SOCIALLY INDUCED RED GROUSE POPULATION CYCLES NEED ABRUPT TRANSITIONS BETWEEN TOLERANCE AND AGGRESSION

Jason Matthiopoulos,[1,4] John M. Halley,[2] and Robert Moss[3]

[1]*NERC Sea Mammal Research Unit, Gatty Marine Lab, University of St Andrews, St Andrews, Fife, KY16 8LB Scotland, UK*
[2]*Department of Ecology, School of Biology, Aristotle University, U.P. Box 119, 54006 Thessaloniki, Greece*
[3]*Centre for Ecology and Hydrology, Hill of Brathens, Banchory, AB31 4BY Scotland, UK*

Abstract. Recent field experiments tested the hypothesis that variations in the aggressiveness of territorial cocks drive Red Grouse (*Lagopus lagopus scoticus*) population cycles. The implications of these results were previously explored with parametrically flexible models that made specific assumptions about the functional form of direct density dependence and the form and timing of delayed density dependence. Although these models were characterized by apparently different stability conditions, they pointed at the same conclusion: that the occurrence of population cycles under this hypothesis relies on the strength of the interaction between density and aggressiveness around the system's equilibrium. To investigate if this important result is valid more generally, we develop a minimally specified model by lifting most of the assumptions on direct and delayed density dependence. Stability analysis of this functionally flexible model confirms that unstable dynamics are indeed more likely if small perturbations from equilibrium density have a strong impact on aggressiveness, and it unifies the stability conditions previously derived for the more specific models under a single, general condition. Further, we derive global, necessary, and sufficient conditions for instability and express them in terms of proportional changes in aggressiveness and density. For the first time since the inception of the hypothesis, the necessary condition quantifies the minimum strength of the intrinsic mechanism that would be required to cause unstable dynamics. We predict that unstable population dynamics are possible if proportional perturbations from equilibrium density are at least matched by proportional changes in aggressiveness. Existing field data indicate that the necessary condition for intrinsic cycles is satisfied in Red Grouse populations. In contrast, the sufficient condition is considerably more strict, implying that intrinsic instability is not an inevitable feature of the system. We conclude that the model is consistent with the demographic patterns of cyclic population fluctuations in Red Grouse and other birds of the grouse family.

Key words: *aggressive behavior; density dependence; intrinsic hypotheses; kinship hypothesis;* Lagopus lagopus scoticus; *mathematical model; necessary and sufficient conditions for instability; population cycles; Red Grouse; territoriality; unstable population dynamics.*

Introduction

Population cycles fascinate ecologists (Stenseth 1999, Bjornstad and Grenfell 2001, Moss and Watson 2001, Berryman 2002, Turchin 2003). Following Lotka (1925) and Volterra (1926), the most popular causal explanations for cycles involve trophic interactions. Variations on this theme include simple two-part systems such as predator–prey (Rosenzweig and MacArthur 1963) and host–parasite (May and Anderson 1978) interactions, and more complex explanations involving negative feedback loops within ecological communities (Berryman 2001). An alternative explanation is that the animals' own behavior causes their numbers to cycle. Variations of this intrinsic hypothesis, focusing primarily on agonistic and territorial behavior (Chitty

1967, Charnov and Finerty 1980, Watson 1985, Watson et al. 1994, Matthiopoulos et al. 1998, 2000, 2002, Mougeot et al. 2003*a*) have been received with skepticism. This stems partly from the assumption (Lack 1954, Stenseth and Łomnicki 1990) that territorial behavior must be a stabilizing influence, but mostly from a lack of conclusive field evidence and convincing models of how behavior might cause unstable dynamics. Thus, in his recent book on cyclic population dynamics, Turchin (2003) concludes that ''all cases [of population cycles] for which we can reach a reasonably well-supported conclusion belong to one general category: trophic interactions,'' but that, ''in one case, the Red Grouse in Scotland, an intrinsic mechanism remains a viable contender.''

Cyclic population fluctuations have been well studied in several grouse species, particularly Red Grouse, *Lagopus lagopus scoticus* (see reviews by Watson and Moss 1979, Moss and Watson 1991, 2001, Hudson 1992). Field observations (Moss et al. 1984, Watson et

al. 1984, 1994, Moss et al. 1996) gave rise to the idea that changes in Red Grouse population density are caused by changes in territory size, in turn influenced by variations in territorial, aggressive behavior. It has been demonstrated (Moss et al. 1994, Mougeot et al. 2003*a*, Mougeot et al., *in press*) that testosterone implanted into territorial, male Red Grouse can lead to some individuals losing their territories and thus can precipitate big, local declines in breeding population density. This, clearly shows that aggressive, territorial behavior can limit Red Grouse populations. In the predominantly monogamous Red Grouse, breeding population density is determined during the competition for territories that takes place among cocks each autumn. This involves both old, established cocks and young cocks, newly reared that summer. Some old cocks lose their territories to young birds that are thus recruited into the territorial population, and some young cocks fail to get territories (Jenkins et al. 1963, Watson and Jenkins 1968). Territorial cocks defend their territories through the winter (Watson 1985). Nonterritorial cocks suffer severe overwinter mortality (Watson 1985) and therefore do not breed in the following spring. The testosterone implantation of old cocks in autumn (Mougeot et al. 2003*b*, Mougeot et al., *in press*) caused the survivors to expand their territories and prevented the recruitment of young cocks. The implants were exhausted within a few weeks of the manipulation, in autumn of year t, but their effect on population density and age structure lasted at least until the spring of year $t + 2$. This enduring effect of each territorial competition, in effect a population memory, provides a time lag that has the potential to cause unstable population fluctuations.

The behavioral mechanisms that lead to memory at the population level are not yet fully understood and, in particular, the complex ways in which past and present densities might interact with past and present behavior are only just beginning to be explored. However, what is currently known about the life history, behavior, and population dynamics of Red Grouse now enables us to reach general conclusions about the interplay between territorial behavior and population dynamics, without the need for many arbitrary assumptions (e.g., Mountford et al. 1990, Hendry et al. 1997, Matthiopoulos et al. 1998, 2000: Table 1). In a recent paper, Matthiopoulos et al. (2003) examined two parametrically flexible models containing plausible functions for direct and delayed density dependence. Both models were capable of cyclic behavior and, despite having apparently different stability conditions, both models suggested that the occurrence of instability depends on the impact that perturbations from equilibrium density have on aggressiveness. However, it was not clear whether this potentially useful result was a general prediction of the hypothesis or a consequence of the particular implementation of density dependence. To address this question, we develop a mini-

mally specified model by removing most of the structural restrictions on both direct and delayed density dependence. We analyze the local stability properties of the model's equilibria and produce general stability conditions expressed in terms of the strength of direct density dependence and the timing of delayed density dependence. We illustrate how this result unifies the stability conditions of the models in Matthiopoulos et al. (2003). We use this new result to generate necessary and sufficient conditions for instability, expressed in terms of proportional changes in the model's state variables. The necessary and sufficient conditions quantify the strength of the intrinsic mechanism at which instability is, respectively, possible and inevitable. Because these conditions are valid over the entire space of possible parameters and plausible models, they offer us the best, as yet, theoretical criterion for the validity of the intrinsic hypothesis. We interpret these results in the context of grouse demography and population fluctuations.

MODEL DESCRIPTION

In Red Grouse, hens gain territories by associating with territorial cocks. Although a few cocks have two hens and some have none, cock numbers largely govern hen numbers (Watson and Jenkins 1968, Moss et al. 1996, Mougeot et al. 2003*b*). By spring, almost all nonterritorial cocks and hens are dead (Watson 1985), so breeding density is effectively determined in the previous autumn. The main demographic determinants of breeding density are autumn recruitment of young cocks into the territorial population and overwinter losses of young and old cocks (Moss and Watson 1985, Watson 1985, Mougeot et al. 2003*a*). Both processes occur during discrete time periods each year. We therefore model cock density in discrete time. We first introduce a difference equation for autumn population density. We then derive a difference equation for average, per capita aggressiveness. Finally, we define a broad class of functions for density-dependent recruitment of young cocks into the territorial population, and we examine which of the classical forms of density dependence belong to this class.

Autumn population density

We begin with a model of population density in spring of year t (P_t), the start of the breeding season

$$P_{t+1} = (s + bq_t)P_t \qquad (1)$$

where s (a constant) is the per capita probability of survival of adult cocks; b (a constant) is the breeding success, i.e., the per capita production of fully grown male offspring; and q_t is the probability that a young cock, reared in the summer of year t, gets recruited into the territorial population in autumn of year t. Cocks that fail to get a territory emigrate or die in the subsequent winter (Watson 1985, Mougeot et al. 2003*b*; but see Park et al. 2002) so that P_{t+1} is determined by

the competition for territories in autumn of year t. Eq. 1 is based on the life history of Red Grouse and is explained in more detail elsewhere (Matthiopoulos et al. 1998, 2002, 2003). To facilitate modeling of density-dependent recruitment, we shift this model to autumn before the occurrence of the territorial contest. In autumn, the total density of competing cocks is the sum of the spring density of established adults (P_t) and the autumn density of newly matured young (bP_t). Cock density will also depend on environmental factors such as habitat quality. To examine the potential for socially induced cycles in isolation from such extrinsic factors, we assume their influence to be constant. Hence, all environmental factors scale the density by a constant K. This has no effect on the dynamics of the model, but allows for different average densities in different habitats. To simplify notation, we replace the state variable P_t by the state variable $h_t \equiv KP_t(1 + b)$:

$$h_{t+1} = (s + bq_t)h_t. \qquad (2)$$

Hence, whereas Eq. 1 models the absolute density of territorial cocks in spring, Eq. 2 models the relative (habitat-independent) density of competing cocks in autumn.

Average aggressiveness

Aggressiveness is an attribute of a cock manifested in the agonistic acts that cause it to get and keep a territory. It is related to the animal's physiological state (e.g., levels of testosterone in the blood or comb size). We use a_t to denote the aggressiveness of an average cock in the autumn territorial contest of year t. Field studies, lasting more than a year and involving testosterone implants (Mougeot et al. 2003b, Mougeot et al., *in press*), have shown that aggressiveness in autumn $t + 1$ is correlated with aggressiveness in autumn t. In nature, given an otherwise constant environment, average aggressiveness within a closed population will be affected by the density of cocks competing for territories. However, the timing of this response is not known. Aggressiveness during the territorial contest of year $t + 1$ might be modified in response to the density prevailing in the same territorial contest, or, existing territory holders might enter the contest with aggressiveness set by last year's density. More generally, we examine a model in which aggressiveness is modified in response to ψ_t, a linear combination of this and last year's density:

$$\psi_t = wh_t + (1 - w)h_{t+1} \qquad (0 \le w \le 1). \qquad (3)$$

Note that $\psi_t = h_t + (1 - w)(h_{t+1} - h_t) = h_t + (1 - w)\Delta h$. Population change ($\Delta h$) equals recruitment (a variable rate) minus mortality (a constant rate). This gives rise to two other interpretations of Eq. 3: First, recruitment determines the age structure of the territorial population (the ratio of young to old cocks). Hence, aggressiveness might respond to age structure. Second, aggressiveness might respond to the rate of

recruitment, which, given philopatric establishment of new territory owners (Watson et al. 1994), modifies the size of kin clusters of territorial cocks (Piertney et al. 1999). Consequently, Eq. 3 encompasses the idea that aggressiveness responds to certain alterations in the spatial arrangement of kin (MacColl et al. 2000), as we shall discuss further.

The annual modification of aggressiveness by density may be multiplicative, say $a_{t+1} = a_t f(\psi_t)$, or additive, say $a_{t+1} = a_t + g(\psi_t)$, for f and g, increasing functions of ψ_t. In general

$$a_{t+1} = a_t f(\psi_t) + g(\psi_t) \quad \text{where } f = 1 \text{ or } g = 0. \quad (4)$$

Eq. 4 does not cover all conceivable models. However, it encompasses linear, power, bounded, and sigmoidal formulations (Fig. 1), and therefore offers considerable generality.

Density-dependent recruitment

The experimental results of Mougeot et al. (2003a) and Mougeot et al. *in press* indicate that autumn aggressiveness depresses recruitment into the territorial population. The probability that a young cock successfully claims a unit of area for itself will depend on whether the same unit of area is being defended by another cock, young or old. On average, the number of such defensive responses in each unit of area will be the product of density by aggressiveness. In general, we write the recruitment function as:

$$q_t = q(a_t h_t). \qquad (5)$$

Future work will examine the effects of immigration on models of the intrinsic hypothesis, but in the present paper, we restrict our attention to proportion-valued functions for recruitment:

$$0 \le q(x) \le 1. \qquad (6)$$

We also assume that recruitment is a decreasing function of its argument, for there is no evidence that, in any part of its domain, recruitment should increase with increasing total aggressiveness:

$$\frac{dq(x)}{dx} < 0. \qquad (7)$$

Finally, with Red Grouse, "we are interested in what mechanisms explain second-order oscillations" (Turchin 2003). We must therefore exclude instability that results from overcompensating forms of direct density dependence. To do this, we briefly examine a population model similar to Eq. 2, but containing no aggressiveness term

$$x_{t+1} = [s + bq(x_t)]x_t \qquad (8)$$

where x_t is proportional to population density. Any unstable solutions of Eq. 8 will be the result of direct density dependence in the recruitment function $q(x_t)$. The asymptotic stability condition for Eq. 8 (see Gurney and Nisbet 1998) is:
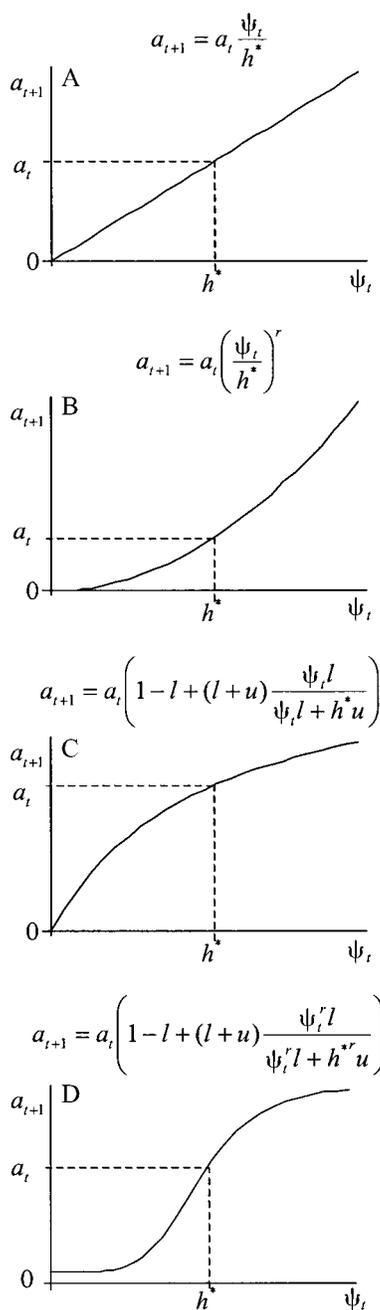
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$$a_{t+1} = a_t \frac{\psi_t}{h^*}$$

A

$$a_{t+1} = a_t \left(\frac{\psi_t}{h^*}\right)^r$$

B

$$a_{t+1} = a_t \left(1 - l + (l+u)\frac{\psi_t l}{\psi_t l + h^* u}\right)$$

C

$$a_{t+1} = a_t \left(1 - l + (l+u)\frac{\psi_t^r l}{\psi_t^r l + h^{*r} u}\right)$$

D

FIG. 1. Four examples of models in the family of Eq. 4 describing the update of aggressiveness (a) on the basis of past and present density as expressed by the variable ψ_t. In the simplest case (A), it might be assumed that aggressiveness increases in proportion to density. When ψ_t is equal to the equilibrium population density h^*, then aggressiveness in the next year remains the same as in the present. Alternatively (B), it may be argued that aggressiveness is updated as a power function of density with exponent r. For example, setting r to two might be used to model a response proportional to the number of pairwise aggressive interactions in the population. It may further be argued that animals can only increase or decrease their aggressiveness up or down to a certain proportion of present aggressiveness. Using a bounded formulation (C) with the parameters l and u determining the

$$\left.\frac{d\{[s + bq(x)]x\}}{dx}\right|_{x=x^*} > -1. \tag{9}$$

This does not exclude damped oscillations arising from direct density dependence. Systems with damped oscillations can exhibit statistically periodic fluctuations in the presence of environmental stochasticity. Our analysis in this paper is purely deterministic, but we return to this topic in the *Discussion*. At the equilibrium x^*, Eq. 8 becomes $s + bq(x^*) = 1$. We therefore focus on systems with density-dependent recruitment functions and parameters that satisfy the requirement

$$\left.-bx\frac{dq}{dx}\right|_{x=x^*} < 2. \tag{10}$$

To illustrate the assumptions in Eqs. 5–7 and 10 and their biological relevance to Red Grouse, we look at the four functions most commonly used in the literature to model density dependence.

1) *The logistic function* ($q(x) = 1 - x$) will violate Eq. 6 when it becomes negative ($x > 1$). In our model, this is not possible because it implies that fewer young cocks than available get recruited. Furthermore, this particular property of the logistic function can, in discrete-time models such as ours, lead to negative population numbers. This makes it biologically inappropriate.

2) *The depensation function* ($q(x) = x/(1 + x^2)$) violates the monotonicity assumption in Eq. 7. There is no biological evidence for depensation effects in Red Grouse. It is therefore plausible to exclude this function by means of Eq. 7.

3) *The generalized Beverton-Holt* ($q(x) = 1/(1 + x^\theta)$) satisfies Eqs. 5–7. The left-hand side of Eq. 10 is written $b\theta x^{*\theta}/(1 + x^{*\theta})^2$, with $x^{*2} = (b + s - 1)/(1 - s)$. Therefore, Eq. 10 is satisfied for $\theta < 2b/((b + s - 1)(1 - s))$. For parameter values outside this range, direct density dependence is strong enough to cause cycles without the need of delayed density dependence. As previously discussed, (Eq. 8), we exclude such parameterizations from our analysis, not because they are biologically unrealistic, but because they would confound the effects of direct and delayed density dependence. We return to this topic in the *Discussion*. Note that the simple Beverton-Holt (obtained for $\theta = 1$) always satisfies this condition.

4) *The generalized Ricker* ($q(x) = \exp[-x^\theta]$) satisfies Eqs. 5–7. The left-hand side of Eq. 10 is written $b\theta x^{*\theta}/\exp[x^{*\theta}]$, with $x^{*\theta} = \ln(b/(1 - s))$. Therefore, Eq. 10 is satisfied for $\theta < 2/[(1 - s)\ln(b/(1 - s))]$. Note that the simple Ricker function (obtained for $\theta = 1$)

←

upper and lower bounds of the update rule incorporates this added complication. Finally (D), an exponent may be used on the bounded formulation to give a variable slope around the system's equilibrium density.

satisfies Eq. 10 when $b < (1 - s)\exp[2/(1 - s)]$. As with the Beverton-Holt, these limitations are intended to exclude the destabilizing effects of strong, direct density dependence from our analysis (but see *Discussion*).

Eqs. 2–4, together with conditions 5–7 and 10, complete the derivation of the model relating density to aggressiveness and aggressiveness to density:

$$h_{t+1} = [s + bq(a_t h_t)]h_t$$

$$\text{where } f = 1 \quad \text{or} \quad g = 0 \quad \text{and}$$

$$a_{t+1} = a_t f(\psi_t) + g(\psi_t)$$

$$\text{where } \psi_t = wh_t + (1 - w)h_{t+1}. \quad (11)$$

In Eqs. 11, the functional form and parameters of the recruitment function q control the strength of direct density dependence. The functions f and g determine the strength of delayed density dependence. The parameter w determines the relative timing of delayed density dependence.

LOCAL STABILITY OF EQUILIBRIA

The system in Eqs. 11 has an extinction equilibrium (0,0) and a nontrivial equilibrium (h^*, a^*) that satisfies the relationship

$$q(a^* h^*) = \frac{1 - s}{b}. \quad (12)$$

That is, at equilibrium, the proportion of reared young that get recruited equals the mortality of established adults.

Local stability analyses of the equilibria (Appendix A) indicate that extinction occurs when $b + s < 1$, and they produce analytical conditions for instability in terms of the ''timing'' parameter w and the ''behavioral'' parameter c, the slope of the aggressiveness function at equilibrium:

$$c \equiv \left[a^* \frac{\partial f}{\partial \psi}(h^*) + \frac{\partial g}{\partial \psi}(h^*) \right]$$

$$\text{where } f = 1 \quad \text{or} \quad g = 0. \quad (13)$$

When the variable ψ takes values below the equilibrium density (h^*), animals reduce their aggressiveness according to the rule in Eq. 4, and therefore become more tolerant. In contrast, when the variable ψ takes values above the equilibrium density (h^*), animals increase their aggressiveness. Therefore, the parameter c determines the abruptness of transitions between tolerant and aggressive behavior around the population's equilibrium density.

Algebraic manipulation can simplify the conditions for instability derived in Appendix A to the following fundamental result

$$c > \begin{cases} \dfrac{q_h}{q_a w} & \text{if } -\dfrac{q_h}{4} < w \le 1 \\[2ex] \dfrac{2(2 + q_h)}{q_a(2w - 1)} & \text{if } 0 \le w < -\dfrac{q_h}{4} \end{cases} \quad (14)$$

where $q_h = bh^*(\partial q/\partial h)$ and $q_a = bh^*(\partial q/\partial a)$ (both partial derivatives are estimated at equilibrium). The general stability condition in Eq. 14 unifies the results obtained previously for more specific models (Matthiopoulos et al. 2003). In Appendix B, we illustrate Eqs. 14 using these models as examples.

From Eq. 7, we know that both q_h and q_a will be negative. The value of q_a is otherwise unrestricted. For q_h we observe that

$$q_h = bh^* \frac{\partial q}{\partial h}\bigg|_{h=h^*} = bh^* \frac{dq}{d(ah)}\bigg|_{ah=a^* h^*} \frac{\partial(ah)}{\partial h}\bigg|_{h=h^*}$$

$$= ba^* h^* \frac{dq}{d(ah)}\bigg|_{ah=a^* h^*} \quad (15)$$

and therefore $q_h > -2$ from Eq. 10. Choosing values for q_h and q_a from the ranges $(-2, 0)$ and $(-\infty, 0)$, respectively, and plotting Eqs. 14 in the w–c plane (Fig. 2) gives a more intuitive view of this result. Notice that the occurrence of unstable dynamics consistently requires high values of c. This establishes the first major result of this paper: *socially induced instability requires abrupt transitions between tolerant and aggressive behavior.*

GLOBAL IMPLICATIONS OF THE STABILITY CONDITIONS

In Eqs. 14, the occurrence of cycles requires that the sensitivity (as expressed by the parameter c) of aggressiveness to density exceeds some critical threshold (the boundary between stability and instability in Fig. 2). Although this pattern is now shown to be general, the value of the threshold depends on the values of w, q_a, q_h, and the units used to measure the state variables. We seek instability conditions that are independent of these. To this end, we derive maximum and minimum values for the instability threshold and use them to derive necessary and sufficient conditions for the onset of instability. We denote these by c_{min} and c_{max}, and use w_{min} and w_{max}, respectively, to denote the values of the timing parameter w at which they occur. For any particular values of b and s, the maximum value of the threshold for c is (also see Fig. 2):

$$c_{max} = -4/q_a \quad \text{attained at} \quad w_{max} = -q_h/4. \quad (16)$$

In the space of all models and parameterizations examined here, if c exceeds c_{max}, unstable dynamics are guaranteed to occur. On either side of w_{max}, the value of the threshold declines monotonically (see Eqs. 14 and Fig. 2) so that the minimum value c_{min} occurs either at $w = 0$ or $w = 1$, depending on the value of q_h, such that
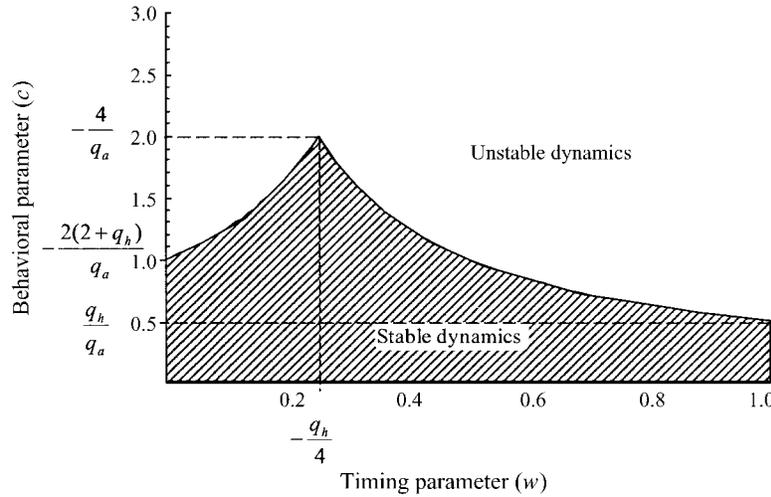
Fig. 2. Graphical representation of Eq. 14. The quantities $q_h = bh^*(\partial q/\partial h)$ relate to the response of recruitment to changes in density and aggressiveness around the equilibrium and have been fixed to $q_h = -1$ and $q_a = -2$ to facilitate visualization. The hatched region corresponds to stable solutions of the general model. For $c = -4/q_a$, the slope of the aggressiveness function is 2.0. For $w = -q_h/4$, the relative timing of delayed density dependence is 0.25.

$$c_{\min} = \begin{cases} \dfrac{q_h}{q_a} & \text{attained at } w_{\min} = 1 \quad \text{if } 0 < -q_h < \dfrac{4}{3} \\ \dfrac{2(2 + q_h)}{-q_a} & \text{attained at } w_{\min} = 0 \quad \text{if } \dfrac{4}{3} < -q_h < 2. \end{cases} \quad (17)$$

Eqs. 16 and 17 are, respectively, the sufficient and necessary conditions for the occurrence of unstable dynamics, expressed in terms of q_a, q_h and the units of aggressiveness and density. This result can be expressed more simply in terms of proportional perturbations from equilibrium density and aggressiveness, defined as:

$$\delta \equiv \frac{\psi - h^*}{h^*} \quad \text{and} \quad \Delta \equiv \frac{A(\psi) - A(h^*)}{A(h^*)}. \quad (18)$$

Using these unitless quantities (see Appendix C) yields

$$\Delta_{\max} > -\frac{4}{q_h}\delta \quad \text{and} \quad (19)$$

$$\Delta_{\min} < \begin{cases} \delta & \text{if } 0 < -q_h < \dfrac{4}{3} \\ -2\dfrac{2 + q_h}{q_h}\delta & \text{if } \dfrac{4}{3} < -q_h < 2. \end{cases} \quad (20)$$

Eqs. 19 and 20 are the sufficient and necessary conditions expressed in terms of the strength of direct density dependence in recruitment (q_h) and proportional changes in density and aggressiveness. Systems that satisfy the sufficient condition are certain to give unstable solutions. Systems that fail to satisfy the necessary condition will always be stable. The sufficient condition, Eq. 19, is of less interest because we are aware that not all grouse populations are unstable (Haydon et al. 2002). We are more interested in the necessary conditions (Eq. 20), because they set the minimum requirements for instability to occur at all under the hypothesis. For the second part of Eq. 20, notice that, within the stated range of q_h, we have

$$0 \le -2\frac{2 + q_h}{q_h} \le 1. \quad (21)$$

Eqs. 20 and 21 establish the following. (1) when direct density dependence in recruitment is weak ($0 < -q_h < 4/3$), instability can occur when proportional changes in density close to equilibrium are *at least matched* by proportional changes in individuals' aggressiveness. (2) when direct density dependence in recruitment is strong ($-q_h > 4/3$), although not strong enough to cause first-order oscillations ($-q_h < 2$), instability may occur *even* if proportional changes in density are not matched by proportional changes in aggressiveness.

Thus, the second important result of this paper can be stated as follows: *irrespective of the functional and parametric specification of the general model, intrinsically unstable dynamics can occur if proportional changes from equilibrium population density are at least matched by proportional changes in per capita aggressiveness.*

A Numerical Example

We illustrate the results of the previous section with a specific example. We seek the necessary and sufficient conditions for cycles in a population model of the form

FIG. 3. Setting the vital rates to the realistic (for grouse) values of $b = 1.5$ (breeding success) and $s = 0.5$ (survival) in the model of Eq. 28 allows us to express the necessary and sufficient conditions for cycles for that model in terms of the strength of density dependence, θ. This provides a unitless measure of how strong the behavioral response to perturbations from equilibrium density (h^*) must be, and delineates the three regions in which population cycles are impossible, possible, and certain.
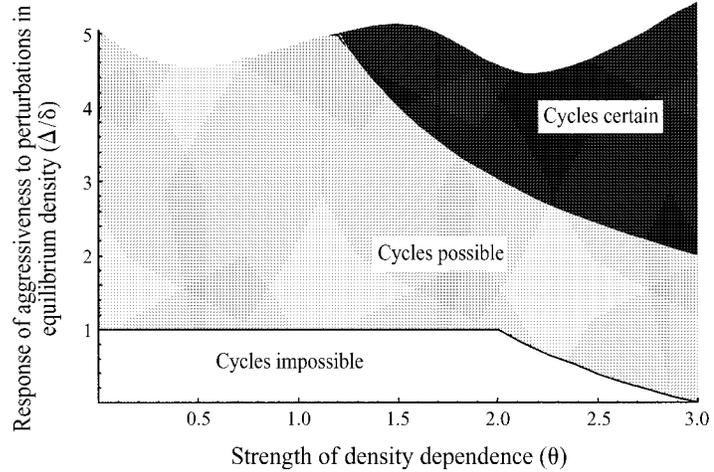
$$h_{t+1} = \left[s + \frac{b}{1 + (a_t h_t)^\theta}\right] h_t$$

$$a_{t+1} = a_t f(\psi_t) + g(\psi_t). \qquad (22)$$

For this, still rather general, system, $q_h = -\theta(b + s - 1)(1 - s)/b$. The parameter θ is restricted to values between 0 and 3 (see our earlier examination of the generalized Beverton-Holt). We fix the demographic parameters to the plausible, for Red Grouse, values of $b = 1.5$ and $s = 0.5$. Breeding success in our model refers to male chicks only, and is therefore taken as half of the average breeding success for male and female chicks. From Eqs. 19 and 20, we obtain

$$\Delta_{max} > \frac{6}{\theta}\delta \quad \text{and}$$

$$\Delta_{min} > \begin{cases} \delta & \text{if } 0 < \theta < 2 \\ 2\dfrac{3 - \theta}{\theta}\delta & \text{if } 2 < \theta < 3. \end{cases} \qquad (23)$$

We can use this to visualize the necessary and sufficient strength of the behavioral mechanism in terms of the strength of density dependence, as measured by θ (Fig. 3). It is worthwhile noting the large gap between necessary and sufficient conditions in Fig. 3. The necessary condition is unresponsive to weak forms of direct density dependence (small values of θ), whereas the sufficient condition tends to infinity as θ tends to zero.

DISCUSSION

To investigate the dynamical consequences of the documented (Mougeot et al. 2003*a*, *b*, Mougeot et al., *in press*) interaction between aggressiveness and density in Red Grouse, we examined a general model that makes minimal assumptions about the form and timing of density dependence. It was not our intention to build a purely mechanistic model, but one that would be specified only to the extent allowed by current evidence. Such functional and parametric generality make

it impossible to obtain numerical solutions of the model. Hence, this minimally specified model is unsuitable for investigating the period, amplitude, and shape of the cycles produced.

Instead, we have demonstrated that a mechanism involving memory in those aspects of aggressive behavior that affect recruitment can lead to unstable population fluctuations, and that this becomes more likely if the mechanism is strong, i.e., if the slope of the response of aggressiveness to perturbations from equilibrium density is steep. This is a consistent result throughout the large class of models and space of parameters considered in this paper.

By introducing the assumption in Eq. 10, we have ensured that, in all functional and parametric versions of the model examined here, instability arises only as a result of the interaction between aggressiveness and density. However, relaxing this assumption does not negate our results. Analyses not presented in this paper indicate that the conditions described here continue to be valid even under overcompensating forms of direct density dependence. Under such conditions, instability occurs more readily and, predictably, it does not always rely on the interaction of aggressiveness and density.

A global overview of the model's properties reveals that sufficient conditions for instability are strict, but necessary conditions are not. We have concluded that, although not inevitable, instability becomes possible when proportional deviations from equilibrium density are, at least, matched by the resulting proportional changes in aggressiveness. This condition applies to weak forms of direct density dependence in recruitment. When density dependence in recruitment is strong (but not strong enough to cause instability on its own), instability can occur even if changes in aggressiveness do not match changes in density. These results are in agreement with the observation that not all grouse populations cycle (Hudson et al. 1985, Williams 1985). They contradict the view (Dobson and Hudson 1992) that the response of aggressiveness to

density required to cause unstable dynamics is unrealistically strong.

For example, Watson et al. (1994) reported on a 14-year (1964–1977) study of two population cycles on Kerloch moor in northeastern Scotland, during which population density fluctuated fivefold. Meanwhile, the rate at which cocks gave territorial songs fluctuated sixfold among years, and the rate at which they had territorial boundary disputes with each other fluctuated more than 20-fold. Hence, proportional changes in density were more than matched by proportional changes in two measures of aggressiveness.

This comparison of our results with field data is indicative only, because measurements of aggressiveness were made after territory establishment in autumn, not during establishment. Also, it has not been shown that rates of singing and disputing are directly related to the acts of aggression that determine changes in territory size.

Another caveat is that the observations of Watson et al. (1994) were not made at equilibrium density. However, most plausible rules for updating aggressiveness will be bounded above and below because average aggressiveness cannot tend to infinity or be negative. Therefore the ratio of changes in aggressiveness to changes in density is likely to be greater at equilibrium than over the course of a full population cycle.

In the present paper, the units of the state variable of aggressiveness are not specified. Indeed, by expressing our results in terms of proportional changes in aggressiveness, we aimed to make them independent of any particular measure. This is because measures of aggressiveness take many forms, some only weakly related to each other (Moss et al. 1979). The difficulty associated with defining and measuring behavioral attributes such as aggressiveness has been one of the main impediments to testing intrinsic hypotheses in the field. Future fieldwork might usefully focus on defining measures of aggressiveness that quantify a bird's ability to get and keep a territory. In parallel, future modeling work should confront our theoretical conclusions with data. This could be done by fitting numerically solvable versions of our general model, such as Eqs. 22, to population time series for Red Grouse. Such time series data originate either from hunting records or from dedicated population studies, each of which presents obstacles to model fitting. Bag data are affected by human behavior and are thus highly biased estimators of population density. They also provide no direct information on Red Grouse behavior or age structure. Data from population studies are, by design, not subject to such faults, but they are relatively short-term and hence lead to low precision in parameter estimation. However, recent developments in state–space methodology (Buckland et al. 2004) and Bayesian model fitting (Gilks et al. 1996) enable us to (1) address the issue of bias by explicitly modeling the data collection process, (2) fit models to incomplete data sets, and (3) combine data

from different studies, hence increasing estimation precision. By using these computer-intensive techniques, it should be possible to estimate the behavioral parameters required to give dynamics with the observed characteristics (stability, cyclicity, period, amplitude, cycle symmetry). These estimates can then be used to pinpoint, within different parameter regions (such as those in Fig. 3), the position of particular Red Grouse populations from different places in the UK. Thus, we will be able to gauge whether the occurrence of cycles is consistent with our model. The same computer-intensive techniques will quantify uncertainty in parameter estimates for different populations, and thus allow us to test hypotheses about the invariance of some of these parameters (e.g., strength of direct density dependence) across different populations.

Our model formalizes the observed interaction between aggressiveness and density, and our analysis demonstrates that, in general, this interaction can lead to unstable population dynamics. This still leaves the question of what behavioral mechanism mediates this interaction and serves as the social basis for the population memory documented by Mougeot et al. (2003b) and Mougeot et al. (in press). Of the many possible biological explanations, the "kinship" hypothesis (Mountford et al. 1990, Watson et al. 1994, Hendry et al. 1997, Matthiopoulos et al. 1998, 2000, 2002) is currently the best developed because it was one of the first to be proposed, and has not yet been discounted by field data. It is based on the concept (Charnov and Finerty 1980) of differential aggressiveness between kin and non-kin and changes in the kin structure of philopatric male populations incurred by variations in density. Territorial cocks are less aggressive toward kin than non-kin and facilitate their recruitment, thus leading to the formation of clusters of related territorial cocks (Watson et al. 1994, MacColl et al. 2000). As population density increases, tolerance among relatives is thought to decrease and recruitment to lessen, until recruitment is no longer sufficient to compensate for mortality. Hence, kin clusters disintegrate and the ensuing low level of recruitment drives density into a trough. In terms of the demographic parameters considered in the present model, this involves positive feedback between recruitment in years t and $t + 1$, and negative feedback between density and recruitment. As explained following Eq. 8, our model encompasses this idea.

The observation (Mougeot et al. 2003, Mougeot et al., in press) that testosterone implantation of old cocks in autumn of year t caused the survivors to expand their territories and prevented the recruitment of young cocks, affecting density at least until spring $t + 2$, is consistent with the kinship hypothesis. More generally, it implies that the timing parameter w (Eq. 8) should be greater than zero.

Previous attempts to model this specific hypothesis (Mountford et al. 1990, Hendry et al. 1997, Matthio-

poulos et al. 1998) found it necessary to make many arbitrary assumptions about how kinship might mediate the interaction between density and aggressiveness. In this way, they have revealed how little is known about the functional form of the behavioral interactions that are implicated in the hypothesis. Of these past attempts, the simpler, age-structured model of Matthiopoulos et al. (1998) is the only one that can be readily recast in the state variables of aggressiveness and density. Throughout that model, linear relationships were employed to describe the responses of aggressiveness to kinship, of aggressiveness to crowding, and of kinship to kin cluster size. Despite that model's realistic output (Matthiopoulos et al. 1998, Mougeot et al. 2003b), these assumptions have since been criticized (Matthiopoulos et al. 2000, 2003, Turchin 2003) as simplistic. Ironically, although these assumptions were motivated by parsimony, recasting that model in the state variables of density and aggressiveness (Matthiopoulos et al. 2003) leads to an analytically intractable formulation. This is because assumptions of linearity in that model can lead to average family clusters consisting of less than one individual. The correction made to eliminate this unrealistic feature yields a relationship between aggressiveness and density that is both multiplicative and additive. We consider this an unnecessarily complex relationship and have not included it in the present paper. Hence, although our results are consistent with a mechanism involving kinship, they do not encompass previous attempts to model the kinship hypothesis.

Certainly, in the light of these new results, the kinship hypothesis deserves further experimental investigation, but its precedent in the literature should not divert us from considering alternative hypotheses, possibly involving aspects other than kinship, philopatry, and territoriality. Indeed, the process modeled here encompasses other unspecified intrinsic mechanisms, in which recruitment is moderated by some process that interacts with density. For example, it is possible that demographic (e.g., age structure), rather than behavioral, mechanisms can mediate the same general process. It is therefore worth examining whether the model is consistent with cycles in other species within or outside the grouse family, even though their behavior differs from that of Red Grouse.

A conclusion from our analysis is that instability can occur with different values of breeding success (b) and survival (s). An extreme case is given in Example 1 (Appendix A), in which the condition for instability is independent of survival and breeding success. This is consistent with long-term studies (reviewed by Moss and Watson 2001) on *Lagopus lagopus* (called Red Grouse, Willow Grouse, or Willow Ptarmigan) and *Lagopus mutus* (called Ptarmigan or Rock Ptarmigan). In various parts of their worldwide range, these species show population cycles associated with very different levels of breeding success and survival. In seven long-term studies (Moss and Watson 2001), a main demographic cause of population declines during the cycles was a lower proportion of the reared young being recruited, as in our model.

In the real world, b and s are very likely to vary during a population cycle. In particular, b typically shows delayed density dependence. This effect (Moss and Watson 2001) can contribute to population cycles, but is generally not strong enough to cause them without reduced recruitment of reared young during population declines, as modeled here. Delayed density dependence in b could be due to the impact of natural enemies such as parasites (Dobson and Hudson 1992, Hudson et al. 2002), or because hens invest less in reproduction during the decline phase of population cycles (Watson et al. 1998).

Also, stochastic input to deterministic models that give rise to damped population cycles can often cause the cycles to continue indefinitely. Delayed density dependence in b or erratic environmental variations, in conjunction with the reduced recruitment of reared young modeled here, might well make population cycles more likely than suggested by our necessary and sufficient conditions. In addition, interaction between strongly damped intrinsic cycles and irregular environmental variations might result in erratic fluctuations that reflect the environmental variations modified by the birds' intrinsic tendency to cycle (Watson et al. 2000).

We claim neither that our model explains all of the demographic variations in all population cycles nor that it is necessarily incompatible with other proposed mechanisms. Rather, by focusing on a single process, we have delimited the requirements for intrinsic population cycles due to interactions between density and aggressiveness, and have shown them to be realistic.

Literature Cited

Berryman, A. A. 2001. Functional web analysis: detecting the structure of population dynamics from multi-species time series. Basic and Applied Ecology **2**:311–321.

Berryman, A. A. 2002. Population cycles: the case for trophic interactions. Oxford University Press, New York, New York, USA.

Bjornstad, O. N., and B. T. Grenfell. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science **293**:638–643.

Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models for the dynamics of wild animal populations. Ecological Modelling **171**:157–175.

Charnov, E., and J. P. Finerty. 1980. Vole population cycles: a case for kin-selection? Oecologia **45**:1–2.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proceedings of the Ecological Society of Australia **2**:51–78.

Dobson, A., and P. J. Hudson. 1992. Regulation and stability of a free-living host–parasite system: *Trichostrongylus ten-*

uis in red grouse. II. Population models. Journal of Animal Ecology **61**:487–498.

Gilks, W. R., S. Richardson, and D. J. Spiegelhalter, editors. 1996. Markov chain Monte Carlo in practice. Chapman and Hall, London, UK.

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological dynamics. Oxford University Press, Oxford, UK.

Haydon, D. T., D. J. Shaw, I. M. Cattadori, P. J. Hudson, and S. J. Thirgood. 2002. Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse. Proceedings of the Royal Society of London, Series B **269**: 1609–1617.

Hendry, R., P. J. Bacon, R. Moss, S. C. F. Palmer, and J. McGlade. 1997. A two-dimensional individual-based model of territorial behaviour: possible population consequences of kinship in red grouse. Ecological Modelling **105**:23–29.

Hudson, P. J. 1992. Grouse in space and time. The Game Conservancy Trust, Fordingbridge, UK.

Hudson, P. J., A. P. Dobson, I. M. Cattadori, D. Newborn, D. T. Haydon, D. J. Shaw, T. G. Benton, and B. T. Grenfell. 2002. Trophic interactions and population growth rates: describing patterns and identifying mechanisms. Philosophical Transactions of the Royal Society of London Series B **357**:1259–1271.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1985. Cyclic and non-cyclic populations of red grouse: a role for parasitism? Pages 79–89 *in* D. Rollinson and R. M. Anderson, editors. Ecology and genetics of host parasite interactions. Academic Press, London, UK.

Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on red grouse *Lagopus lagopus scoticus* (Lath.). Journal of Animal Ecology **40**:367–383.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, Oxford, UK.

Lotka, A. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

MacColl, A. D. C., S. B. Piertney, R. Moss, and X. Lambin. 2000. Spatial arrangement of kin affects recruitment success in young male red grouse. Oikos **90**:261–270.

Matthiopoulos, J., R. Moss, and X. Lambin. 1998. Models of red grouse cycles. A family affair? Oikos **82**:574–590.

Matthiopoulos, J., R. Moss, and X. Lambin. 2000. The kin-facilitation hypothesis for red grouse population cycles: territory sharing between relatives. Ecological Modelling **127**:53–63.

Matthiopoulos, J., R. Moss, and X. Lambin. 2002. The kin-facilitation hypothesis for red grouse population cycles: territorial dynamics of the family cluster. Ecological Modelling **147**:291–307.

Matthiopoulos, J., R. Moss, F. Mougeot, S. Redpath, and X. Lambin. 2003. Territorial behaviour and population dynamics in red grouse *Lagopus lagopus scoticus*. II. Population models. Journal of Animal Ecology **72**:1083–1096.

May, R. M., and R. M. Anderson. 1978. Regulation and stability of host–parasite population interactions. II. Destabilizing processes. Journal of Animal Ecology **47**:249–267.

Moss, R., H. H. Kolb, M. Marquiss, A. Watson, B. Treca, D. Watt, and W. Glennie. 1979. Aggressiveness and dominance in captive cock red grouse. Aggressive Behavior **5**: 59–84.

Moss, R., R. Parr, and X. Lambin. 1994. Effects of testosterone on breeding density, breeding success and survival of red grouse. Proceedings of the Royal Society of London Series B **258**:175–180.

Moss, R., and A. Watson. 1991. Population cycles and kin selection in red grouse *Lagopus lagopus scoticus*. Ibis **133**(Supplement 1):113–120.

Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research **32**:53–111.

Moss, R., A. Watson, and R. Parr. 1996. Experimental prevention of a population cycle in Red Grouse. Ecology **77**: 1512–1530.

Moss, R., A. Watson, and P. Rothery. 1984. Inherent changes in the body size, viability and behavior of a fluctuating red grouse (*Lagopus lagopus scoticus*) population. Journal of Animal Ecology **53**:171–189.

Mougeot, F., S. B. Piertney, F. Leckie, S. Evans, R. Moss, S. Redpath, and P. J. Hudson. *In press*. Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. Journal of Animal Ecology.

Mougeot, F., S. M. Redpath, F. Leckie, and P. J. Hudson. 2003*a*. The effect of aggressiveness on the population dynamics of a territorial bird. Nature **421**:737–739.

Mougeot, F., S. M. Redpath, R. Moss, J. Matthiopoulos, and P. J. Hudson. 2003*b*. Territorial behaviour and population dynamics in red grouse *Lagopus lagopus scoticus*. I. Population experiments. Journal of Animal Ecology **72**:1073–1082.

Mountford, M. D., A. Watson, R. Moss, R. Parr, and P. Rothery. 1990. Land inheritance and population cycles of red grouse. Pages 78–83 *in* A. N. Lance and J. H. Lawton, editors. Red grouse population processes. Royal Society for the Protection of Birds, Sandy, Bedfordshire, UK.

Park, K. J., M. M. Hurley, and P. J. Hudson. 2002. Territorial status and survival in red grouse *Lagopus lagopus scoticus*: hope for the doomed surplus? Journal of Avian Biology **33**:56–62.

Piertney, S. B., A. D. C. MacColl, X. Lambin, R. Moss, and J. F. Dallas. 1999. Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). Biological Journal of the Linnean Society **68**:317–331.

Rozenzweig, M. L., and R. H. MacArtur. 1963. Graphical representation and stability conditions of predator–prey interactions. American Naturalist **97**:209–223.

Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. Oikos **87**:427–461.

Stenseth, N. C., and A. Łomnicki. 1990. On the Charnov-Finerty hypothesis: the unproblematic transition from docile to aggressive and the problematic transition from aggressive to docile. Oikos **58**:234–238.

Turchin, P. 2003. Complex population dynamics. Princeton University Press, Princeton, New Jersey, USA.

Volterra, V. 1926. Fluctuations in the abundance of species considered mathematically. Nature **118**:558–660.

Watson, A. 1985. Social class, socially-induced loss, recruitment and breeding of red grouse. Oecologia **67**:493–498.

Watson, A., and D. Jenkins. 1968. Experiments on population control by territorial behaviour in red grouse. Journal of Animal Ecology **37**:595–614.

Watson, A., and R. Moss. 1979. Population cycles in the Tetraonidae. Ornis Fennica **56**:87–109.

Watson, A., R. Moss, R. Parr, M. D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology **63**:39–50.

Watson, A., R. Moss, and S. Rae. 1998. Population dynamics of Scottish Rock Ptarmigan cycles. Ecology **79**:1174–1192.

Watson, A., R. Moss, and P. Rothery. 2000. Weather and synchrony in 10-year population cycles of Rock Ptarmigan and Red Grouse in Scotland. Ecology **81**:2126–2136.

Watson, A., R. Moss, P. Rothery, and R. Parr. 1984. Demographic causes and predictive models of population fluctuations in red grouse. Journal of Animal Ecology **53**:639–662.

Williams, J. 1985. Statistical analysis of fluctuations in red grouse bag data. Oecologia **65**:269–272.

Month 2005   SOCIALLY INDUCED POPULATION CYCLES

APPENDIX A

Local stability analysis of the general model equation (Eq. 11) is available in ESA's Electronic Data Archive: *Ecological Archives* XXXXXXXXX.

APPENDIX B

Application of stability conditions in Eq. 14 to specific examples is available in ESA's Electronic Data Archive: *Ecological Archives* XXXXXXXXX.

APPENDIX C

Perturbation analysis of the necessary and sufficient conditions for cycles is available in ESA's Electronic Data Archive: *Ecological Archives* XXXXXXXXX.