Effects of tick Ixodes ricinus infestation on pheasant Phasianus colchicus breeding success and survival

Authors: Hoodless, Andrew N., Kurtenbach, Klaus, Nuttall, Patricia A., and Randolph, Sarah E.

Source: Wildlife Biology, 9(3) : 171-178

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.046

Effects of tick *Ixodes ricinus* infestation on pheasant *Phasianus colchicus* breeding success and survival

Andrew N. Hoodless, Klaus Kurtenbach, Patricia A. Nuttall & Sarah E. Randolph

Hoodless, A.N., Kurtenbach, K., Nuttall, P.A. & Randolph, S.E. 2003: Effects of tick *Ixodes ricinus* infestation on pheasant *Phasianus colchicus* breeding success and survival. - Wildl. Biol. 9: 171-178.

In some parts of Britain, pheasants *Phasianus colchicus* are infested by *Ixodes ricinus* ticks in the spring and summer. The effects of experimental reduction of tick infestation levels on the breeding success and survival of reared female pheasants were studied on two estates in southern England during 1995-1997. Females were radio-tagged and half of the birds, selected at random, were fitted with a slow-release acaricide, which substantially reduced their tick burdens. Clutch survival was significantly higher for treated females throughout the three-year study period, and hence more chicks were hatched by treated females (3.30 ± 0.86) than by control females (0.70 ± 0.36), even though treated and control birds produced the same numbers of clutches and eggs. During April-July, the female survival rate was significantly higher for acaricide-treated birds, showing an improvement of 10-15% over that of control birds each year. While these impacts will be of minor importance where annual pheasant releasing takes place to supplement autumn stocks for shooting, they might reduce the potential harvest on estates with wild pheasants or on those aiming to re-establish self-sustaining naturalised populations.

Key words: breeding success, Ixodes ricinus, Phasianus colchicus, pheasant, survival, ticks

Andrew N. Hoodless, The Game Conservancy Trust, Fordingbridge, Hampshire SP6 1EF and Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK - e-mail: ahoodless@gct.org.uk
Klaus Kurtenbach, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK, and NERC Centre for Ecology and Hydrology, Mansfield Road, Oxford OX1 3SR, UK - e-mail: k.kurtenbach@ic.ac.uk*
Patricia A. Nuttall, NERC Centre for Ecology and Hydrology, Mansfield Road, Oxford OX1 3SR, UK - e-mail: pan@ceh.ac.uk
Sarah E. Randolph, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK - e-mail: sarah.randolph@zoology.oxford.ac.uk

**Present address: Department of Infectious Disease Epidemiology, Imperial College of Science, Technology and Medicine, St. Mary's Campus, Norfolk Place, London W2 1PG, UK*

Corresponding author: Andrew N. Hoodless

Received 19 December 2001, accepted 10 February 2003

Associate Editor: Steve Redpath

Ectoparasites have been shown to have a considerable impact on a variety of hole nesting and colonial birds, which suffer high infestations as a consequence of using the same nest sites year after year. High parasite burdens can cause increased nest desertion (Feare 1976, King, Blankinship & Paul 1977, King, Keithe & Mitchell 1977, Duffy 1983) and reductions in mating success, hatching success, brood size, nestling growth and survival, fledging success and the number of broods per season (Brown & Brown 1986, Møller 1990, Chapman & George 1991, Møller 1993, Richner, Opplinger & Christe 1993). In contrast, there is very little information concerning the impact of ectoparasites on birds, such as gamebirds, that use different nests per breeding attempt.

In Britain a common ectoparasite on gamebirds is the sheep tick *Ixodes ricinus*, which may have both direct and indirect effects on fitness. Direct effects documented in other groups of birds include exsanguination, causing anaemia in extreme cases (Janovy 1997), irritation resulting in increased preening and decreased anti-predator vigilance (Clayton 1991a, Cotgreave & Clayton 1994), and reduction of visual perception when ticks are aggregated around the eyes. Additionally, indirect impacts may result from the transmission of bacteria and viruses. In red grouse *Lagopus lagopus scoticus* substantial chick mortality caused by the tick-borne flavivirus that causes louping ill has been documented (Hudson & Dobson 1991), but there is no published evidence of deaths resulting from high tick burdens in the absence of louping ill. Nevertheless, tick infestations may reduce fitness in other more subtle ways, just as other groups of parasites reduce productivity in galliforms. Experimental reductions of intestinal nematodes resulted in improved hatching success of pheasants *Phasianus colchicus* (Woodburn 1995, 1999) and increased clutch size, hatching success and brood size in red grouse (Hudson 1986).

Densities of the tick *Ixodes ricinus* vary markedly between sites (Gray, Kahl, Robertson, Daniel, Estrada-Pena, Gettinby, Jaenson, Jensen, Jongejan, Korenburg, Kurtenbach & Zeman 1998), partly due to variable abiotic constraints on their survival and partly due to variable success rates in finding hosts upon which to feed. High population densities of deer, a significant host for larvae and nymphs, and the most important host for adult female ticks, are associated with high densities of ticks, both *I. ricinus* in Europe and *I. scapularis* in the USA (Wilson, Telford, Piesman & Spielman 1988, Gray, Kahl, Janetski & Stein 1992, Daniels, Fish & Schwartz 1993, Stafford 1993). Pheasants share the woodland habitats of deer and ticks in Britain and up to 25 million are released annually to satisfy game shooting interests (estimate based on Tapper 1999 and subsequent unpublished Game Conservancy Trust records). Pheasants are frequently infested with immature stages of *I. ricinus*, males often heavily so (Hoodless, Kurtenbach, Peacey, Nuttall & Randolph 1998, Hoodless, Kurtenbach, Nuttall & Randolph 2002), and are also competent amplifying hosts for the Lyme disease spirochaete *Borrelia burgdorferi* (Kurtenbach, Carey, Hoodless, Nuttall & Randolph 1998). Despite the considerable economic investment in rearing and releasing pheasants in Britain, and the renewed interest in managing self-sustaining populations of wild pheasants, there is currently no information on the effects of tick infestation on the survival and breeding success of these precocial birds.

The aim of our study was to examine the impact of tick infestation on the breeding success and survival of reared female pheasants in the wild following the shooting season. This was achieved by experimental manipulation of tick burdens by treating birds with an acaricide. The results of the study are discussed in the context of pheasant management.

Methods

Study sites

Fieldwork was conducted at two sites; one consisted of approximately 2.5 km^2 on the Wimborne St. Giles estate (Wimborne), Dorset (50°54'N, 1°56'W) during 1995-1996, and the second was an area of 8 km^2 on the Clarendon Park estate (Clarendon), Wiltshire (51°04'N, 1°43'W) in 1997. Both areas consist of deciduous and coniferous woodland (making up ca 40% of each study area) surrounded by agricultural fields. Pheasants are reared by the gamekeepers on both estates and transferred to release pens as six-week old poults at the end of July. There are few, if any, truly wild pheasants, and naturalised birds (those surviving at least two winters following release) comprise about 10% of the spring populations. Red foxes *Vulpes vulpes* are culled, but there is considerable immigration from outside. Carrion crows *Corvus corone* and magpies *Pica pica* are trapped or shot in spring on both estates, and stoats *Mustela erminea* and weasels *Mustela nivalis* are trapped at Wimborne. No spring feeding of the pheasants takes place, and no conservation headlands (Sotherton 1991) or other specifically designed brood-rearing habitats are incorporated into the farming.

Assessment of tick infestations, radio-tagging and acaricide treatment

Female pheasants were live-trapped during mid-February

- mid-March each year and ticks were counted on their heads. Total body counts of ticks on male pheasants shot under licence during the summer showed that 96 ± 1% (N = 42) of the ticks occurred on the head. Data on tick infestations of female pheasants in April were obtained from birds shot under licence at Clarendon in 1995 and on the farm adjoining Wimborne in 1996.

The pheasants were fitted with 17-g necklace radio-tags (Biotrack Ltd., Wareham, Dorset), and approximately half of those trapped each year were treated with permethrin acaricide, a contact and stomach poison against a wide range of insects, mites and ticks. Permethin (a synthetic pyrethroid: (3-phenoxyphenyl) methyl (±)-cis, trans-3-(2,2-dichloroethenyl)-2,2-dimethylcyclopropane-carboxylate) has very low avian and mammalian toxicity (Elliott 1977), and there is no evidence that dermal applications increase avian metabolic rate. This method of application will have had no effect on any intestinal parasites. Each year, 84-97 male pheasants were also fitted with coded poncho-tags and approximately half of these were treated with acaricide. Although these birds are not considered here, it is important to understand the context in which the effects on females were studied. The effects of tick infestation on male pheasant territoriality are discussed in Hoodless et al. (2002).

Birds were assigned to the two treatment groups on the basis of the order in which they were captured according to a predetermined sequence of N/2 random numbers within the range 1...N, where N was the target number to be caught. The permethrin was administered in the form of strips of cattle ear tag (Expar, manufactured by Coopers Animal Health Inc., Kansas, USA and supplied by Mallinckrodt Veterinary Ltd., Middlesex, UK) attached to the underside of the radio-tags, giving a dose of approximately 40 mg kg^{-1}. This method has been shown to reduce tick infestations on red grouse chicks (Laurenson, Hudson, McGuire, Thirgood & Reid 1997). At Wimborne, 59 females (28 treated) were radio-tagged in 1995 and 60 (30 treated) were radio-tagged in 1996. In 1997, 54 females (27 treated) were radio-tagged at Clarendon. Acaricide strips were still attached to radio-tags recovered up to one year later. The birds were aged according to the shaft diameter of the proximal primary feather (Greenberg, Etter & Anderson 1972, Hill & Robertson 1988), which was removed at capture. All the females marked were first-year birds, i.e. released the previous July.

Pheasant survival and breeding success

Dates of nest establishment, the outcome of nesting attempts and the timing of mortality of female pheasants were determined as follows. Using a TR2 receiver (Telonics, Arizona, USA) and a three-element Yagi antenna, tagged females were pin-pointed to within a 5-m radius once a week during April-August. Any female that did not move between radio-locations was approached to ascertain whether it was nesting or dead. Nests were visited at 3-4-day intervals and clutch sizes recorded when hens were absent. The causes of nest failure were separated into desertion and predation and, where possible in the case of predated nests, a predator was attributed on the basis of puncture marks in eggs or other signs left in the vicinity of the nest. The number of chicks hatched from successful nests was recorded, and broods were located on alternate days. Brood size was determined when the chicks were 10 days old, the female being flushed if necessary to obtain an accurate count. Broods were monitored at 3-7-day intervals thereafter.

Statistical analysis

As ticks typically show over-dispersed distributions on their host populations (Randolph 1975, Craine, Randolph & Nuttall 1995), comparisons of tick burdens were made by using a generalised linear model (GLM) with negative binomial errors (Wilson & Grenfell 1997). Survival functions of radio-tagged females during April-July were estimated by using a non-parametric method allowing censoring of birds whose radio-tags failed (Kaplan & Meier 1958, Pollock, Winterstein, Bunck & Curtis 1989). The number of birds at risk was modified to account for uncertain relocation of individuals (Bunck, Chen & Pollock 1995). The survival rates of females during April-July were compared with a logistic regression model. Analyses of the number of nesting attempts and of nest success were based on the numbers of females alive on 15 April. Clutch sizes were corrected for laying date, as the mean clutch size of pheasants declines during the breeding season (Robertson 1991). Because some nests were not detected during egg-laying, the timing of nesting was analysed using estimated dates of the start of incubation (details in Hoodless, Draycott, Ludiman & Robertson 1999). Owing to the fact that site and year were confounded, the effect of acaricide treatment on pheasant survival and breeding success was examined using models incorporating treatment and site as factors and female pheasant density as a covariate. Statistics were calculated in SYSTAT 9 (SPSS Inc. 1999). Generalised linear models with Poisson errors and a logarithmic link function were performed in GENSTAT 5.3 (Lawes Agricultural Trust 1993), instead of analysis of covariance, in cases where transformation of the dependent variable failed to achieve normality.

Results

Tick infestation levels and efficacy of acaricide treatment

In Dorset, nymphal *I. ricinus* quest in increasing numbers from February to a peak in April/May, while very few larvae start to quest before May and this stage typically reaches a peak in July/August (Hoodless et al. 1998). This was reflected in increasing infestation levels of nymphs on female pheasants during February, March and April, and greater numbers of nymphs than larvae during these months (Table 1). No adult female ticks were recorded on pheasants. Ticks could not be counted on nesting pheasants, but tick infestations on males reflected the seasonal trend in questing ticks described above (Hoodless et al. 2002).

Tick infestation levels at the time of capture were similar on the birds destined for each treatment (GLM treatment $F_{1,157} = 1.23$, $P = 0.270$, month × treatment $F_{1,157} = 0.01$, $P = 0.936$). There was a significant difference in infestations at the time of capture between years, the highest burdens being in 1997 and the lowest in 1996 (GLM year $F_{2,157} = 19.93$, $P < 0.001$). On the same individual birds, tick infestation levels decreased significantly between tagging and 7-36 days later (recaptured in February-March) on treated birds, but remained similar on control birds (see Table 1). It was not possible to measure the effect of acaricide treatment on female pheasants after March, but treatment had a significant effect on tick infestations on male pheasants until August (Hoodless et al. 2002).

Pheasant survival

The survival rates of female pheasants during April-July were not constant, with birds in both treated and control groups experiencing greater mortality during late April and early May, the time when they started nesting (Fig. 1). Survival of acaricide-treated females was significantly better than that of control females (logistic regression: $\chi^2_1 = 5.42$, $P = 0.020$), with density, site and treatment × site effects unimportant ($\chi^2_1 = 1.69$, $P = 0.194$, $\chi^2_1 = 3.30$, $P = 0.069$ and $\chi^2_1 = 0.18$, $P = 0.671$ respectively). Survival of acaricide-treated females varied between 32 and 43% and that of control females between 12 and 31%, with a mean difference of 12.3 ± 1.5%. There was no difference between the proportions of treated (22%, N = 23) and control (32%, N = 28) females killed when clutches were predated (logistic regression: treatment $\chi^2_1 = 0.70$, $P = 0.402$, density $\chi^2_1 = 0.01$, $P = 0.938$, site $\chi^2_1 = 0.13$, $P = 0.723$, treatment × site $\chi^2_1 = 3.26$, $P = 0.071$).

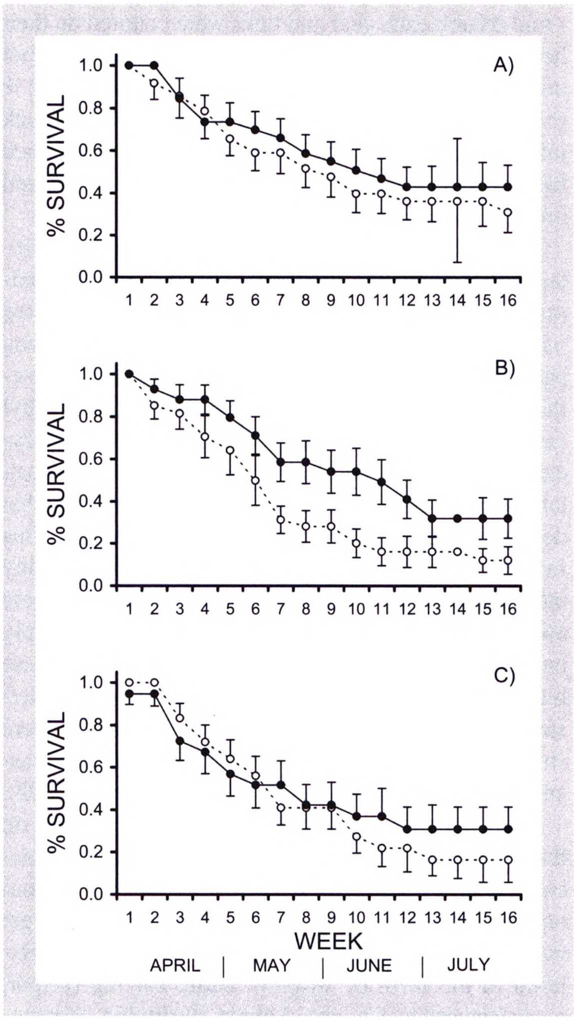

Figure 1. Female pheasant survival functions during April-July, estimated by the Kaplan & Meier (1958) method at Wimborne 1995 (A), Wimborne 1996 (B) and Clarendon 1997 (C). Control birds are open circles and dashed line, acaricide-treated birds are filled circles and solid line. Error bars show ± 1 SE, and week 1 is the beginning of April.

Table 1. Median (and quartiles) tick infestations of female pheasants with a comparison of the numbers of larvae and nymphs during February, March and April (A), and a comparison of total tick infestations (larvae + nymphs) on acaricide-treated and control birds when radio-tagged and when recaptured 7-36 days later (B). Test statistic is the Wilcoxon matched-pairs signed-rank test, with two-tailed significance for (A) and one-tailed for (B).

(A) Month	N	Larvae	Nymphs	Statistic
February	72	0 (0-0)	2 (0-3)	z = 6.29, P < 0.001
March	81	0 (0-0)	3 (1-5)	z = 6.99, P < 0.001
April	42	0 (0-1)	7 (2-17)	z = 5.53, P < 0.001
(B) Treatment	**N**	**Tagging**	**Recapture**	**Statistic**
Acaricide	9	2 (2-5)	0 (0-2)	z = -2.41, P = 0.008
Control	13	3 (1-6)	5 (2-7)	z = -0.04, P = 0.485

Table 2. Nesting performance of female pheasants at Wimborne St. Giles (1995, 1996) and Clarendon Park (1997) in relation to experimental reduction of tick infestations with permethrin acaricide.

	Acaricide-treated birds		Control birds				
	N*	Mean ± SE	N*	Mean ± SE	Test	Statistic	P
Proportion of females nesting†	62	0.49 ± 0.06	72	0.41 ± 0.05	Chi-square	$\chi^2_1 = 0.11$	0.745
Number of clutches/female	30	1.17 ± 0.07	30	1.17 ± 0.08	GLM	$F_{1,54} = 0.004$	0.950[a]
Date of start of incubation	30	9 May ± 2.6 days	27	9 May ± 2.9 days	ANCOVA	$F_{1,52} = 0.29$	0.591[a,b]
Clutch size	15	11.62 ± 0.79	14	10.36 ± 0.77	ANOVA	$F_{1,25} = 1.29$	0.267[c]
Proportion of nesting females that hatched a clutch	30	0.39 ± 0.09	30	0.13 ± 0.06	Logistic regn	$\chi^2_1 = 4.63$	0.032[a,d]
Chicks hatched/female	30	3.30 ± 0.86	30	0.70 ± 0.36	GLM	$F_{1,55} = 9.62$	0.003[a,e]

* Sample size refers to all females pooled for both sites for the three years. Clutch size could not be recorded for all nesting females because some were never off the nest when visited and some were predated before clutch size could be determined.
† Means ± SE based on values for each year and site separately.
[a] Density, site and treatment × site effects not significant.
[b] Analysis based on day number post 15 April and restricted to first clutches.
[c] Clutch sizes corrected for laying date according to Robertson (1991). Density covariate excluded from the model because clutch sizes were only obtained in 1995 and 1997. Site and treatment × site effects not significant.
[d] Statistics similar for the subset of females that survived to 15 June (treatment $\chi^2_1 = 4.89$, P = 0.027).
[e] Statistics similar for the subset of females that survived to 15 June (treatment $F_{1,31} = 8.10$, P = 0.008).

Breeding performance of female pheasants

Similar proportions of females from each group nested and the mean number of clutches laid per female was similar (Table 2). There was no significant difference in clutch size (although treated females laid on average one more egg) or in the timing of the start of incubation. In all years, nesting success was very low, as habitually observed on these estates (Hoodless et al. 1999, Game Conservancy Trust, unpubl. records). However, in all three years the survival of clutches produced by treated females was higher than that of clutches belonging to control females (Fig. 2), and hence more chicks were hatched per treated female. The proportion of birds that hatched a clutch and the number of chicks hatched were still significantly higher for acaricide-treated females than for controls when the analyses were repeated on the subset of females that survived until 15 June (about two weeks after the peak hatch date, see Table 2). This demonstrates that the difference in clutch survival was not simply a product of the differential mortality of females. The only chicks that survived their first 10 days were those from two broods reared by treated females, and five of these from one brood survived to at least eight weeks of age.

Of predated clutches where the identity of the predator was clear, the proportions taken by foxes, rather than corvids, did not differ significantly between groups (treated females: 85% fox predation of nests, N = 13; controls: 79% fox predation, N = 19; Yates' $\chi^2_1 = 0.003$, P = 0.956). Nest desertion was a rare cause of failure, occurring in less than 3% of all cases.

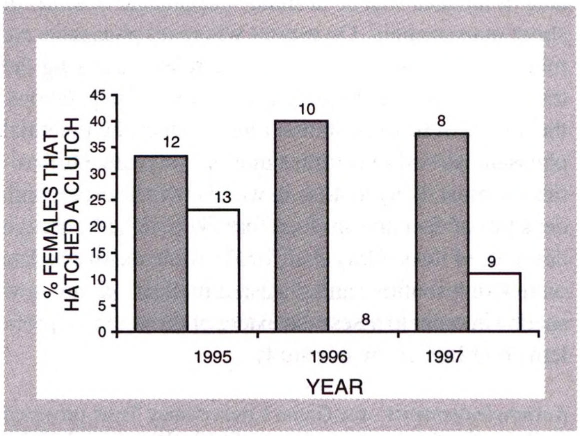

Figure 2. Proportions of nesting females that hatched a clutch of eggs at Wimborne St. Giles (during 1995 and 1996) and Clarendon Park (during 1997). Control birds are open bars, acaricide-treated birds are grey bars. The figures above the bars are sample sizes. Note that no control birds hatched clutches in 1996.

Discussion

Using experimental manipulation of tick burdens by treating birds with an acaricide, we have already shown that high tick burdens have a negative impact on wattle development, harem acquisition and territoriality in male pheasants (Hoodless et al. 2002). We now report that infestations of ticks have significant adverse effects on female pheasant survival and productivity, despite the fact that female pheasants typically harbour lower tick burdens than males.

Pheasants were assigned to the acaricide-treated or control groups without any prior knowledge of their natural tick burdens. This and the fact that all the females were the same age, means that the observed differences in nesting success between the two groups can be attributed directly to the treatment. It proved impractical to clear spirochaetal infections from a sample of pheasants by treating them with antibiotics, and thus to distinguish between the effects of spirochaetes and ticks on pheasant fitness. Nevertheless, given a) the numbers of nymphal ticks that would have fed on female pheasants between their leaving release pens in August and the start of acaricide treatment in late February (Hoodless et al. 1998), and b) the 2.6% mean infection prevalence of *Borrelia burgdorferi* in questing nymphs at these sites (Kurtenbach, Peacey, Rijpkema, Hoodless, Nuttall & Randolph 1998), it can be estimated that about 70% of the birds in this study would have been bitten by a spirochaete-infected tick prior to capture and assignment to the experimental groups. Therefore the observed differences in pheasant fitness were more likely to be due to tick infestations than to spirochaete infection.

Due to high predation rates by foxes, survival rates were low for all the pheasants at our study sites during April-July. Nevertheless, acaricide treatment revealed that tick infestations reduced survival by a further 12% during the three years of the study. This observation is consistent with reports which indicate that ectoparasites affect both survival and reproductive success in birds (reviewed in Clayton 1991b, Brown, Brown & Rannala 1995, Clayton & Moore 1997). A similar manipulative study of intestinal parasites, notably the caecal nematode *Heterakis gallinarum*, resulted in a difference in the survival functions of reared female pheasants during incubation (Woodburn 1999). The observed reduced survival rate during late April and May agrees with previous findings that female pheasants are most vulnerable to predation when nesting (Brittas, Marcström, Kenward & Karlbom 1992, Leif 1994). Treated and control females were observed to be off the nest with similar frequency (treated: 15.4% of observations, N = 104; control: 11.6%, N = 86). However, these data are biased towards birds that survived until at least mid-way through the nesting period and it is not known whether the control birds predated earlier were killed because they were prone to spending more time away from the nest.

Females carrying ticks suffered a slightly higher predation rate at the nest, which is consistent with lower anti-predator vigilance if ectoparasites cause birds to spend more time preening (Clayton 1991a, Cotgreave & Clayton 1994). The majority of *I. ricinus* larvae and nymphs that feed on birds are attached to their heads, often around the eyes. The head is the one area of the body where ticks cannot easily be removed by preening and ticks around the eyes may impair vision. Possibly, even for the females that escaped predation at the nest, a delayed escape might have been the cause of the higher rate of predation observed on the clutches of control females. We know that clutches belonging to treated females survived better as a result of a lower rate of predation on the clutches *per se*, rather than simply because of differential mortality of the females. Thus it seems that even the relatively low infestation levels of ticks observed on these female pheasants may have an impact on fitness, although the mechanism is not yet clear.

On many estates where pheasants are released, the number of chicks that survive to fledging is typically low because of inadequate brood-rearing habitats and availability of invertebrates for chicks to feed on. However, ticks are also present on some of these estates and may further reduce chick survival. Owing to the small sample size in our study, it is unclear whether the greater predation rate of control females or a higher pick-up of ticks by control bird chicks was responsible for the poor survival of chicks belonging to control females. This area would merit further work because any adverse effects of tick infestation on the survival of chicks hatched from nests in woodlands, where most ticks live, would apply equally to wild populations of pheasants. Female pheasants (N = 5-17) on three out of six wild-bird estates in Hampshire, Norfolk and Suffolk were found to carry ticks in April 1996, with median infestations of 1-10 ticks per female (R.A.H. Draycott, pers. comm.) which are comparable to the tick burdens observed in our study.

The implications of tick infestations for pheasant management may differ for estates with wild populations as opposed to estates where birds are released annually. As pheasant release serves to supplement autumn stocks for shooting, rather than to restock wild breeding populations, the impact of ticks on the breeding success of females will be of minor importance in terms of shoot management. On estates where no pheasants are released, or where only males are released during the transition back to self-sustaining naturalised populations, the effects of tick infestation might reduce the potential pheasant harvest in certain situations or years. Difficulties are most likely to arise in woods which sustain high densities of deer and are therefore likely to harbour high densities of ticks (Gray et al. 1992). More extensive data on tick distributions and pheasant infestations are now needed in order to assess the extent of the potential problems highlighted by our study.

Acknowledgements - the Game Conservancy Trust provided facilities for this study and Lord Shaftesbury and A.W.M. Christie-Miller kindly allowed us to work at Wimborne St. Giles and Clarendon Park. The gamekeepers, Ron Thorpe, Paul Morrish and Roy Perks, were particularly helpful. Dave Butler and Neville Kingdon assisted with radiotracking. We thank Nicholas Aebischer, Isabella Cattadori and two anonymous referees for helpful comments on the manuscript. Mike Matthewson, Schering-Plough, UK supplied the acaricide tags and the project was financed by the Natural Environment Research Council, UK (GR3/09626). Sarah Randolph was supported by the Royal Society and the Wellcome Trust.

References

Brittas, R., Marcström, V., Kenward, R.E. & Karlbom, M. 1992: Survival and breeding success of reared and wild ring-necked pheasants in Sweden. - Journal of Wildlife Management 56: 368-376.

Brown, C.R. & Brown, M.B. 1986: Ectoparasitism as a cost of coloniality in cliff swallows (Hirundo pyrrhonata). - Ecology 67: 1206-1218.

Brown, C.R., Brown, M.B. & Rannala, B. 1995: Ectoparasites reduce long-term survival of their avian host. - Proceedings of the Royal Society, London B 262: 313-319.

Bunck, C.M., Chen, C. & Pollock, K.H. 1995: Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. - Journal of Wildlife Management 59: 790-794.

Chapman, B.R. & George, J.E. 1991: The effects of ectoparasites on cliff swallow growth and survival. - In: Loye, J.E. & Zuk, M. (Eds.); Bird-Parasite Interactions: Ecology, evolution and behaviour. Oxford University Press, pp. 69-92.

Clayton, D.H. 1991a: Coevolution of avian grooming and ectoparasite avoidance. - In: Loye, J.E. & Zuk, M. (Eds.); Bird-Parasite Interactions: Ecology, evolution and behaviour. Oxford University Press, pp. 258-289.

Clayton, D.H. 1991b: The influence of parasites on host sexual selection. - Parasitology Today 7: 329-324.

Clayton, D.H. & Moore, J. 1997: Host-Parasite Evolution. General principles and avian models. - Oxford University Press, 473 pp.

Cotgreave, P. & Clayton, D.H. 1994: Comparative analysis of time spent grooming by birds in relation to parasite load. - Behaviour 131: 171-187.

Craine, N.G., Randolph, S.E. & Nuttall, P.A. 1995: Seasonal variation in the role of grey squirrels as hosts of Ixodes ricinus, the tick vector of the Lyme disease spirochaete, in a British woodland. - Folia Parasitologica 42: 73-80.

Daniels, T.J., Fish, D. & Schwartz, I. 1993: Reduced abundance of Ixodes scapularis (Acari: Ixodidae) and Lyme disease risk by deer exclusion. - Journal of Medical Entomology 30: 1043-1049.

Duffy, D.C. 1983: The ecology of tick parasitism on densely nesting Peruvian seabirds. - Ecology 64: 110-119.

Elliott, M. 1977: Synthetic Pyrethroids. - American Chemical Society Symposium Series No. 42, 241 pp.

Feare, C.J. 1976: Desertion and abnormal development in a colony of sooty terns Sterna fuscata infested by virus-infected ticks. - Ibis 118: 112-115.

Gray, J.S., Kahl, O., Janetzki, C. & Stein, J. 1992: Studies on the ecology of Lyme disease in a deer forest in County Galway, Ireland. - Journal of Medical Entomology 29: 915-920.

Gray, J.S., Kahl, O., Robertson, J.N., Daniel, M., Estrada-Pena, A., Gettinby, G., Jaenson, T.G.T., Jensen, P., Jongejan, F., Korenburg, E., Kurtenbach, K. & Zeman, P. 1998: Lyme borreliosis habitat assessment. - Zentralblatt fur Bakteriologie 287: 211-228.

Greenberg, R.E., Etter, S.L. & Anderson, W.L. 1972: Evaluation of proximal primary feather criteria for ageing wild pheasants. - Journal of Wildlife Management 36: 700-705.

Hill, D. & Robertson, P. 1988: The Pheasant: Ecology, Management and Conservation. - Blackwell Scientific Publications Professional Books, 281 pp.

Hoodless, A.N., Draycott, R.A.H., Ludiman, M.N. & Robertson, P.A. 1999: Effects of supplementary feeding on territoriality, breeding success and survival of pheasants. - Journal of Applied Ecology 36: 147-156.

Hoodless, A.N., Kurtenbach, K., Nuttall, P.A. & Randolph, S.E. 2002: The impact of ticks on pheasant territoriality. - Oikos 96: 245-250.

Hoodless, A.N., Kurtenbach, K., Peacey, M., Nuttall, P.A. & Randolph, S.E. 1998: The role of pheasants as hosts for ticks and Lyme disease spirochaetes in southern England. - Gibier Faune Sauvage 15: 477-489.

Hudson, P.J. 1986: The effect of a parasitic nematode on the breeding production of red grouse. - Journal of Animal Ecology 55: 85-92.

Hudson, P.J. & Dobson, A.P. 1991: Control of parasites in natural populations: nematode and virus infections of red grouse. - In: Perrins, C.M., Lebreton, J-D. & Hirons, G.J.M. (Eds.); Bird Population Studies. Oxford University Press, pp. 413-432.

Janovy, J. Jr. 1997: Protozoa, helminths and arthropods of birds. - In: Clayton, D.H. & Moore, J. (Eds.); Host-Parasite Evolution. General principles and avian models. Oxford University Press, pp. 303-337.

Kaplan, E.L. & Meier, P. 1958: Nonparametric estimation from incomplete observations. - Journal of the American Statistical Association 53: 457-481.

King, K.A., Blankinship, D.R. & Paul, R.T. 1977: Ticks as a factor in the 1975 nesting failure of Texas brown pelicans. - Wilson Bulletin 89: 157-158.

King, K.A., Keithe, J.O. & Mitchell, G.A. 1977: Ticks as a factor in nest desertion of California brown pelicans. - Condor 79: 507-509.

Kurtenbach, K., Carey, D., Hoodless, A., Nuttall, P.A. & Randolph, S.E. 1998: Competence of pheasants as reservoirs for Lyme disease spirochaetes. - Journal of Medical Entomology 35: 77-81.

Kurtenbach, K., Peacey, M., Rijpkema, S.G.T., Hoodless, A.N., Nuttall, P.A. & Randolph, S.E. 1998: Differential transmission of the genospecies of Borrelia burgdorferi sensu lato by game birds and small rodents in England. - Applied and Environmental Microbiology 64: 1169-1174.

Laurenson, M.K., Hudson, P.J., McGuire, K., Thirgood, S.J. & Reid, H.W. 1997: Efficacy of acaricidal tags and pouron as prophylaxis against ticks and louping ill in red grouse. - Medical and Veterinary Entomology 11: 389-393.

Lawes Agricultural Trust 1993: Genstat 5 Release 3 Reference Manual. - Oxford University Press, 812 pp.

Leif, A.P. 1994: Survival and reproduction of wild and pen-reared ring-necked pheasant hens. - Journal of Wildlife Management 58: 501-506.

Møller, A.P. 1990: Effects of parasitism by the haematophagous mite on reproduction in the barn swallow. - Ecology 71: 2345-2357.

Møller, A.P. 1993: Ectoparasites increase the cost of reproduction in their hosts. - Journal of Animal Ecology 62: 309-322.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.

Randolph, S.E. 1975: Patterns of distribution of the tick Ixodes trianguliceps Birula on its hosts. - Journal of Animal Ecology 44: 451-474.

Richner, H., Opplinger, A. & Christe, P. 1993: Effect of an ectoparasite on the reproduction of great tits. - Journal of Animal Ecology 62: 703-710.

Robertson, P.A. 1991: Estimating the nesting success and productivity of British pheasants Phasianus colchicus from nest-record schemes. - Bird Study 38: 73-79.

Sotherton, N.W. 1991: Conservation headlands: a practical combination of intensive cereal farming and conservation. - In: Firbank, L.G., Carter, N., Derbyshire, J.F. & Potts, G.R. (Eds.); The Ecology of Temperate Cereal Fields. - Blackwell Scientific Publications, Oxford, pp. 373-397.

SPSS Inc. 1999: SYSTAT 9. - SPSS Inc., Chicago.

Stafford, K.C. III 1993: Reduced abundance of Ixodes scapularis (Acari: Ixodidae) with exclusion of deer by electric fencing. - Journal of Medical Entomology 30: 86-996.

Tapper, S. 1999: A Question of Balance. Game animals and their role in the British countryside. - The Game Conservancy Trust, Fordingbridge, 288 pp.

Wilson, K. & Grenfell, B.T. 1997: Generalized linear modelling for parasitologists. - Parasitology Today 13: 33-38.

Wilson, M.L., Telford, S.R. III, Piesman, J. & Spielman, A. 1988: Reduced abundance of immature Ixodes dammini (Acari: Ixodidae) following elimination of deer. - Journal of Medical Entomology 25: 224-228.

Woodburn, M. 1995: Do parasites alter pheasant breeding success? - Game Conservancy Annual Review 26: 96-97.

Woodburn, M.I.A. 1999: Comparative population dynamics of wild and reared pheasants (Phasianus colchicus). - Unpubl. PhD thesis, University of Southampton, 237 pp.