Territorial behaviour and population dynamics in red grouse *Lagopus lagopus scoticus*. II. Population models

JASON MATTHIOPULOS*, ROBERT MOSS†, FRANÇOIS MOUGEOT†, XAVIER LAMBIN‡ and STEVE M. REDPATH†

*NERC Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK; †Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BY, Scotland, UK; ‡Aberdeen Population Ecology Research Unit, School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland, UK

Summary

1. Recent experiments on cyclic red grouse populations discovered that aggressiveness, induced by testosterone implants, depressed population density for more than a year after the implants were exhausted.

2. This confirms the observation, also made in previous studies of this territorial species, that aggressiveness can determine population density. Additionally, it hints at a form of social memory that sustains the effect of episodes of high aggressiveness after their cause has ceased to exist.

3. We explore the logical consequences of this observation with a simple model of the interaction between population density and aggressiveness. A flexible function describes how aggressiveness changes from year to year as a function of population density. At low densities animals are tolerant to conspecifics and aggressiveness falls from one year to the next. Conversely, at high densities aggressiveness rises.

4. In the model, current aggressiveness is set by aggressiveness in the previous year, and modified by last year’s population density (first version) or by current population density (second version).

5. We assume no particular behavioural mechanism underlying this process but derive conditions under which changes in aggressiveness, effected by density, can generate unstable dynamics.

6. The two versions of the model give fluctuations that differ in period and amplitude but have similar conditions for unstable dynamics. Specifically, the more abrupt the transition from tolerant to intolerant behaviour with increasing density, the more likely are cycles to occur.

7. We show how a previous model of the kinship hypothesis for red grouse cycles can be recast in the current terminology, and how the new models offer a more general way of examining red grouse population dynamics.

Key-words: aggressiveness, kinship hypothesis, territorial behaviour, unstable population dynamics.


Introduction

In territorial animals, spacing behaviour is an important determinant of population density. The establishment of territorial boundaries and the resultant size of territories are mediated by agonistic behaviour and so changes in aggressiveness of territory-holders are crucial to the dynamics of such populations.

There have been two main schools of thought. One relates territory size to resource density so that, on ground fully occupied by territories, mean territory size and its inverse, population density, are in effect attributes of the environment. An early suggestion (Lack 1954) was that territorial behaviour is simply a
way in which animals divide up ground after their numbers have been limited by resources or natural enemies. Others, such as Davies (1978), developed the theme that the size of a territory results from a balance between the costs (energy expenditure and mortality risk) and benefits (access to resources) of holding it. A problem with this viewpoint is that in some species territorial boundaries are fixed before resource limitation occurs. Thus, red grouse (Lagopus lagopus scoticus L.) territories on heather moorland are determined largely in autumn (Watson 1985), well before resource limitation occurs in late winter or spring (Moss & Watson 1990).

The second school regards territory size as primarily an attribute of the animal, relating territory size to the intensity of aggressive behaviour (e.g. Watson 1964). More generally, Wynne-Edwards (1962) and Chitty (1967) argued that animal populations can regulate their density below any immediate limit set by resources or natural enemies. Until recently, however, it has proved difficult to provide unequivocal evidence of mechanisms.

Recent experiments on red grouse (Mougeot et al. 2003a, 2003b) confirm previous evidence (Watson & Jenkins 1968; Watson 1985; Moss, Parr & Lambin 1994) that aggressive behaviour can limit population density. For 3 months in autumn, the aggressiveness of territorial cocks was increased by testosterone implants. This reduced population density for more than a year after the implants were exhausted. Hence aggressiveness in autumn influenced population density, not just in the following spring (Mougeot et al. 2003a), but also in the one after that (Mougeot et al. 2003b). Here, we explore the consequences of this striking observation.

Most previous red grouse population models have investigated how two competing hypotheses explained the cycles observed in time-series of certain shooting records (Potts, Tapper & Hudson 1984; Williams 1985; Moss, Watson & Parr 1996) and population counts (Watson et al. 1984; Moss & Watson 1991; Moss et al. 1996). One hypothesis (Dobson & Hudson 1992; Hudson, newborn & Dobson 1992; Hudson, Dobson & Newborn 1999) focuses on the parasite Trichostrongylus tenuis (Eberth.), the other (Mountford et al. 1990; Watson et al. 1994; Hendry et al. 1997; Matthiopoulos, Moss & Lambin 1998, 2000, 2002) on differential behaviour between kin and non-kin. Both aim to explain the demographic pattern of delayed density-dependent recruitment of young birds to the territorial population. The former invokes primarily variation in breeding success, the latter variation in recruitment of reared young (Mougeot et al. 2003b).

Here, we take a process-free approach to the role of aggressive behaviour in population dynamics. Rather than postulating a specific mechanism, and seeing how it explains past observations, we start with current knowledge of red grouse territorial behaviour and explore implications for population dynamics.

**BIOLOGICAL BACKGROUND**

Red grouse are territorial, monogamous birds. Cocks take up territories in autumn (Watson & Jenkins 1964) and most hold them until spring. Territorial cocks killed in autumn or winter are replaced by previously non-territorial individuals (Watson & Jenkins 1968). By spring, however, almost all non-territorial birds have emigrated or died (Watson 1985; Mougeot et al. 2003b) and the breeding population consists of territorial birds. Effectively all the available habitat is filled with territories, such that mean territory size is the inverse of cock breeding density. There are exceptions to these generalizations (Hudson & Renton 1988; Hudson 1990) but we model conditions in which they apply.

Hens gain territories by associating with cocks and so cock numbers govern hen numbers (Watson & Jenkins 1968; Moss et al. 1996; Mougeot et al. 2003, 2003b). We therefore confine the model to cocks and assume that hen numbers follow cock numbers.

Pair formation begins in autumn as territories become established, and families break up in the following autumn. Male chicks born in spring and reared in summer compete with each other and with old cocks for a territory in the same autumn (Watson & Jenkins 1968) and a variable proportion of youngsters obtain territories. Old cocks that lose their territories die or emigrate.

**MODEL DEVELOPMENT**

The discrete nature and relative timing of fecundity, mortality and recruitment in red grouse dictate a discrete-time population model (Fig. 1). We focus on closed populations denoted by the density of territory-holding cocks at the end of the territorial contest in year \( t \), and use the following, general population model as a starting point:

\[
P_{t+1} = P_t(s + bq_t),
\]

where \( s \) is the (constant) annual survival rate of adult cocks, \( b \) is the (constant) breeding success, i.e. the per capita production of reared, male young and \( q_t \) the proportion of young cocks, born in the spring of year \( t \), that become recruited into the territorial population in

![Fig. 1. The relative timing of events in the model. In year \( t \), each male in the territorial population (\( P_t \)) rears \( b \) male offspring, of which a proportion \( q_t \) obtain territories. The territorial population in year \( t+1 \) consists of these new recruits and those territory holders that survived (at a rate \( s \)) from year \( t \).](image-url)
autumn \( t \). Population change in red grouse is driven by recruitment of young and loss of old cocks to the territorial population, with recruitment of young playing the main part. [Adult survival varies from year to year but shows no consistent pattern during cyclic fluctuations, being lower during declines than during increases in some cyclic fluctuations (Moss & Watson 1991) and vice versa in others (Moss et al. 1996).] For simplicity, we assume that a constant proportion of older, territorial cocks retain their territories in the autumn contest. We also assume that mortality in territorial cocks between autumn and spring is negligible, as territorial cocks that die are replaced immediately by other cocks that have lost, or failed to obtain, territories during the autumn contest. This pool of non-territorial cocks suffers heavy mortality over winter and hardly any are left by spring.

The central idea is that, during the autumn territorial contest, cocks occupy territories whose size is related, not necessarily linearly, to aggressiveness in the population. Aggressiveness (denoted \( a \)) can be measured (Watson et al. 1994) as the average number of boundary disputes per individual, per unit time (but see Discussion) and is related positively to comb size, which is directly related to levels of testosterone (Moss et al. 1979). Aggressiveness is affected by the density of cocks, old and young combined, taking part in current and, in the case of old cocks, past territorial contests. In turn, aggressiveness affects the future density of territorial cocks by moderating recruitment of young into the territorial population. The impact of territorial behaviour on long-term population dynamics emerges from this interaction between aggressiveness and population density.

Young animals are less likely to establish a territory in a population of many, aggressive competitors. Hence, we assume that the proportion \( q \) is a decreasing function of autumn density and aggressiveness. Suitable mathematical formulations of this statement are the Ricker and Beverton–Holt functions. They have similar properties but, to avoid predisposing the model towards unstable dynamics (Gurney & Nisbet 1998), we chose the Beverton–Holt.

\[
q_t = \frac{1}{1 + Ka_P(1 + b)}
\]

where \( P_t(1 + b) \) is the density of animals competing for territories in the autumn of year \( t \) and \( K \) an arbitrary constant determined by the characteristics of the environment. Combining eqns 1 and 2 we obtain:

\[
P_{t+1} = P_t \left( s + \frac{b}{1 + Ka_P(1 + b)} \right)
\]

To simplify notation, eqn 3 is written in terms of \( h = KP_t(1 + b) \), a rescaling of the density of competing birds \( P_t(b + 1) \). For brevity, we refer to \( h \) as ‘autumn density’ henceforth.

\[
h_{t+1} = h_t \left( s + \frac{b}{1 + a_t h_t} \right)
\]

From field observations we make three basic inferences.

**Aggressiveness this year is influenced by aggressiveness in last year’s territorial contest**

In the population experiments of Mougeot et al. (2003b) old cocks were implanted with testosterone in autumn \( t \). This depressed recruitment of young and population density, and increased mean territory size. These effects lasted for over a year after the testosterone was exhausted and so the populations had, in effect, a memory of the experimental manipulation that continued to influence territorial behaviour, not only in autumn \( t \) but also in autumn \( t + 1 \).

**Aggressiveness needed by young cocks to be recruited into the territorial population is set by the territorial behaviour of old, established cocks**

In early autumn most of the surviving old cocks resume their previous territories with approximately the same boundaries as in the previous spring, often before young birds challenge for territories (Watson 1967, 1985; Watson & Jenkins 1968). Although the mean size of young and old cocks’ territories can differ within years, the direction of such differences varies and observed differences between age classes are small relative to differences in average territory size between years (Watson 1967; Watson & Miller 1971; A. Watson, unpublished data). It seems that young cocks, having no previous experience of staking out a territory, effectively mimic the territorial and, hence, aggressive behaviour of old cocks.

**Changes in aggressiveness are correlated positively with population density**

Territory size – the inverse of density – and aggressiveness in red grouse cocks influence each other. Comparisons among individuals within years and study areas show that more aggressive individuals have bigger territories (Watson & Jenkins 1968), and experimental testosterone implants increase individuals’ territory size, aggressiveness and comb size (Watson & Parr 1981; Moss et al. 1994). Comparisons among years within areas, however, show that mean comb size and aggressiveness are greater at higher densities, when mean territory sizes are smaller (Watson et al. 1994; Moss et al. 1996).

In cyclic population fluctuations, the relationship between aggressiveness and density is not linear. For example, peak aggressiveness follows peak densities with a lag of 1 year. Watson et al. (1994) suggested that aggressiveness was related directly to density and inversely to the size of kin clusters of territorial cocks, and that kin clusters were larger during the increase
phase of a cycle, lower during the decline. Here, we make no assumptions about kin clusters and simply assume a positive monotonic relationship between autumn density and changes in aggressiveness.

In short, we examine a population of territorial animals in which recruitment, and therefore future density \((h_{t+1})\), is regulated by present density \((h_t)\) and aggressiveness \((a_t)\). Current aggressiveness is set by the aggressiveness experienced by old cocks in the previous territorial contest, modified by density. Modification might occur before or during the current territorial contest. In the first case, the appropriate assumption is that density in autumn \(t\) modifies aggressiveness in autumn \(t+1\), in the second that density modifies aggressiveness in the same autumn. We investigate both possibilities. All the models comprise two coupled difference equations in the state variables and \(h_t\) and \(a_t\).

**MODEL 1: PAST DENSITY MODIFIES PRESENT AGGRESSIVENESS**

In this case, the difference equation tracking average, per capita aggressiveness is of the general form:

\[
a_{t+1} = f(a_t, h_t)
\]

(i) \(\lim_{h_t \to \infty} f(a_t, h_t) = a_t + U(a_t)\)

(ii) \(\lim_{h_t \to 0} f(a_t, h_t) = a_t - L(a_t)\)

(iii) If \(f\) is a continuous function, there exists a critical value of \(h_t\), say \(h_{cm}\), such that \(f(a_t, h_{cm}) = a_c\).

These properties describe an increasing, sigmoidal function of density with upper and lower bounds \(a_c + U(a)\) and \(a_c - L(a)\), and an inflection point at the density \(h_{cm}\). These requirements are satisfied (Fig. 2) by the general formulation:

\[
a_{t+1} = a_t - L(a_t) + (L(a_t) + U(a_t)) \frac{h_t^n}{h_t^n U(a_t) + h_t^n}
\]

where \(C\) is a control parameter affecting the slope of the function around the value \(h_{cm}\).

The functions \(U(a_t)\) and \(L(a_t)\) can be formulated in several ways and there is no evidence to support one over another. We return to this question below, but now focus on the simple case in which next year’s aggressiveness can only increase up to, or decrease down to, a constant proportion of current aggressiveness, i.e. \(U(a_t) = u a_t (u \geq 0, a\) constant) and \(L(a_t) = l a_t (0 \leq l < 1, a\) constant). This gives:

\[
h_{t+1} = h_t \left( s + \frac{1}{1 + a_t h_t} \right)
\]

\[
a_{t+1} = a_t \left(1 - l (1 + u) \frac{h_t^n}{h_t^n u + h_t^n l} \right)
\]

The system has two equilibria, the first corresponding to population extinction. We derived analytical conditions for local stability (Appendix I) of the equilibria in terms of the parameters \(b, s, C, u, l\), which fall
naturally into two groups, those relating to demography (breeding success \( b \) and survival rate \( s \)) and those relating to aggressive behaviour (shape parameter \( C \) and bounding parameters \( u \) and \( l \)). These are used to construct the ‘demographic parameter’ \( w = (1 - s)(b + s - 1)/b \) and the ‘behaviour parameter’ \( \gamma = Clu/(l + u) \), which simplify presentation of results from local stability analysis.

The qualitative properties of solutions within the regions of the parameter space defined by these conditions were explored numerically and the results are summarized in Fig. 3.

There exists a parameter region in which the model gives unstable solutions. These (e.g. Fig. 4) take the form of periodic fluctuations. In graphical realizations of the model throughout the paper we use autumn density \( h_t \). In some cyclic realizations, especially those arising from high values of the parameter \( C \), we observed small variations in amplitude.

The instability condition \( \gamma > 1 \) (see Fig. 3 and Appendix I) has an interesting biological interpretation. In this model, the expression

\[
g(h_t) = -l + (l + u) \frac{C}{h_m(l + u) + h_m^*l}
\]

eqn 8

gives the proportion by which aggressiveness alters from year \( t \) to year \( t + 1 \) as a function of autumn density. When autumn density \( (h_t) \) is below the equilibrium density \( (h_m) \) aggressiveness falls. In contrast, when autumn density exceeds the equilibrium density \( h_m \), aggressiveness rises. If, during two successive years, autumn density overshoots the equilibrium density the model produces a transition from decreasingly aggressive to increasingly aggressive behaviour, which is likely to produce unstable dynamics. The sharpness of this transition can be described in terms of \( m \), the slope of \( g(h) \) at \( h_m \):

\[
m = \frac{dg}{dh}(h_m) = \frac{Clu}{h_m(l + u)} = \frac{\gamma}{h_m}
\]

eqn 9

Overshooting of \( h_m \) by \( h_t \) is more likely when \( \gamma \) is greater (Appendix I) which implies that, for a given equilibrium density, the onset of unstable dynamics is more likely when the slope of \( g(h_t) \) is greater, such that eqn 6 tends to a stepwise function. This can be achieved by increasing the maximum proportions \( (l \) and \( u \)) by which aggressiveness varies from year to year, or by increasing the value of \( C \).
We explored the quantitative properties of the cycles in different regions of the parameter space (defined in Table 1). For realistic values of the vital rates \(0.2 < s < 0.8\) and \(0.5 < b < 2.0\) the period of the cycles always exceeded 9 years. Setting \(s\) and \(b\) to the middle of these ranges, with values of \(l\) and \(u\) in the ranges \((0.1, 0.9)\) and \((0.1, 2.5)\), respectively, gives cycles with mean period 15.8 years (standard deviation 4.0 years) and mean amplitude (max/min ratio of population size during a cycle) of 42.5 (standard deviation 60.7). The subset of these parameter combinations that gave realistic amplitudes (max/min ratio in population size < 10) gave cycles with periods in the range 10–14 years. In this subset, the sum of the proportions \(l\) and \(u\) was in the range 0.3–0.9 (from a possible range of 0.2–3.4) and the ratio \(l/u\) was in the range 0.5–1.4 (from a possible range of 0.1–2.5) indicating that, with this model, cycles of realistic amplitude are generated by relatively small and symmetric bounds to annual changes in aggressiveness.

**Table 1.** Parameter space examined in realizations of the models

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival rate</td>
<td>(s)</td>
<td>0.2–0.8</td>
</tr>
<tr>
<td>Breeding success</td>
<td>(b)</td>
<td>0.5–2.0</td>
</tr>
<tr>
<td>Maximum annual proportionate increase in aggressiveness</td>
<td>(u)</td>
<td>0.1–2.5</td>
</tr>
<tr>
<td>Maximum annual proportionate decrease in aggressiveness</td>
<td>(l)</td>
<td>0.1–0.9</td>
</tr>
<tr>
<td>Shape parameter</td>
<td>(C)</td>
<td>1–5000</td>
</tr>
<tr>
<td>Autumn density at which (a_{t+1} = a_t)</td>
<td>(h_m)</td>
<td>10</td>
</tr>
</tbody>
</table>

In this case territorial requirements are given by the general expression:

\[
a_{t+1} = f(a_t, h_{t+1})
\]

**eqn 10**

The model in eqn 7 is then modified:

\[
h_{t+1} = h_t \left( s + \frac{b}{1 + a_t h_t} \right)
\]

**eqn 11a**

\[
a_{t+1} = a_t \left( 1 - l + (l + u) \frac{h_t^c l}{h_t^c u + h_t^c u} \right)
\]

**eqn 11b**

The conclusions from local stability analysis of this system (Appendix II) are summarized in Fig. 5.

Once again, large values of \(\gamma\) are needed for instability. For example, setting \(b\) and \(s\) to plausible (for red grouse) values of 1.3 and 0.5, respectively, results in the condition \(\gamma > 11\), even stricter than the condition \(\gamma > 1\) for the previous version of the model. Again, for a given equilibrium density \(h_m\), we can interpret \(\gamma\) as the slope at \(h_m\) of the response of aggressiveness to density.

Unstable realizations of this system fluctuate with irregular amplitude and period. The value of the constant \(C\) is important in determining the regularity of the fluctuations. For example, in the bifurcation diagram in Fig. 6 values of \(C\) between 25 and 40 give highly irregular fluctuations. Outside this region, fluctuations are more regular.

However, spectral analysis of unstable solutions indicates that, despite irregularities, there always exists a clearly dominant period. Hence, even though this is a chaotic system, the period of the fluctuations is more regular than their amplitude (e.g. Fig. 7).

For realistic vital rates \((0.2 < s < 0.8\) and \(0.5 < b < 2.0\) the dominant period of the fluctuations lies
Fig. 6. Bifurcation diagram with respect to the parameter $C$. The other parameters were fixed at $s = 0.5$, $b = 1.4$, $u = 3$, $l = 0.6$ and $h_m = 10$.

Fig. 7. Sample output from two 10 000-year-long realizations of the model in eqn 11 with $s = 0.5$, $b = 1.4$, $u = 3$, $l = 0.6$ and $h_m = 10$, the first using $C = 35$ and the second $C = 90$. (a) and (b) display 50-year segments from each solution. (c) and (d) show the phase-spaces of the solutions. The phase-space of the first realization has a complicated structure and, to make this more clearly visible, the points have not been connected by lines. Plates (e) and (f) show the results from spectral analysis of 500-year segments of the two realizations. Note the clearly defined peaks at 3 and 5 years, respectively.
between 2 and 75 years (mean 8.4 years, standard deviation 9.9 years). Setting \( s \) and \( b \) to the middle of these ranges and examining values of \( l \) and \( u \) in the ranges (0.1, 0.9) and (0.1, 2.5), respectively, gives fluctuations with mean dominant period 6.0 years (standard deviation 3.9 years) and mean amplitude (max/min ratio of cycles) of 6/8 (standard deviation 3.4). The subset of these parameter combinations that gave realistic amplitudes (max/min ratio in population size < 10) gave fluctuations with dominant period in the range 2–12 years. In this subset, the sum of the proportions \( l \) and \( u \) was in the range 0.2–3.3 (from a possible range of 0.2–3.4) and the ratio \( u/l \) was in the range 0.1–24 (from a possible range of 0.1–25) indicating that, in contrast to Model I, fluctuations of realistic amplitude can be generated by asymmetrical and large values of \( l \) and \( u \).

**Comparison with a Previous Model on Kin-Facilitation**

Young cocks tend to take territories close to their natal territory, leading to clusters of related cocks. Members of such kin clusters facilitate the recruitment of their joint offspring (MacColl et al. 2000). The kinship hypothesis suggests that population cycles result from the build-up and decay of such clusters (Mountford et al. 1990; Moss & Watson 1991; Watson et al. 1994; Hendry et al. 1997). Matthiopoulos et al. (1998) formalized the kinship hypothesis by an age-structured model, making simple assumptions about the behavioural mechanisms involved.

The present models are not primarily about kinship but it is interesting to see how the kinship model compares with them. We therefore reformulate the kinship model:

\[
O_{t+1} = s(O_t + Y_t) \quad \text{eqn 12a}
\]

\[
Y_{t+1} = \frac{Ab(O_t + Y_t)}{A + K \frac{O_t^2}{sY_t}(O_t + Y_t)(b + 1)} \quad \text{eqn 12b}
\]

in terms of the state variables of autumn density and aggressiveness. Here, \( A, s \) and \( b \) are the total available area, the survival rate and breeding success, \( Y \) is the number of young cocks in the territorial population, \( O \) is the number of older cocks and \( K \) is an arbitrary rescaling constant. The expression for recruitment (equivalent to \( q \), in eqn 2) was derived from assumptions on the mechanism of kin-facilitation. Setting \( P_t = (O_t + Y_t)/A \) and combining the eqn 12a and 12b, we can re-write them in the notation of this paper (compare with eqn 3) as:

\[
P_{t+1} = P_t \left( \frac{s + \frac{b}{1 + Ka_P(1 + b)}}{sY_t} \right) \quad \text{eqn 13}
\]

where, in this case,

\[
a_t = \frac{O_t^2}{sY_t} \quad \text{eqn 14}
\]

Writing eqn 12 in terms of \( O_t, Y_t, O_{t-1}, Y_{t-1} \), and replacing into eqn 14 gives

\[
a_t = \frac{A}{b} P_t (1 + Ka_P P_t(b + 1)) \quad \text{eqn 15}
\]

Equations 13 and 15 can be written as a system of coupled, difference equations with state variables \( h_t = KP_t(1 + b) \) and \( a_t \).

\[
h_{t+1} = h_t \left( s + \frac{b}{1 + a_t h_t} \right) \quad \text{eqn 16a}
\]

\[
a_{t+1} = \frac{A}{K(b + 1)} h_t (1 + a_t h_t) \quad \text{eqn 16b}
\]

Equation 16a is the same as eqns 7a and 11a. The models differ in the way they update aggressiveness from year to year. The update rules in eqns 7b and 11b have upper and lower bounds as, in both cases, \( a_{t+1} \in [a_t(1 - l), a_t(1 + u)] \). In contrast, the update rule in eqn 16b has no upper bound and an unrealistic lower bound as \( a_{t+1} \in [0, \infty) \). This implies that, from year to year, aggressiveness can either increase without check or practically vanish. Even though this never happened in realizations of this earlier model it does, in theory, make it more prone to unstable dynamics. In this sense, the models presented in the present paper are more conservative.

Furthermore, the fact that the upper and lower bounds are determined by the parameters \( u, l \) and the shape of the curve in eqns 7b and 11b is determined by the parameter \( C \), affords greater control over the models’ properties. This enables us to quantify the generic form of the behavioural mechanism required for the occurrence of unstable dynamics (see previous sections) without specifying that mechanism.

In terms of their dynamical properties, the two models in the present paper give the same conditions for population extinction as the kinship model, and each is capable of generating population cycles. However, the transition from stable to unstable dynamics in the present models occurs at lower values of breeding success \( b \).

A comparison of the relative timing of population events in different models (Fig. 8) reveals similarities and differences. We plotted the relative magnitude of population density, aggressiveness and annual proportional changes in aggressiveness against time for two consecutive population cycles. All models indicate that peak aggressiveness should occur after peak population density and during the decline phase of the cycle. This agrees with field observations (Watson et al. 1994; Moss et al. 1996). Further, for low values of the constant \( C \), the output of Model I, which is structurally closer than Model II to the kinship model, resembles the output of the kinship model. For high values of \( C \), Models I and II display stepwise, annual changes in aggressiveness which cannot be produced by the kinship model.
In Models I and II upper and lower bounds limited the amount by which aggressiveness could change each year. This, however, does not guarantee that aggressiveness will not increase or decrease indefinitely over many years even though this did not happen in realizations of the model. For simplicity, we ignored this complication previously but now return to it.

We introduce long-term upper (\(M_u\)) and lower bounds (\(M_l\)) to aggressiveness (\(a\)) and redefine the functions \(U(a)\) and \(L(a)\) in eqn 6:

\[
U(a) = \begin{cases} 
M_u - a & \text{if } M_u < a(1 + u) \\ 
u a_i & \text{otherwise}
\end{cases}
\]

**MODELS WITH FIXED, UPPER AND LOWER LIMITS TO AGGRESSIVENESS**

In Models I and II upper and lower bounds limited the amount by which aggressiveness could change each year. This, however, does not guarantee that aggressiveness will not increase or decrease indefinitely over many years even though this did not happen in realizations of the model. For simplicity, we ignored this complication previously but now return to it.

We introduce long-term upper (\(M_u\)) and lower bounds (\(M_l\)) to aggressiveness (\(a\)) and redefine the functions \(U(a)\) and \(L(a)\) in eqn 6:

\[
U(a) = \begin{cases} 
M_u - a & \text{if } M_u < a(1 + u) \\ 
u a_i & \text{otherwise}
\end{cases}
\]
Using these definitions, we explored the behaviour of Model I:

\[ h_{t+1} = h_t \left( s + \frac{b}{1 + a_t h_t} \right) \]

\[ a_{t+1} = a_t - L(a_t) + (L(a_t) + U(a_t)) \frac{h_t C L(a_t)}{h_m U(a_t) + h_t C L(a_t)} \]

numerically. We present some conclusions and an example (Fig. 9) from this set of realizations.

The addition of fixed limits affected the behaviour of the model as follows. If the boundaries \( M_U \) and \( M_L \) contained the range of values taken by \( a_t \) in solutions of the model in eqn 7 then solutions were unaffected. For high values of \( C \), if the fixed limits were set closer to the equilibrium value \( a^* = (b + s - 1)/(h_m(1 - s)) \), the period and amplitude of the fluctuations decreased (Fig. 10). In Model II, however, the fluctuations were not damped, irrespective of how tightly the limits \( M_U \) and \( M_L \) bracketed the equilibrium value \( a^* \).

Adding fixed limits to aggressiveness to Model II gave similar results to Model I. If the limits were wide enough the solution evolved unaffected. If the limits were closer to the equilibrium value \( a^* = (b + s - 1)/(h_m(1 - s)) \), the period and amplitude of the fluctuations decreased (Fig. 10). In Model II, however, the fluctuations were not damped, irrespective of how tightly the limits \( M_U \) and \( M_L \) bracketed the equilibrium value \( a^* \).

**Discussion**

The models developed here assume only that population change is due to variations in the recruitment of young cocks to the territorial population, that recruitment is related inversely to population density and to aggressiveness during the autumn territorial contest, that aggressiveness one year affects aggressiveness the next, and that annual changes in aggressiveness are influenced by population density. Each assumption is justified by field observations which, however, are not detailed enough to define the functional form and relative timing of some of these relationships. To address these gaps in our knowledge, we made our general model parametrically flexible and explored four structurally different versions of it, with particular emphasis on population cycles, making no further assumptions about the behavioural mechanisms involved. Hence, predictions from these models are generic in that they can emerge from any putative mechanism consistent with our assumptions.

**OVERVIEW OF RESULTS**

Qualitatively, the different versions of the basic model are in agreement. All four (Models I and II, with and
without fixed, long-term limits to aggressiveness) readily generate unstable dynamics and all make an important testable prediction: cyclic population fluctuations should be accompanied by sudden shifts in the direction of annual changes in aggressiveness, from decreases in aggressiveness at low (< \( h_m \)) densities to increases at high (> \( h_m \)) densities.

In particular, Model I predicts that cycles are more likely when annual changes in aggressiveness show stepwise, delayed density dependence. Interestingly, Moss et al. (1996) gave evidence that the delayed density dependence in population growth observed during a red grouse population cycle was stepwise.

Testing of this prediction will require care when measuring aggressiveness. Aggressiveness takes many forms, some related only weakly to each other (Moss et al. 1979). Here, we are interested in those aggressive acts that contribute to occupying a territory.

In contrast to their qualitative consensus, different versions of the basic model displayed a wide range of quantitative properties. With parameter values reasonable for red grouse (Table 1), Model I generated regular cycles with long periods while Model II gave more chaotic fluctuations with shorter dominant periods. Furthermore, Models I and II are the extremes of a range of intermediate models in which changes in aggressiveness at \( +1 \) depend upon some combination of \( h_t \) and \( h_{t+1} \). These were not investigated here but preliminary explorations of such models gave trajectories with period and regularity, intermediate between those of Models I and II.

The wealth of quantitative properties displayed by this class of models suggests that it contains at least one model which, suitably parameterized, will emulate observed dynamics. However, there are likely to be many versions of the model that fit the data and therefore attempts at model-fitting may suffer from problems of identifiability (Lambin et al. 2002) until more of the functional relationships have been pinned down by experimental work.

Furthermore, factors other than territorial behaviour and vital rates shape population trajectories. For example, cycle period varies widely in the same grouse species, in no obvious relation to vital rates (Moss & Watson 2001). There is evidence from rock ptarmigan (\( \text{Lagopus mutus} \)), red grouse (Watson, Moss & Rothery 2000) and snowshoe hares (\( \text{Lepus americanus} \)) (Sinclair et al. 1993) that ∼10-year cycles have been entrained by cyclic weather patterns. This is a big topic which we do not explore, but preliminary investigations indicate that external influences can affect the period of the aggressiveness models.

**Fig. 10.** Realizations from the models in eqns 11 and 20. In this example we used the parameter values \( s = 0.5, b = 1.4, C_H = 0.6, C_L = 0.6, C = 200 \) and \( h_m = 10 \). Examples of autumn density \( (h_t) \) and aggressiveness \( (a_t) \) for a model with no fixed limits on aggressiveness are shown in (a) and (b), respectively. The addition of fixed limits \( (M_H = 0.5, M_L = 0.1) \) reduces the amplitude and period of the fluctuations in autumn density (c) and aggressiveness (d).

The sudden changes in aggressiveness associated with high values of \( m \) (eqn 9) could occur through the breakdown of cock kin clusters at high densities, as envisaged by the kinship hypothesis. Furthermore, the effective population memory implied by the experiment of Mougeot et al. (2003b) could, as they explain, be mediated through kin clusters.

**RELEVANCE TO THE KINSHIP HYPOTHESIS**

The present aggressiveness models and the kinship model of Matthiopoulos et al. (1998) each assumed that changes in breeding density were determined by variations in recruitment during the territorial contest. Otherwise, the biological assumptions might seem quite different. In fact, the 1998 model can be formulated as an aggressiveness model without postulating kinship as a driving mechanism. Conversely, the aggressiveness models are consistent with the kinship mechanism, although some of the assumptions made in 1998 might need changing.
Models of the kinship hypothesis at the organizational level of the kin cluster (Matthiopoulos et al. 2000, 2002) focused on ‘territory sharing’ between philopatric red grouse. This was postulated to occur through reductions in aggressiveness between related, neighbouring, territory-holders. The amount by which territories could contract was calculated using arguments on the geometry of territories and the degree of relatedness between cluster members. The fact that aggressiveness can lead to territory expansion (Mougeot et al. 2003a, 2003b) was not considered in these papers but two useful conclusions were reached. First, territory-sharing alone cannot lead to fluctuations of the amplitude observed in nature (Matthiopoulos et al. 2000) and, secondly, as population density increases family clusters break down abruptly and irreversibly (Matthiopoulos et al. 2002).

Empirically, the 1998 kinship model has been successful. Parameterized versions gave reasonable accounts of three different population cycles (Matthiopoulos et al. 1998), even though factors other than kinship certainly influenced observed trajectories. This model was also quantitatively consistent with the experimental results of Mougeot et al. (2003b).

None the less, the 1998 model has methodological drawbacks. The functional forms used to relate crowding, kin cluster size and age structure were inflexible. Therefore, in contrast to the models presented here, there was no way of quantifying the critical strength of the postulated mechanism required for the occurrence of instability (Turchin 2003). In addition, by reformulating that model in terms of density and aggressiveness, it transpires that the rule used for updating aggressiveness (eqn 16b) has no fixed bounds and so could, in theory, allow aggressiveness to become unrealistically strong or weak. This could predispose the model towards unstable dynamics. However, the present aggressiveness models show that cyclicality does not depend on this property and is likely to occur with other, less volatile, updating rules.

Conclusion

We have explored the dynamical consequences of recent field observations and reached a clear conclusion: interactions between aggressive behaviour and population density can cause unstable population dynamics. We provide general and analytical conditions for the occurrence of unstable dynamics and express them in terms of aggressive behaviour. The general prediction that the occurrence of cycles depends critically on the abruptness of the transition from tolerant to aggressive behaviour around the equilibrium population density now awaits validation in the field. The cyclic output of the models has a wealth of quantitative properties (period, amplitude and regularity) that augurs well for future attempts to fit such models to observed time series. First, we need to know more about the precise form and mechanisms that link density and aggressiveness. This could be the focus of future experimental work.

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References


Appendix I

LOCAL STABILITY ANALYSIS OF EQN 7A, B

The system in eqn 7a, b has two equilibria, \((h^*, a^*) = (0, 0)\) and \((h^*, a^*) = (h_m, (b + s - 1)(h_m(1 - s))).\) The condition for local stability of the extinction point is obtained as \(\text{Max}(s + b), (1 - l) < 1.\) Since \((1 - l) < 1,\) the condition simplifies to \(s + b < 1.\)

Using the substitution \(w = (1 - s)(b + s - 1)/b\) and \(\gamma = C \cdot \frac{lu}{u + l}\) the condition for stability of the non-trivial equilibrium becomes:

\[
\text{Max} \left\{ \left[ \frac{1}{2} (2 - w \pm \sqrt{w(w - 4\gamma)}) \right] \right\} < 1 \quad \text{eqn AI.1}
\]

Assuming that \(w > 0,\) i.e. that \(s + b > 1,\) there are two possibilities depending on whether the discriminant in eqn AI.1 is positive or negative. The discriminant is positive when \(\gamma < w/4,\) in which case condition AI.1 is written

\[
\frac{1}{2} \left(2 - w + \sqrt{w(w - 4\gamma)}\right) < 1 \quad \text{as} \quad 2 - w = (s + 1)(1 - s)/b > 0.
\]

This simplifies to \(\gamma = C \cdot \frac{lu}{u + l} > 0\) which is always true because \(C, l, u > 0.\) Therefore stability is always attained when \(\gamma < w/4.\)

The discriminant in (I.2) will be negative when \(\gamma > w/4.\) In this case condition AI.1 is written

\[
\frac{1}{4} \left(2 - w + 4w\gamma\right) < 1 \quad \text{which simplifies to} \quad \gamma < 1.
\]

Appendix II

LOCAL STABILITY ANALYSIS OF EQN 11A, B

Eqn 11a, b have the same two equilibria as eqn 7a, b. The characteristic equation for the trivial equilibrium is the same, and hence the condition for extinction is \(s + b < 1.\) Once again, using the substitutions \(w = (1 - s)(b + s - 1)/b\) and \(\gamma = C \cdot \frac{lu}{u + l},\) the condition for stability becomes:

\[
\text{Max} \left[ \left\{ \frac{1}{2} \left(2 - w + \gamma + \sqrt{w^2(1 + \gamma)^2 - 4w\gamma}\right) \right\} \right] < 1 \quad \text{eqn AII.1}
\]

If the discriminant in (II.1) is negative then the condition for stability is written

\[
\frac{1}{4} \left(2 - w + (1 + \gamma)^2 + 4w\gamma - w^2(1 + \gamma)^2\right) < 1.
\]

This simplifies to \(w > 0\) which is always true if \(s + b > 1.\)
The discriminant in (II.1) is positive when \( w/4 > \gamma/(1 + \gamma)^2 \). We further distinguish two cases depending on whether \( 2 - w(1 + \gamma) \) is positive or negative. If it is positive, i.e. if \( \gamma < 2/w - 1 \), then the condition for stability is written

\[
\frac{1}{2} \left( 2 - w(1 + \gamma) + \sqrt{w^2(1 + \gamma)^2 - 4w\gamma} \right) < 1,
\]

which simplifies to \( 4w\gamma > 0 \). For \( s + b > 1 \), this will always be true.

On the other hand, if \( \gamma > 2/w - 1 \), then the condition for stability is written

\[
\frac{1}{2} \left( w(1 + \gamma) - 2 + \sqrt{w^2(1 + \gamma)^2 - 4w\gamma} \right) < 1.
\]

This simplifies to \( \gamma < \frac{4}{w} - 2 \) which is not necessarily true and the non-trivial equilibrium is unstable when this condition does not hold. It is easy to check that \( 0 < (2/w - 1) < (4/w) - 2 \) and hence that \( \gamma > (4/w) - 2 \) is a necessary and sufficient condition for the occurrence of unstable solutions.