	Healthy	1	0	0	0	0	0	0
А	2002	I11	6	1	0	1	0	0	0
А	2003	Healthy	0	0	0	0	0	0	0
А	2003	Ill	3	1	1	0	0	0	0
В	2001	Healthy	35	1	0	0	0	0	1
В	2001	Ill	6	3	2	1	3	3	0
С	2002	Healthy	5	0	0	0	0	0	0
С	2002	I11	1	1	1	0	0	0	0
С	2003	Healthy	1	1	0	1	0	0	0
С	2003	Ill	4	4	4	0	0	0	0
Total hea	lthy		46	3 (7%)	0 (0%)	1 (2%)	0 (0%)	0 (0%)	2 (4%)
Total ill			33	19 (58%)	14 (42%)	3 (9%)	7 (21%)	7 (21%)	0 (0%)
Overall to	otal		79	22 (28%)	14 (18%)	4 (5%)	7 (9%)	7 (9%)	2 (3%)

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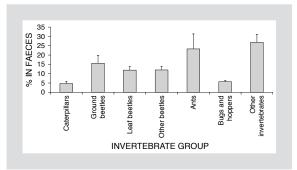


Figure 1. Mean composition (% by number \pm SE) of invertebrates in grey partridge chick faeces at three sites in Norfolk in 2001-2003.

1.45, P > 0.182) or site ($\Lambda = 0.481$, $F_{12,42} = 1.55$, P = 0.145).

The average percentage of each invertebrate group eaten by the partridge broods in the three years at the three sites is shown in Figure 1. Overall, at all three sites the main invertebrate group eaten was 'other invertebrates'. Of the remaining groups, ants were the second highest consumed, with smaller but similar numbers of the other groups being taken.

Association between diet and chick survival

When considering the effect of diet on brood survival using logistic regression neither year, site or their interaction was significant (all P > 0.05), so data were pooled across sites and years. There was a significant negative relationship ($F_{1,27} = 7.77$, P = 0.010) between the percentage of ants in the diet and chick survival, such that as the percentage of ants in the diet increased, the survival of chicks in the brood decreased (Fig. 2). The association between the percentage of invertebrate groups

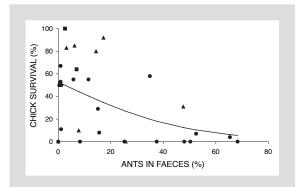


Figure 2. Relationship between brood survival (in %) and the percentage (by number) of ants in chick faeces averaged within broods for the three sites Hilborough (\bullet), West Barsham (\blacksquare) and Holkham (\blacktriangle) in Norfolk in 2001-2003. The logistic regression line is logit(%survival) = -0.0431 %ants + 0.108.

in the diet thought to represent good grey partridge chick food (caterpillars, leaf beetles and weevils) and chick survival was positive, but not significant ($F_{1,27} = 0.50$, P = 0.485). When using the ratio of ants to 'good' food as an indicator of diet quality, the relationship with chick survival was significantly negative ($F_{1,27} = 9.56$, P =0.005); low survival was associated with a high ratio of ants to 'good' food.

Laboratory nutrition study

By six weeks, 189 chicks had survived out of the original 240 (78.8%). The corresponding average survival rates were, for the 60 chicks on a diet supplemented with ants, 83.3 ± 3.3%, with snails 76.7 ± 1.7%, with beetles 78.3 ± 3.2%, and for the unsupplemented diet (control) 76.7 ± 2.7%. There were no significant differences in survival rate between these groups ($\chi^2_3 = 1.11$, P > 0.775).

The experimentally reared grey partridge chicks had significantly different growth rates in relation to diet for body mass ($F_{3,16} = 7.81$, P = 0.002) and tarsus length ($F_{3,16} = 6.37$, P = 0.005), but not for wing ($F_{3,16} = 0.51$, P = 0.681). The body mass and tarsus growth rates of chicks fed on ants and beetles followed a similar pattern, which was higher, by 4-9%, than the growth rates of chicks fed on snails and the standard diet of chick crumb.

When considering mean daily food consumption per chick during the entire study period the interaction between treatment and age was not significant ($F_{114,626} =$ 1.13, P = 0.186). Mean daily food consumption per chick increased significantly with age ($F_{38,740} = 23.39$, P < 0.001) and was significantly different between treatments ($F_{1,740} = 11.01$, P = 0.001), however, no systematic pattern was apparent.

At necropsy, none of the chicks that died in the course of the experiment was found to be infected with parasites, nor were any of the chicks that survived to the age of six weeks.

Discussion

Field-based study

The parasite burden of the adult radio-tagged grey partridges, which was assessed by faecal worm egg counts, was low and thought by a veterinary surgeon to represent the normal background level of parasites found in wild grey partridges (C. Knott, pers. comm.). The wild grey partridges submitted for necropsy contained a range of parasitic worms, predominately tapeworms, but in addition gapeworms, threadworms, nematodes and

roundworms. Only 15% of the birds in the sample were thought to have died directly as a result of high parasite levels, and the overall incidence of parasitic infection was 28%. However, given the biased nature of this information, which resulted from a disproportionate number of birds found ill or dead, the actual prevalence of parasites at levels high enough to cause illness and death was likely to be much lower within the wild grey partridge population. The subset of partridges found dead in circumstances where disease was unlikely to be the cause of death was probably much more representative: the level of parasite infection there was 7%. On this basis, the probability of both members of a pair being free of parasites was $(1-0.07)^2 = 0.86$, or 86%, not very different from the value of 81% of broods whose adults had low levels of internal parasites.

The grey partridge chicks studied here had a diet that was similar to that reported by other studies (e.g. Ford et al. 1938, Green 1984). They ate a range of invertebrates commonly found in lowland agriculture, although ants were recorded at higher levels than in previous studies. Several of the insect species eaten are known to be intermediate hosts for worms that are internal parasites of grey partridges. In particular ants and carabid beetles are intermediate hosts of tapeworms (Jordan & Pattison 1996). Additionally, the remains of earthworms, which are an intermediate or transport host for parasitic nematode worms, were also identified.

The survival of chicks in a brood declined, on average, as the percentage of ants in the diet increased. It is possible that as ants are one of the main intermediate hosts for tapeworms, parasite infection is higher and chick survival is lower for those that consumed more ants. However, it is also possible that grey partridge chicks that ate more ants were consuming a poorer overall diet.

Laboratory nutrition study

The invertebrate groups fed to chicks in this study were potential hosts of grey partridge parasites. The study showed that parasite infection rates were very low, given the complete absence of parasites after six weeks in chicks fed a diet supplemented with invertebrates.

In total the chicks consumed over 3,000 beetles, 3,000 snails and at least 10,000 ants. It is thus most unlikely that insufficient numbers of invertebrates were provided to allow exposure to any parasites carried by the hosts. Moreover, the quantity of invertebrates fed to the chicks sufficiently supplemented the diet to produce better growth (body mass, tarsus length) among the chicks fed ants and beetles.

The lack of subsequent parasitic infection shows that

either the incidence of infective stages in the host invertebrates must be very low or that some other factor may be controlling the contraction of disease. The laboratory chicks had all the requirements for good growth, namely continual warmth, light, water and an ad libitum high-protein diet. It is possible that under these ideal conditions grey partridge chicks have a much better immunity to parasitic infection than chicks reared in the wild. Adult partridges, however, fed in a similar way, proved susceptible to experimental infection by the internal parasite Heterakis gallinarum (Sage et al. 2002), and it is unlikely that the immunity of chicks is better than that of adults.

Conclusions

Disease has been cited as one of the possible, although unlikely, causes of the recent declines experienced by a range of farmland birds in the UK (Fuller et al. 1995), although very little evidence exists within the literature to support this hypothesis. For grey partridges there is evidence from the early 1930s (Portal & Collinge 1932) that a disease epidemic amongst wild grey partridges (in that case Trichostrongylus tenuis) could cause mass mortality and population decline amongst wild birds, although generally it is accepted that losses of wild grey partridges to disease are usually low. This study has shown that wild grey partridges are susceptible to parasitic infection and at levels that may result in death. Overall, however, it seems that the parasitic infection rates and levels are low. The poor brood survival experienced in recent years is most likely due to a poor overall diet, or if parasitic infection is the cause, it is likely to be a result of a poor diet reducing immunity and increasing the deleterious effects of parasites. It was, however, not possible to dismiss the role of disease in affecting a small part of the wild grey partridge population or the role of ants in the diet in reducing chick survival, either as vectors of disease or indicators of a poor diet. Overall it is considered most likely that the perceived increase in the number of grey partridges with parasites, and the apparent decreases in brood survival, are indicative of an overall reduction in habitat suitability and food availability for grey partridges, rather than an absolute increase in parasite levels. Accordingly, management to conserve and increase wild grey partridge numbers should concentrate on improving brood-rearing habitat quality, i.e. increasing invertebrate chick-food abundance, rather than directing efforts at reducing the smallscale effects of disease.

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References

- Aebischer, N.J. 1997: Gamebirds: management of the grey partridge in Britain. - In: Bolton, M. (Ed.); Conservation and the Use of Wildlife Resources. Chapman & Hall, London, pp. 131-151.
- Aebischer, N.J. & Potts, G.R. 1998: Spatial changes in grey partridge (Perdix perdix) distribution in relation to 25 years of changing agriculture in Sussex. - Gibier Faune Sauvage 15: 293-308.
- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993: Compositional analysis of habitat use from animal radiotracking data. - Ecology 74: 1313-1325.
- Aitchison, J. 1986: The Statistical Analysis of Compositional Data. - Chapman & Hall, New York, 448 pp.
- Anonymous 1996: UK Biodiversity Group Tranche 2 Action Plans. - English Nature, Peterborough, 267 pp.
- Anonymous 1998: Partridge Count Scheme. The Game Conservancy Trust Review of 1998, 30: 112 pp.
- Anonymous 1999: Partridge Count Scheme. The Game Conservancy Trust Review of 1999, 31: 112 pp.
- Baillie, S.R., Crick, H.Q.P., Balmer, D.E., Beaven, L.P., Downie, I.S., Freeman, S.N., Leech, D.I., Marchant, J.H., Noble, D.G., Raven, M.J., Simkin, A.P., Thewlis, R.M. & Wernham, C.V. 2002: Breeding Birds in the Wider Countryside: Their Conservation Status 2001. - BTO Research Re-

port 278, British Trust for Ornithology, Thetford. Available at www.bto.org/birdtrends.

- Ford, J., Chitty, H. & Middleton, A.D. 1938: The food of partridge chicks (Perdix perdix) in Great Britain. - Journal of Animal Ecology 7: 251-265.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. & Carter, N. 1995: Population declines and range contractions among lowland farmland birds in Britain. - Conservation Biology 9: 1425-1441.
- Gibbons, D.W., Reid, J.B. & Chapman, R.A. 1993: The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991.
 T. & A.D. Poyser, London, 520 pp.
- Green, R.E. 1984: The feeding ecology and survival of partridge chicks (Alectoris rufa and Perdix perdix) on arable farmland in East Anglia. - Journal of Applied Ecology 21: 817-830.
- Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D., Gibbons, D.W. & Galbraith, C. 2002: The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. - British Birds 95: 410-448.
- Jordan, F.T.W. & Pattison, M. 1996: Poultry diseases (4th edition). - W.B. Saunders, London, 546 pp.
- Middleton, A.D. & Chitty, H. 1937: The food of adult partridges Perdix perdix and Alectoris rufa, in Great Britain. -Journal of Animal Ecology 6: 322-336.
- Moreby, S.J. 1988: An aid to the identification of arthropod fragments in the faeces of gamebird chicks (Galliformes). Ibis 130: 519-526.
- Portal, M. & Collinge, W.E. (Eds.) 1932: Partridge disease and its causes. - Country Life Ltd. London, 96 pp.
- Potts, G.R. 1980: The effects of modern agriculture, nest predation and game management on the population ecology of Partridges Perdix perdix and Alectoris rufa. - Advances in Ecological Research 11: 2-79.
- Potts, G.R. 1986: The Partridge: Pesticides, Predation and Conservation. - Collins, London, 276 pp.
- Sage, R.B., Woodburn, M.I.A., Davis, C. & Aebischer, N.J. 2002: The effect of an experimental infection of the nematode Heterakis gallinarum on hand-reared grey partridges Perdix perdix. - Parasitology 124: 529-535.
- Tapper, S. 1992: Game Heritage: An ecological review from shooting and gamekeeping records. - Game Conservancy Ltd, Fordingbridge, 140 pp.