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Fitting Models of Multiple Hypotheses to Partial Population Data: Investigating the Causes of Cycles in Red Grouse

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ABSTRACT: There are two postulated causes for the observed periodic fluctuations (cycles) in red grouse (*Lagopus lagopus scoticus*). The first involves interaction with the parasitic nematode *Trichostrongylus tenuis*. The second invokes delayed regulation through the effect of male aggressiveness on territoriality. Empirical evidence exists to support both hypotheses, and each hypothesis has been modeled deterministically. However, little effort has gone into looking at the combined effects of the two mechanisms or formally fitting the corresponding models to field data. Here we present a model for red grouse dynamics that includes both parasites and territoriality. To explore the single and combined hypotheses, we specify three versions of this model and fit them to data using Bayesian state-space modeling, a method that allows statistical inference to be performed on mechanistic models such as ours. Output from the three models is then examined to determine their goodness of fit and the biological plausibility of the parameter values required by each to fit the population data. While all three models are capable of emulating the observed cyclic dynamics, only the model including both aggression and parasites does so under consistently realistic parameter values, providing theoretical support for the idea that both mechanisms shape red grouse cycles.

Keywords: aggressiveness, Bayesian statistics, cyclic population dynamics, *Lagopus lagopus scoticus*, state-space modeling, *Trichostrongylus tenuis*.

Introduction

Periodic fluctuations (cycles) in populations attract considerable research from both empiricists and theoreticians (Berryman 2002; Turchin 2003). This is partly due to the lack of a single unifying theory for the causes of cycles, which has meant that mechanisms must be postulated for each species separately. Other species' cycles can only pro-

vide a backdrop of information from which to develop possible hypotheses, creating ever-opening avenues of new research. To make things more difficult, competing explanations for population cycles are abundant and, often, equally well supported by both theoretical and empirical data. Even broad generalizations about population cycles are difficult to make. Almost all studies on cyclic species have invoked extrinsic mechanisms to create periodic fluctuations. However, there is a single species, the red grouse (*Lagopus lagopus scoticus*), whose population cycles can be driven by an intrinsic mechanism (Turchin 2003).

Although the statistical properties of cycles in red grouse have been studied for many decades (Moran 1952; Haydon et al. 2002), the cause of fluctuations has been a topic of considerable debate. Several mechanisms, such as food quality or maternal nutrition, have been postulated to explain the cycles, and most have been ruled out (Hudson 1992). Only two hypotheses remain: the intrinsic "territorial-behavior hypothesis" (Moss et al. 1996; Matthiopoulos et al. 1998, 2003, 2005; Mougeot et al. 2003a) and the extrinsic "parasite hypothesis" (Dobson and Hudson 1992; Hudson 1992; Hudson et al. 1992b). There is empirical and theoretical support for both (Dobson and Hudson 1992; Hudson 1992; Hudson et al. 1992a, 1992b, 1998; Matthiopoulos et al. 1998, 2000, 2002, 2003; Mougeot et al. 2005a, 2003a), thereby providing fuel for a long-running debate.

Red grouse population densities are driven by cock territory numbers. Cocks that fail to establish territories in the autumn suffer considerably greater overwinter mortality than do territory-holding cocks (Jenkins et al. 1967; Watson 1985). According to the territorial-behavior hypothesis, fluctuations in aggressiveness result in varying levels of juvenile recruitment into the territorial population. Theory and experiments have shown that the interactions between aggressiveness, recruitment, and density can cause instability in red grouse populations. High aggressiveness occurs at peak grouse densities, reducing re-

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cruitment. This decreases the population density, lowering aggressiveness and allowing recruitment to rise (Moss et al. 1996; Matthiopoulos et al. 2003, 2005; Mougeot et al. 2003a).

In contrast, according to the parasite hypothesis, the nematode *Trichostrongylus tenuis* reduces the grouse's chick-rearing success (Dobson and Hudson 1992). The number of successfully reared chicks is lower in birds with higher parasite burdens (Hudson 1992; Hudson et al. 1998; Newborn and Foster 2002). While there is evidence that increased parasite burdens make adult grouse more vulnerable to predation, these burdens have the same effect on grouse population size as random predation (Hudson et al. 1992a), so parasite burdens do not increase adult grouse mortality. Theory and experiments have shown that the interactions between parasites and population density can also cause instability in red grouse populations, although parasites are not a requirement for cycles (Moss et al. 1993; Redpath et al. 2006). As rearing rate is reduced, so are the numbers of young available for recruitment, causing grouse density to decline. As host numbers decline, so does the transmission rate, decreasing the average parasite burdens. With fewer parasites, grouse rear more young, resulting in increased grouse density. *Trichostrongylus tenuis* affects autumn population densities by limiting the number of young reared per pair, so its influence is not gender specific.

Recent research indicates a connection between aggressiveness and parasite load (Fox and Hudson 2001; Mougeot et al. 2005b, 2006; Seiwright et al. 2005; Redpath et al. 2006), giving rise to a combined hypothesis. Experiments have shown that parasites ultimately reduce territorial behavior in male red grouse (Fox and Hudson 2001; Mougeot et al. 2005b). Further experiments have shown that increased aggressiveness leads to high parasite intensities (Seiwright et al. 2005). The relationship between aggression and parasites can also be seen in comb size, which can be used as a proxy for aggression: cocks with larger combs are more likely to gain territories. The larger comb may also be an indication of higher levels of immunocompetence, making cocks better able to cope with high levels of parasites (Mougeot and Redpath 2004).

Matthiopoulos et al. (2007) demonstrated the effect of different model assumptions regarding the cause of red grouse cycles on the interactions between the grouse and a generalist predator, the hen harrier (*Circus cyaneus*). They found that some predictions were robust to model and parameter uncertainty, while others, such as the maximum effect of harrier predation, were not. These differences highlighted the importance of model choice and specification, but comparisons could only be made between single-mechanism models (intrinsic, extrinsic, and a general phenomenological model) because no theoretical form of the combined hypothesis existed. The exact nature

of the interaction between aggressiveness and parasites is still not completely understood, making it difficult to explicitly include it in any model. However, the abilities of aggressiveness and parasites to act simultaneously in red grouse populations is unquestionable. Until now, deterministic models have aimed to uncover necessary and sufficient mechanisms for cyclic behavior. Yet finding out how these determine the detailed shapes of the cycles is an equally legitimate next question. This question can be answered by confronting with field data a model in which both of these influential mechanisms coexist. In this article, we develop and validate such a model.

We begin by specifying three specific versions of a general model: aggressiveness only, parasites only, and a combination of the two. All three models are implemented in a state-space estimation framework, enabling us to integrate them with data while incorporating observation uncertainty and systematic stochasticity (Buckland et al. 2007). We describe our implementation and the specification of the necessary Bayesian priors. We then explore the ability of each of the three models to fit the observations from a multiannual, replicated field study in southern Scotland. We compare the three models on the bases of their abilities to recreate the observed dynamics and the biological plausibility of the estimated parameter values. Finally, we place our results in the wider context of population ecology and grouse management.

Model Development

Aggressiveness

Aggressiveness in grouse cocks affects population density by limiting the number of juvenile cocks that can be recruited into the territorial population. Aggressiveness and density are coupled because aggressiveness both modifies and is dependent on density. Furthermore, experiments have shown that aggressiveness depends on both current density and density in the previous year (Mougeot et al. 2005a, 2003b). These relationships were modeled on the basis of observations of within-year variation in aggressiveness by Matthiopoulos et al. (2003, 2005). With a longer time series, it is possible to map aggressiveness across years according to the function

$$a_t = \frac{\exp(\xi_0 + \xi_1 0.5G_{f,t} + \xi_2 0.5G_{f,t-1})}{1 + \exp(\xi_0 + \xi_1 0.5G_{f,t} + \xi_2 0.5G_{f,t-1})}, \quad (1)$$

where a_t is the aggressiveness index for year t , constrained to lie between 0 and 1, and G_f is autumn grouse density in years t and $t - 1$ before hunting and recruitment, both of which occur in the autumn. Only male birds contribute to aggressiveness; therefore, given the 1 : 1 sex ratio (Jen-

kins et al. 1963), autumn grouse density is halved in equation (1).

Parasites

The parasite *Trichostrongylus tenuis* reduces the ability of red grouse to rear their young (Newborn and Foster 2002). Changes in average *T. tenuis* burden (W_t) per bird must therefore be tracked from spring to spring, when grouse start breeding. Yearly changes in spring parasite load are due to parasite density in the previous year (Hudson 1992) and seasonal changes within a year, which must also be considered (McGladdery 1984; Shaw and Moss 1989).

Given a worm burden W in year t , an average number of eggs (E) are produced per worm. A percentage ν_s of these develop into infective larvae, which survive with probability ϕ_p . A portion of the infective larvae, ω , are then ingested by the adult grouse, where they establish as adult worms at the end of the summer. Assuming that no adult worms die between spring and autumn, the average autumn worm burden per bird ($W_{a,t}$) is

$$W_{a,t} = W_t(1 + E\nu_s\phi_p\omega). \tag{2}$$

Studies of *T. tenuis* have focused on estimating ν_s , ϕ_p , and ω values separately (Shaw et al. 1989; Dobson and Hudson 1992; Hudson et al. 1992b); we therefore refer to them individually in equation (2).

In the autumn, the parasite reproduces again. The proportion of eggs that develop into infective larvae (ν_t) is season specific, while the number of eggs produced (E), the larvae's survival (ϕ_p), and their ingestion and establishment in red grouse (ω) are not. Rather than establish as adult worms, the infective larvae that are ingested by the red grouse in autumn establish as arrested larvae. This gives the average number of arrested larvae in autumn per bird (A_t):

$$A_t = W_{a,t}E\nu_t\phi_p\omega. \tag{3}$$

Survival of the adult worms and arrested larvae occurs over the winter. While *T. tenuis* has been found in other game birds, the parasite's life cycle is direct, without any intermediate hosts (Hudson 1992), so the continued existence of the parasite depends on the grouse. Additionally, parasite burdens are heterogeneous in the host, so the removal of a few highly parasitized birds will have a disproportionately large effect on average worm burden (Hudson et al. 1992a). While the survival of parasites within a living bird is not affected by the death of another bird, the death does affect the average survival for the *T. tenuis* population, which is the parameter of interest. Thus, the average worm burden is affected by the grouse's overall

survival. However, adult and juvenile birds survive at different rates, with juvenile survival varying yearly (see eqq. [7], [8]). As a result, the combined overwinter survival of adult and juvenile grouse is handled in terms of the proportional change in grouse density from autumn (time t ; $G_{f,t}$) to spring (time $t + 1$; G_{t+1}):

$$\begin{aligned} \phi_{1,t} &= \frac{\exp[\delta_1 - \delta_0(G_{t+1}/G_{f,t})]}{1 + \exp[\delta_1 - \delta_0(G_{t+1}/G_{f,t})]}, \\ \phi_{w,t} &= \frac{\exp[\delta_w - \delta_0(G_{t+1}/G_{f,t})]}{1 + \exp[\delta_w - \delta_0(G_{t+1}/G_{f,t})]}, \end{aligned} \tag{4}$$

where δ_1 and δ_w are measures of survival rates in the absence of any effect of changing grouse densities for arrested larvae and adult worms, respectively, and δ_0 is a measure of the effect of grouse density on survival. The model, as presented here, tracks the average parasite burden per bird and not the distribution of parasites across individuals, and it assumes that the survival of arrested larvae and adult worms have logistic relationships with grouse survival and with the constant presence of red grouse.

After the winter, the surviving larvae come out of arrest and combine with the surviving adult worms to form the spring worm burden at time $t + 1$:

$$W_{t+1} = W_{a,t}\phi_{w,t} + A_t\phi_{1,t}. \tag{5}$$

Grouse

The punctuated nature of annual demographic events in a grouse population allows us to model its dynamics in discrete time. Given that the birds rarely disperse or establish far from their natal territory (Jenkins et al. 1967), we assume that the population is closed. There is also the assumption that a grouse population's boundary is defined by a feature of the natural habitat, such as farmland or pasture; this is often the case.

The discrete grouse model first suggested by Matthiopoulos et al. (2003) and generalized by Matthiopoulos et al. (2005) formalizes only the intrinsic hypothesis. The continuous model, developed by Dobson and Hudson (1992) and based on the prototype by Anderson and May (1978), examines the extrinsic hypothesis. To model both hypotheses simultaneously, we modified the model by Matthiopoulos et al. (2005) as follows: The state variable G_t refers to the spring breeding densities of both cocks and hens. The variable $G_{f,t}$ is used as shorthand for autumn density before hunting and recruitment:

$$G_{f,t} = G_t + 0.5G_t\lambda_p \tag{6}$$

where λ_t (eq. [9]) is the rearing rate per grouse pair and $G_t\lambda_t$ is multiplied by 0.5 because, while λ_t is per pair, spring grouse density (G_t) includes both sexes and must be halved. The modified model allows recruitment to vary with autumn cock density before territorial contests and hunting commence. When this autumn density is low, established cocks will not need to defend their territories against as many birds. Conversely, large numbers of young cocks mean that adult males are more vigorous in their defense, increasing aggressiveness even when adult cock density is low:

$$G_{t+1} = \left[\phi_a + 2 \frac{0.25\lambda_t}{1 + (\kappa a_t 0.5 G_{t,t})} \right] G_t, \quad (7)$$

where κ regulates the strength of the density dependence and the territory density (which is set at 0.1 by Matthiopoulos et al. [2007]). The equation tracks male and female densities, but recruitment during the territorial contest depends on only the males, so autumn density ($G_{t,t}$) is multiplied by 0.5. As in equation (6), the rearing rate (λ_t) is multiplied by 0.5 to convert spring density (G_t) to pairs. Additionally, recruitment acts directly on only the male young, so λ_t is multiplied by 0.5 again, resulting in a constant of 0.25, which is the number of male young reared per pair. The number of males recruited into the population is doubled to account for the hens with which they will pair.

Juvenile survival is equivalent to the recruitment of young cocks into the territorial population:

$$\phi_j = \frac{1}{1 + (\kappa a_t 0.5 G_{t,t})}. \quad (8)$$

The rearing rate (λ_t) per pair has also been modified to allow for yearly variation due to fluctuating spring parasite burdens:

$$\lambda_t = \exp(\gamma_0 - \gamma_1 W_t), \quad (9)$$

where γ_0 is the natural log of red grouse brood size and γ_1 measures the effect of the average worm burden on reducing the size of the brood reared.

Stochasticity was added to the model by assigning distributions to the rearing rate, adult survival, and recruitment of red grouse. For the rearing rate, we have a Poisson distribution:

$$R_t \sim \text{Poisson}(\lambda_t), \quad (10)$$

where R_t is the number of young reared per pair in year

t . The number of juvenile males recruited and the number of surviving adults were drawn from a binomial distribution:

$$\begin{aligned} G_{a,t} &\sim \text{binomial}(G_t, \phi_a), \\ G_{j,t} &\sim \text{binomial}(G_{m,t}, \phi_{j,t}), \end{aligned} \quad (11)$$

where $G_{a,t}$ and $G_{j,t}$ are the number of adults (of both genders) and juvenile cocks to survive the winter of year t , respectively, and $G_{m,t}$ is the number of male young reared in year t .

The observation model for red grouse accounted for the fact that the gamekeepers observed only a proportion p_t of the grouse present, according to the effort (number of drives, d_t) put into counting the grouse in year t :

$$p_t = \frac{d_t}{d_t + c}, \quad (12)$$

where c is a constant to be estimated. The red grouse observations were modeled as a binomial distribution, which was approximated using a normal distribution with the same mean and variance:

$$\begin{aligned} \mu_t &= G_{t,t} p_t, \\ \sigma_t^2 &= G_{t,t} p_t (1 - p_t), \\ G_{\text{Obs},t} &\sim N(\mu_t, \sigma_t^2). \end{aligned} \quad (13)$$

Model Fitting

Data

The data used for model fitting came from Langholm Estate in southern Scotland during the period 1975 to 1996. Each autumn, gamekeepers with trained dogs undertook population counts of grouse before shooting. The estate was divided into six beats (areas of the estate managed by different gamekeepers); data are available from four of these (referred to as LC, LD, LM, and LR). The counts represent a proportion of the grouse on the estate. The proportion observed is thought to vary between beats and with the amount of annual effort. From 1993, hen harriers were known to be nesting on the estate in numbers large enough to impact grouse density. Thus, data collected after 1992 are excluded from the analysis to avoid confounding by the effects of predation on grouse cycles (Redpath and Thirgood 1997; Thirgood et al. 2000).

The data from Langholm Estate lack any numerical information regarding aggressiveness and parasites. However, the caeca of some birds that were shot were checked during

the study, confirming the presence of *Trichostrongylus tenuis*. Similarly, while no data on aggressiveness were collected, agonistic encounters between territorial cocks were repeatedly observed (Redpath and Thirgood 1997).

Statistical Methods

The data and equations for the grouse population dynamics were fitted in a state-space model. State-space models describe the evolution of two parallel processes known as the state and observation processes (Newman et al. 2006). In our case, the state process encompasses the biological mechanisms defining how grouse density, parasite burdens, and male aggressiveness change from time t to time $t + 1$. The observation process utilizes the data, matching its components to the components of the state process. The observation model allows us to account for the impact of observation bias and imprecision on the data used for fitting (Buckland et al. 2004).

An advantage of state-space modeling is that not all of the components of the state process have to be directly observed. The method can incorporate unobserved, hidden states (Newman et al. 2006), which allows for the estimation of aggression levels and parasite burdens despite the lack of data.

We fitted our state-space models within a Bayesian framework, which allows for previous biological knowledge to be incorporated into the analysis. Such knowledge takes the form of probability distributions for the model's parameters, referred to as "priors." The result of updating our prior knowledge with data via the model is a posterior belief, which is also a probability distribution known as the "posterior." All inferences about the states and parameters are made from the posterior, which provides a direct measure of the degrees of uncertainty around the parameters or states being estimated (Ellison 2004; McCarthy 2007).

Equations (1)–(9) were fitted to the data in WinBUGS 1.4.2 using BlackBox Component Builder 1.5, which employs Markov chain Monte Carlo (MCMC) methods (Spiegelhalter et al. 2007). MCMC is a computer-intensive algorithm often used in conjunction with Bayesian models. This algorithm draws samples from a distribution via Monte Carlo integration using a Markov chain such that the draw at time t depends solely on that at time $t - 1$. Ideally, the chain will eventually converge to a stationary distribution that is no longer dependent on the starting point assumed for the parameter values or the number of iterations run. This is used as an approximation of the posterior distribution. The sample averages from the distribution form the expected values for the parameters and states of interest. Convergence on the stationary distri-

bution is usually determined visually or through the use of convergence diagnostics (Gilks et al. 1996).

Given the lack of data, two approaches were taken to estimate the parameters of the parasite and aggression models. In the case of the *T. tenuis* model, parameter values were found in the published literature (Gibbs 1986; Shaw et al. 1989; Dobson and Hudson 1992; Hudson 1992; Hudson et al. 1992*b*; Hudson and Dobson 1997) that coincided with those parameters used in the model (table 1). The only parameter for the parasite model that lacked any estimate from earlier research was δ_0 , the effect of changing grouse density on the survival of the parasitic nematode.

Our aggression model does not have an equivalent theoretical form in the published literature. Therefore, simulations were run over a wide spread of parameter values to determine a range of values for ξ_0 , ξ_1 , and ξ_2 , as well as for δ_0 , that were capable of producing biologically realistic cycles. Cycles were deemed biologically realistic if the predicted grouse densities and parasite burdens did not exceed the highest published values for these states. The ranges of values capable of creating realistic population dynamics were then used to determine the ranges of uniform priors (table 1).

For the parameters γ_0 and γ_1 , it was possible to use information available in the published literature to choose weakly informative means and variances for the priors in the grouse population model. Where the available information was limited or conflicting, priors were based solely on biological realism, such as the use of a beta prior on the survival parameters to constrain the values between 0 and 1. All parameter priors are listed in table 1.

To account for variations in habitat quality between the four beats and the mostly sedentary nature of the red grouse, parameters related to demography (ϕ_a , γ_0 , and γ_1) were assumed to be beat specific. However, the parameters pertaining to aggressiveness and parasites (ξ_0 , ξ_1 , ξ_2 , and δ_0) were assumed to be beat independent, since these responses should apply to the entire species (Lambin et al. 2006).

A weak prior was chosen for the observation constant c (table 1). This was because, while we are not explicitly defining a prior for p_p , the value is calculated using an estimated parameter (c), which results in the presence of an implicit prior for p_p . The prior for c was therefore chosen to result in a reasonable implicit prior for p_p defined as a unimodal distribution for p_i for all levels of effort (d_i).

To compare the intrinsic and extrinsic hypotheses, three models were run. The first, as presented in equation (7), incorporated both hypotheses. In the other two models, we switched off the effects of either parasites or aggressiveness as follows: in the case of the intrinsic model, the rearing rate (λ_i) was modified to be a constant that is dependent solely on γ_0 , the brood size of red grouse (see

Table 1: Parameters in the three models and their definitions, values, and priors

Symbol	Definition	Value	Prior
E	Average number of eggs produced per worm	20,000	NA
ν_s	Percentage of <i>Trichostrongylus tenuis</i> eggs that develop into infective larvae in the spring	.001	NA
ν_f	Percentage of <i>T. tenuis</i> eggs that develop into infective larvae in the fall	.0156	NA
ϕ_p	Infective larvae survival	.66	NA
ω	Proportion of infective larvae ingested by grouse	.025	NA
δ_i	Measure of the survival rate of infective larvae	0	NA
δ_w	Measure of the survival rate of adult worms	-.66	NA
κ	Strength of density dependence	.1	NA
δ_0	Effect of overall grouse survival on parasite survival	NA	Uniform (0, 6)
γ_0	Natural log of average brood size	NA	Normal (0, 10)
γ_1	Effect of average worm burden on average brood size	NA	Gamma (1, 50)
ξ_0	Intercept parameter for the aggression model	NA	Uniform (-4, -2)
ξ_1	Effect of grouse density in time t on aggression	NA	Uniform (0, .002)
ξ_2	Effect of grouse density in time $t - 1$ on aggression	NA	Uniform (.005, .04)
ϕ_a	Adult cock survival	NA	Beta (1, 1)
ϕ_j	Juvenile cock survival	NA	Beta (1, 1) ^a
c	Observation constant	NA	Gamma (15, 2)
G_t	Spring grouse density (km^{-2}) in time t	NA	NA
$G_{f,t}$	Autumn grouse density (km^{-2}) in time t , before hunting and recruitment	NA	NA
$G_{a,t}$	Adult cock density (km^{-2}) in time t	NA	NA
$G_{j,t}$	Juvenile cock density (km^{-2}) in time t	NA	NA
$G_{m,t}$	Male young (km^{-2}) reared in time t	NA	NA
$G_{\text{Obs},t}$	Observed autumn grouse density in time t	NA	NA
λ_t	Rearing rate per grouse pair in time t	NA	NA
a_t	Aggression index for time t	NA	NA
W_t	Average spring worm burden per bird in time t	NA	NA
$W_{a,t}$	Average autumn worm burden per bird in time t	NA	NA
A_t	Average number of arrested larvae per bird in autumn	NA	NA
d_t	Amount of gamekeeper effort (drives) in time t	^b	NA
R_t	Stochastic realization of λ_t	NA	NA
p_t	Proportion of grouse observed in time t	NA	NA

Note: NA = not applicable.

^a Extrinsic model only.

^b Value varies from year to year and beat to beat.

eq. [9]). For the extrinsic hypothesis, juvenile survival (ϕ_j) was estimated as a constant with a beta (1, 1) prior, instead of allowing it to vary from year to year with autumn cock density and aggression.

Model selection is usually achieved through information criteria, for example, the Akaike Information Criterion or Bayesian equivalents, such as the deviance information criterion (DIC), which uses the posterior mean deviance, or the Bayesian information criterion (BIC). The BIC is not appropriate here, since the models are hierarchical and the effective number of parameters is not known (Spiegelhalter et al. 2002). However, the DIC also fails to be applicable, since it can result in negative dimensionality when used in conjunction with models involving missing data (Celeux et al. 2006). Given our lack of data on aggressiveness and parasites, the models for the different

hypotheses were compared in three ways. First, the model-fitting diagnostics were examined to assess convergence and mixing. While these cannot be used to select between the hypotheses, inference from a model that displays poor mixing and/or convergence would be questionable. Second, we looked at the model estimates for grouse density to determine whether they were cyclic. Finally, we compared a selection of estimated model parameters with those available in the literature to determine whether the models are capable of creating cyclic dynamics under biologically realistic circumstances.

Results

Each model took 3–6 hours to run three chains for 100,000 iterations using a 3.2-GHz processor. A burn-in of 10,000

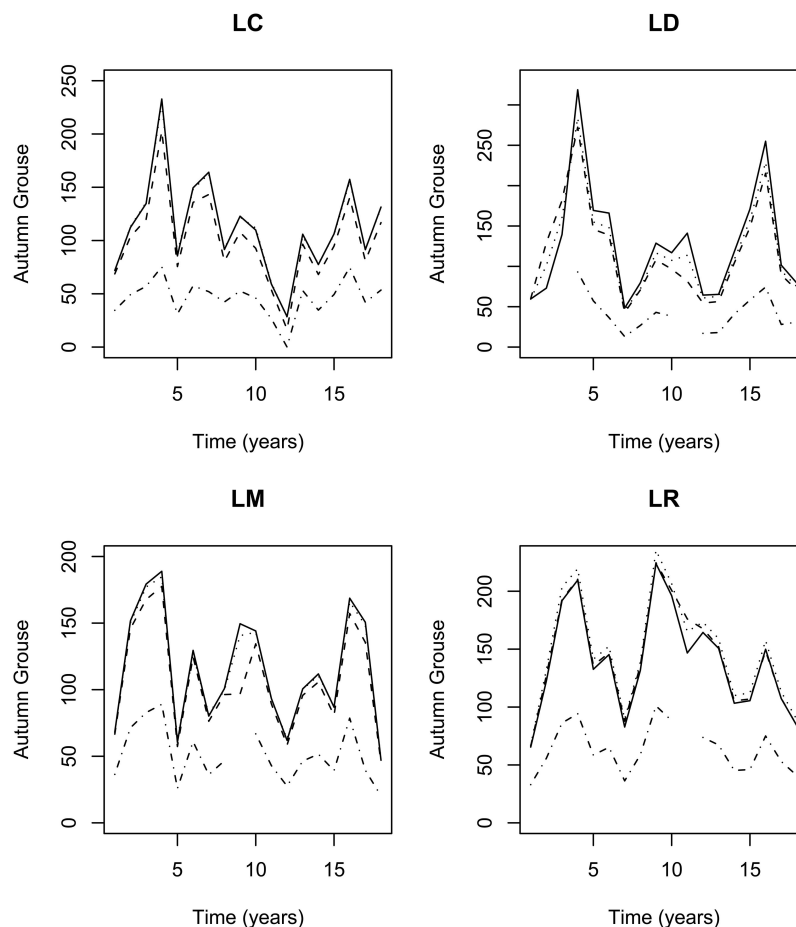


Figure 1: Estimated density of red grouse (km^{-2}) in autumn on each of four beats on Langholm Estate (LC, LD, LM, and LR), from 1975 to 1992, for the combined (solid line), intrinsic (dotted line), and extrinsic (dashed line) models, as compared with the observed data (dotted-dashed line).

iterations was used, and only every tenth iteration was retained to reduce serial autocorrelation between MCMC trials. Time-series plots were used to assess mixing, and the Gelman-Rubin statistic was used as a quantitative diagnostic to assess the convergence of multiple chains to a target distribution (Brooks and Roberts 1998).

The parameters for which it was possible to use informative priors based on previous biological knowledge (γ_0 , γ_1 , ϕ_a , and c) were robust to the choice of prior. Given the lack of data to fit to the aggression and parasite models, it is not surprising that the associated parameters (ξ_0 , ξ_1 , ξ_2 , and δ_0) showed prior sensitivity (app. A in the online edition of the *American Naturalist*). We avoided choosing arbitrary parameter values by providing informative priors with a range of values capable of creating biologically realistic dynamics.

Intrinsic Model

The red grouse model, in the absence of *Trichostrongylus tenuis*, displayed cyclic behavior on all four monitored beats, starting during a cyclic increase and ending in a decline phase. Spring and fall population densities followed the same pattern, with autumn density being higher than spring density (figs. 1, 2). Aggressiveness peaked with, or just after, peak autumn densities, remaining high during the initial decline phase and only later allowing grouse densities to increase (fig. 3). The intrinsic model converged for all tracked parameters and states. Overall, the model displayed good mixing, although for some states, such as adult grouse density on beat LC and most of the estimates for the number of young reared per pair, mixing was generally poor in comparison to the other models.

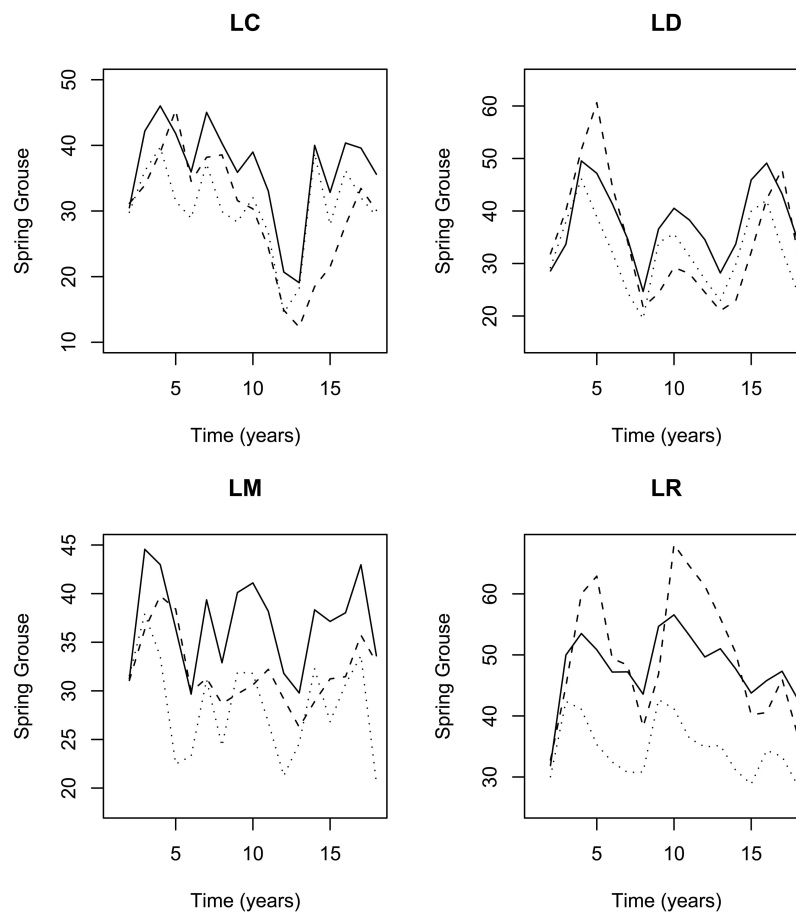


Figure 2: Estimated density of red grouse (km^{-2}) in the spring on each of four beats on Langholm Estate (LC, LD, LM, and LR), from 1976 to 1992, for the combined (solid line), intrinsic (dotted line), and extrinsic (dashed line) models.

Extrinsic Model

The extrinsic model followed a pattern similar to that of the intrinsic model, with evidence of cyclic behavior in both the spring and fall densities of red grouse (figs. 1, 2). The predicted parasite densities lagged behind spring grouse densities, peaking just after grouse reached their peak and remaining low during the initial increase phase of grouse cycles (fig. 4). The predicted values for the worm burdens were comparable across the beats and remained within the biologically realistic bounds of 6–24,850 worms per grouse (Shaw 1988). The model converged for all tracked parameters and states. However, mixing for years 2 and 3 on beat LD was relatively poor for adult, juvenile, chick, and autumn density, as was mixing for adult (ϕ_a) and juvenile (ϕ_j) survival in all beats except beat LC. Otherwise, the model displayed good mixing for most parameters and states.

Combined Model

The combined model showed cyclic behavior. Aggression peaked with, or just after, peak autumn densities, and parasites peaked just after peak spring densities (figs. 3, 4). Both aggression and parasite burden remained high through the initial decline phase of the cycle and crashed shortly after the crash in grouse density, remaining low during the initial growth phase of the grouse population cycle. Parasite burdens were not as consistent across the beats but remained biologically plausible (fig. 4). The combined model converged and displayed good mixing.

Model Comparison

The only parameters to appear in all three models were the natural log of brood size (γ_0), adult survival (ϕ_a), juvenile survival (ϕ_j), and the observation constant (c). The parameter estimates varied across the three models and

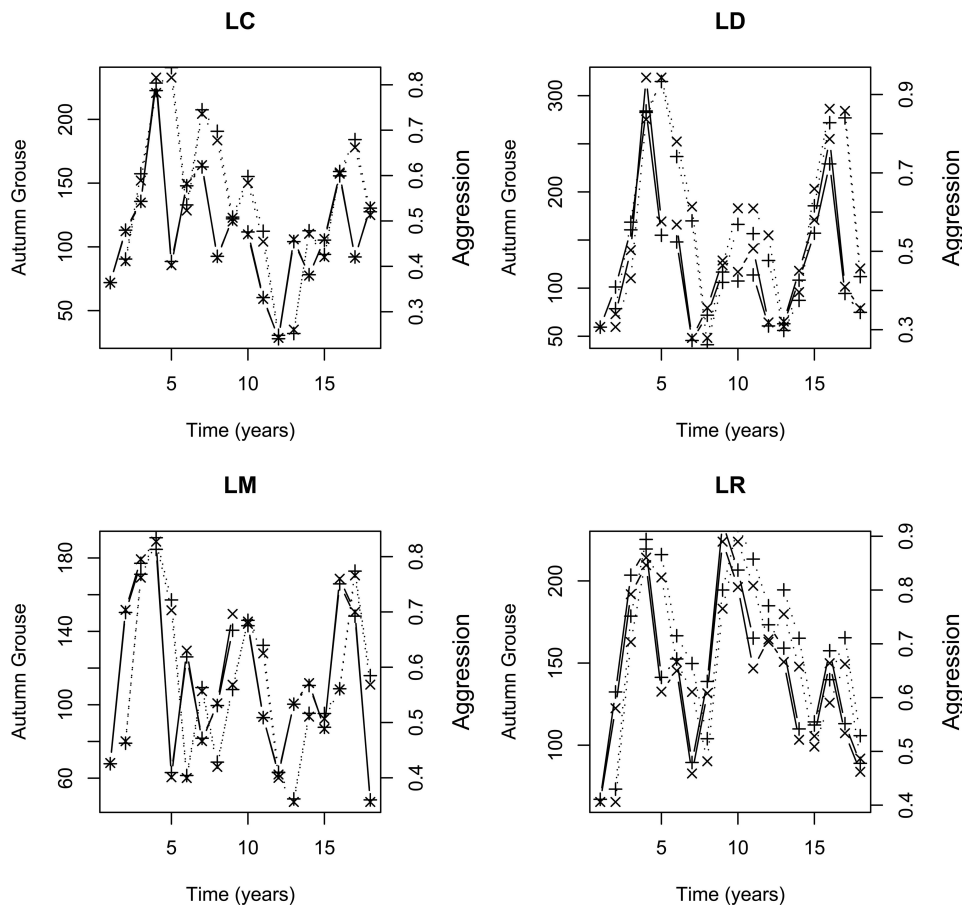


Figure 3: Relative timing of aggression (dotted line) and autumn grouse density (km^{-2} ; solid line) in the intrinsic (plus signs) and combined (crosses) models, in relation to each other, for each of the four beats on Langholm Estate (LC, LD, LM, and LR), from 1975 to 1992.

were compared with ranges of values published in earlier literature from estates in both Scotland and England (table 2). The range of adult survival across the beats was lowest in the intrinsic model (25%–44%) and highest in the extrinsic model (54%–76%). The combined model, whose values fell between those of the other two (50%–66%), was the only model to remain completely within the range of previous estimates for ϕ_a (34% [Jenkins et al. 1967] to 70% [Park et al. 2002]). The exponent γ_0 gave average brood size, which showed a pattern similar to that for ϕ_a : the range of brood size across the beats was lowest in the intrinsic model (5.4–6.9 chicks) and highest in the extrinsic model (6.7–18.8 chicks). The values estimated from the combined model fell between those of the other two models (6.2–9.8 chicks). Our estimates of γ_0 , while less variable than individual brood sizes, should fall between the lowest (one chick; Jenkins et al. 1963) and highest (12 chicks; Moss et al. 1981) observed individual broods. Only the estimates from the intrinsic and combined models were

below 12 chicks. Juvenile survival varied from year to year in the combined and intrinsic models according to changing levels of aggression and grouse density (eq. [8]). The estimates for the range of values across the beats from the intrinsic model (8%–75%) were almost identical to those from the combined model (7%–75%). Juvenile survival was a constant in the extrinsic model, with much lower and less variable estimates (10%–25%) across the beats, and fell below the previous estimate of 48% for ϕ_j (Hudson 1992). The estimates for the observation constant c varied among the three models but showed the same pattern in the relative values for the individual beats. Strong correlations existed between the parameters in the intrinsic and extrinsic models, but all the correlations in the combined model were weak (app. B in the online edition of the *American Naturalist*).

The parameter values for aggression (ξ_0 , ξ_1 , and ξ_2) were similar in the combined and intrinsic models. The estimates related to parasites (δ_0 and γ_1) varied slightly be-

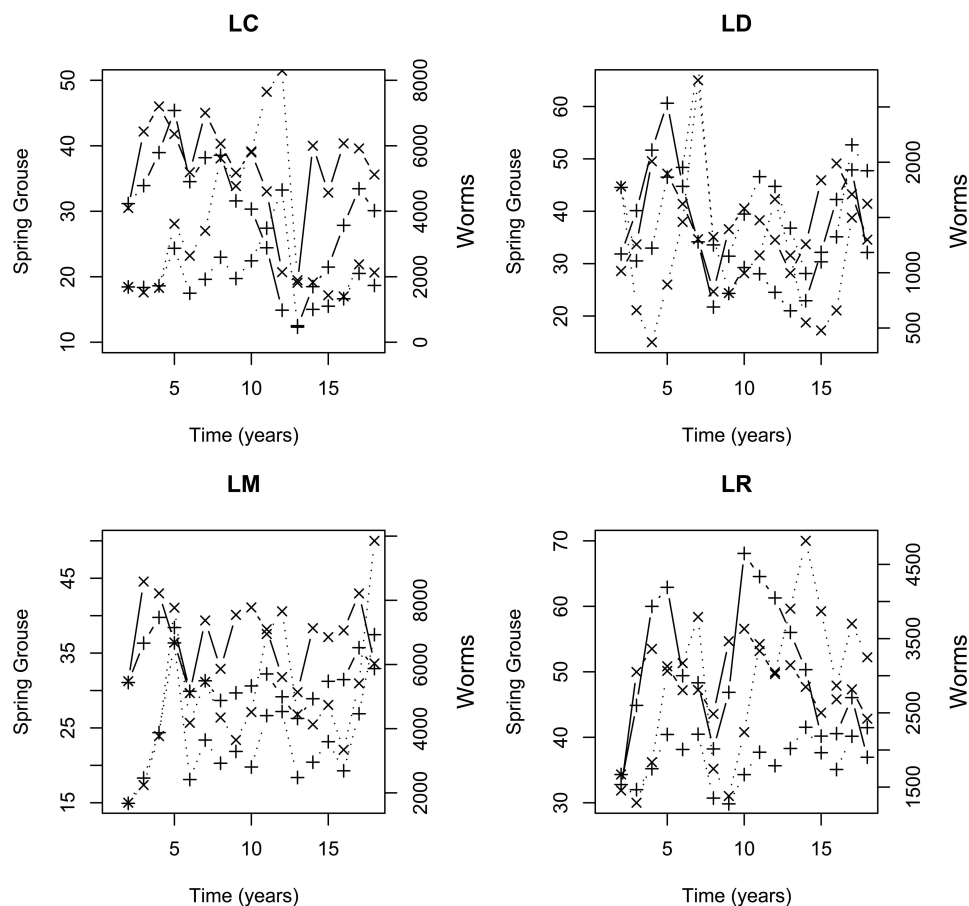


Figure 4: Relative timing of parasites (dotted line) and spring grouse density (km⁻²; solid line) in the extrinsic (plus signs) and combined (crosses) models, in relation to each other, for each of the four beats on Langholm Estate (LC, LD, LM, and LR), from 1976 to 1992.

tween the two models, with the values estimated by the combined model being slightly lower than those for the extrinsic model (table 2). Dobson and Hudson (1992) estimated the reduction in grouse fecundity per worm to be 5×10^{-4} . The estimates for γ_1 , the effect of *T. tenuis* on rearing rate, range from 2.8×10^{-4} to 3.8×10^{-3} across the two models. Given the lack of data on parasite burdens, the estimates of γ_1 were determined to fall within a reasonable range of the previously estimated value.

The autumn densities estimated by the three models were similar, and all matched key features of the data (fig. 1). The highest density estimates were provided by combined model, followed by the intrinsic model and then the extrinsic model, with exceptions for beats LD and LR. On beat LR, the intrinsic model estimated higher densities than the combined model for the entire time series.

Distinct differences among the models were observed in the estimated spring densities (fig. 2). The values estimated in each model for spring density showed few con-

sistent patterns in their relationship to the other models, although the intrinsic model consistently estimated spring densities that were lower than the combined model for all four beats. In contrast, the spring densities estimated by the extrinsic model showed no regular patterns in relation to the other two models. In comparison to the other models, spring density on beat LM had less of a tendency to cycle in the extrinsic model.

The estimates for aggression level were almost identical for the combined and intrinsic models (fig. 3). In contrast, *T. tenuis* burdens were higher for the combined model than for the extrinsic model for all beats except beat LD. While the average worm burden per bird showed the same pattern of increase and decrease for the two models, the estimated values varied appreciably between them (fig. 4).

Discussion

The need for parsimony and computational tractability have meant that single-factor hypotheses have, until now,

Table 2: Posterior means and their 95% confidence intervals for the parameter estimates, as well as their values from published literature

Parameter	Intrinsic	Extrinsic	Combined	Previous estimates
$\gamma_{0, LC}^a$	1.8 (1.1, 2.3)	2.8 (1.9, 3.9)	1.9 (1.3, 2.8)	0–2.5
$\gamma_{0, LC}^a$	1.7 (1.1, 2.3)	2.9 (1.8, 4.8)	2.3 (1.5, 2.9)	0–2.5
$\gamma_{0, LC}^a$	1.8 (1.2, 2.4)	2.5 (1.6, 3.5)	2.3 (1.5, 3.2)	0–2.5
$\gamma_{0, LC}^a$	1.9 (1.2, 2.6)	1.9 (.71, 3.2)	1.8 (1.02, 2.7)	0–2.5
$\phi_{a, LC}$.34 (.019, .67)	.66 (.46, .85)	.52 (.25, .69)	.34–.70 (.50, .83)
$\phi_{a, LD}$.39 (.079, .66)	.59 (.34, .95)	.54 (.32, .71)	.34–.70 (.50, .83)
$\phi_{a, LM}$.25 (.013, .61)	.76 (.49, .98)	.49 (.19, .69)	.34–.70 (.50, .83)
$\phi_{a, LR}$.44 (.11, .73)	.54 (.11, .89)	.66 (.43, .80)	.34–.70 (.50, .83)
$\phi_{j, LC}^b$.14 (.054, .25)		.48
$\phi_{j, LD}^b$.17 (.017, .30)		.48
$\phi_{j, LM}^b$.099 (.0083, .23)		.48
$\phi_{j, LR}^b$.25 (.046, .61)		.48
c_{LC}	6.7 (4.5, 9.3)	5.4 (3.5, 7.9)	6.7 (4.6, 9.3)	^c
c_{LD}	6.8 (3.9, 10.4)	6.2 (3.3, 10.1)	7.7 (4.7, 11.2)	^c
c_{LM}	5.8 (3.6, 8.4)	5.2 (3.2, 7.9)	5.8 (3.8, 8.2)	^c
c_{LR}	5.5 (3.4, 8.1)	5.1 (3.1, 7.6)	4.9 (3.1, 7.4)	^c
ξ_0	–2.3 (–3.0, –2.1)	^d	–2.3 (–2.9, –2.0)	^c
ξ_1	.014 (.0036, .019)	^d	.015 (.0042, .019)	^c
ξ_2	.032 (.014, .039)	^d	.029 (.0099, .039)	^c
δ_0	^d	5.7 (5.0, 5.9)	5.3 (4.4, 5.9)	^c
$\gamma_{1, LC}$	^d	1.1×10^{-3} (4.6×10^{-6} , 5.1×10^{-3})	2.9×10^{-4} (4.1×10^{-6} , 1.6×10^{-3})	5×10^{-4}
$\gamma_{1, LD}$	^d	3.8×10^{-3} (4.9×10^{-3} , 2.9×10^{-2})	1.3×10^{-3} (1.1×10^{-5} , 6.9×10^{-3})	5×10^{-4}
$\gamma_{1, LM}$	^d	4.7×10^{-4} (1.8×10^{-5} , 2.6×10^{-3})	3.1×10^{-4} (8.2×10^{-6} , 1.6×10^{-3})	5×10^{-4}
$\gamma_{1, LR}$	^d	3.4×10^{-4} (4.3×10^{-6} , 1.9×10^{-3})	2.8×10^{-4} (1.6×10^{-6} , 1.5×10^{-3})	5×10^{-4}

^a Values are on the log scale.
^b Estimates vary from year to year.
^c No previous estimate available.
^d Parameter does not appear in the model.

dominated the literature on population cycles (Berryman 2002; Turchin 2003). This is most apparent in the red grouse, where the choice between two single-factor hypotheses has also come to embody the debate on the relative importance of intrinsic and extrinsic population regulation. We have addressed this by formulating an initial model of a combined hypothesis.

A comparison of the proposed explanations requires that they be confronted with field observations. The assumptions inherent in the use of these hypotheses are supported by field observations (e.g., Hudson et al. 1992b; Mougeot et al. 2003b, 2006). We know from past theoretical work (Dobson and Hudson 1992; Matthiopoulos et al. 1998, 2000, 2002, 2003) that each of the two single-factor hypotheses can, under realistic ranges of parameters, generate cycles where period and amplitude are within the observed ranges. A more stringent test of the validity of the models is to fit them to data, since this enables us to express the quality of different models in likelihood terms and study the correlations between different parameters. This is the main contribution of this article.

All three models produced similar estimates of autumn density but differed in their estimates of spring density.

The intrinsic model estimated spring densities that were consistently lower than those from the combined model, but the extrinsic model showed no apparent pattern in its relationship to the other models. The variation in spring densities among the models resulted from a combination of differences in parameter estimates and the interactions between density, aggression, and parasite burdens.

The intrinsic model yields the smallest estimates of adult survival, resulting in low estimated spring densities. However, due to the absence of *Trichostrongylus tenuis* from that model, there is no reduction in the rearing rate. This allowed autumn densities to reach the same values as in the other models, despite the low brood size. Maintaining a relatively high autumn density produces aggression levels that are comparable with those of the combined model, resulting in more limited recruitment than would be expected from the spring densities alone. This reduction, combined with low adult survival, yields the low predictions of spring density for the intrinsic model.

In the extrinsic model, large brood size and high adult survival can produce high spring densities, but only when parasite burdens are low. Otherwise, low juvenile survival combines with the reduced rearing rate to suppress spring

density. Spring density impacts the estimates of *T. tenuis* levels, because the overall survival of grouse from autumn of year t to spring of year $t + 1$ affects parasite survival (eq. [4]). The spring parasite burden then modifies the rearing rate and thus the number of young that are available to be recruited into the next year's breeding population. The extrinsic model's different spring density estimates, combined with a slightly higher estimate for δ_0 , result in the difference in predicted parasite burdens between the combined and extrinsic models.

In the combined model, it is possible to observe the indirect impacts of both aggression and parasites. Autumn density controls aggression, determining the level of juvenile recruitment into the territorial population. Recruitment shapes grouse numbers, which affect parasite survival through changes in grouse density from autumn to spring. The shifting parasite burdens modify the rearing rate, impacting autumn density and aggression during the territorial contests. The estimates of adult survival and brood size are not as high as they are for the extrinsic model, but fluctuating juvenile survival can allow for greater recruitment into the population and thus higher spring densities in many cases.

All three models fitted the data well, and all are capable of creating cyclic dynamics. While good convergence and mixing do not indicate model appropriateness, inference is unreliable if convergence and mixing are poor. In our case, all the models converged on stationary distributions, but only the combined model displayed good mixing for all MCMC chains. This is likely due to the strong correlations between parameters in the intrinsic and extrinsic models, which can slow mixing (app. B). Slow mixing means that posterior densities may not accurately represent the target distribution, leading to questionable inference. However, outputs from multiple chains can be used to improve coverage of the parameter space.

Given that our first two methods of comparison—model diagnostics and the ability to create cycles—fail to show a distinct difference among the models, model choice is dependent on the biological plausibility of the parameter estimates. All three models generate fall grouse densities that fit the main features of the data (fig. 1; app. C in the online edition of the *American Naturalist*). However, only the combined model does so using biologically realistic parameter values. This may be due to the increased flexibility of the combined model. However, if the incorporation of both mechanisms leads to an overparameterized model, identifiability would tend to decrease, which may lead to an apparent lack of biological plausibility. On the contrary, the combined model was the only one to estimate biologically realistic parameter values in all cases, providing support for the combined hypothesis. High levels of uncertainty in the parameters, γ_0 in particular, may be due

to the lack of information regarding aggressiveness and parasites.

In contrast to earlier work that focused on management related to a single hypothesis, these results imply that efficient management of grouse populations requires that both aggression and parasites be taken into account. Managing only for parasites increases the rearing rate (Newborn and Foster 2002), eventually leading to increased aggression and continued cycles. If spring density is lowered to reduce the effects of aggression, parasite loads will still increase (Watson et al. 1988). The density manipulations will keep the grouse population from crashing, so transmission of *T. tenuis* will remain high. This will result in a reduced rearing rate and the eventual continuation of the cycles. Field studies to test the combined hypothesis employing both a reduction of spring density and treatment with anthelmintics to reduce parasites could be used to further test whether the combined hypothesis is the reason for persistent red grouse cycles. Such field tests could also be used to provide data to build a model for an interaction hypothesis, where the direct relationships between aggressiveness and parasites are taken into account. The additional information could also be used to construct a model for the parasites that accounts for the distribution of *T. tenuis* across individuals, rather than tracking the average worm burden per bird.

As well as suggesting further field experiments and increasing understanding of the red grouse population dynamics, the models could be used to directly assess the effects of different management plans on grouse populations. Predictions can be made under alternative management scenarios, such as the one suggested for the field experiment. By use of a Bayesian framework, the level of uncertainty around management decisions can be quantified, allowing for choices to be made on the basis of all the available information.

Although the models were fitted to data from the Langholm Estate, they could readily be applied to data from other grouse estates in the United Kingdom. Beat-specific demographic parameters (ϕ_a , ϕ_j , γ_0 , and γ_1), could be treated as region specific, giving the model the ability to account for spatial variations in grouse cycles. Additionally, weather can give some indication of outbreaks in the relative intensities of *T. tenuis* infections (Cattadori et al. 2005), and it can affect parasite recruitment (Moss et al. 1993). Therefore, the parasite model could be adapted to incorporate local weather data, which may also explain some of the observed regional differences in grouse cycles.

While the models presented here are specific to red grouse, the modeling approach can be easily adapted for other species. Ecologists are already familiar with the building of population models through the use of Leslie and Lefkovich matrices. This format provides an efficient

way to conceptualize state-space models (Buckland et al. 2004). Once the population model has been developed, fitting the model is relatively straightforward using freely available software. The modeling approach has advantages, such as the direct inclusion of uncertainty. However, priors are a double-edged sword, allowing previous biological knowledge to be incorporated into the analysis but still requiring specification when no preceding information is available. The synthesis of the model and the data achieved in state-space modeling provide a unified approach to biological inference that is flexible enough to apply to almost any ecological system.

Acknowledgment

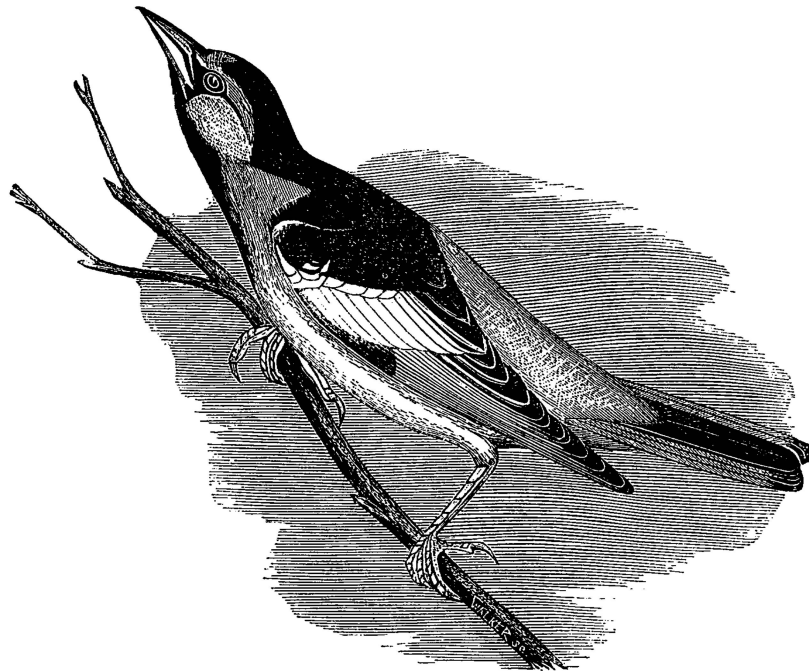
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Xanthothus bullockii from "Bullock's Oriole" by Elliot Coues (*American Naturalist*, 1871, 5:678–682).