

Temporal changes in kin structure through a population cycle in a territorial bird, the red grouse *Lagopus lagopus scoticus*

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Abstract

Populations of red grouse (*Lagopus lagopus scoticus*) undergo regular multiannual cycles in abundance. The 'kinship hypothesis' posits that such cycles are caused by changes in kin structure among territorial males producing delayed density-dependent changes in aggressiveness, which in turn influence recruitment and regulate density. The kinship hypothesis makes several specific predictions about the levels of kinship, aggressiveness and recruitment through a population cycle: (i) kin structure will build up during the increase phase of a cycle, but break down prior to peak density; (ii) kin structure influences aggressiveness, such that there will be a negative relationship between kinship and aggressiveness over the years; (iii) as aggressiveness regulates recruitment and density, there will be a negative relationship between aggressiveness in one year and both recruitment and density in the next; (iv) as kin structure influences recruitment via an affect on aggressiveness, there will be a positive relationship between kinship in one year and recruitment the next. Here we test these predictions through the course of an 8-year cycle in a natural population of red grouse in northeast Scotland, using microsatellite DNA markers to resolve changing patterns of kin structure, and supra-orbital comb height of grouse as an index of aggressiveness. Both kin structure and aggressiveness were dynamic through the course of the cycle, and changing patterns were entirely consistent with the expectations of the kinship hypothesis. Results are discussed in relation to potential drivers of population regulation and implications of dynamic kin structure for population genetics.

Keywords: kin selection, kin structure, *Lagopus*, population cycles, red grouse

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Introduction

Kin selection offers an extremely elegant and beguilingly simple explanation for much of the altruistic behaviour observed in natural populations (Hamilton 1963, 1964). Individuals will behave more altruistically and less aggressively toward relatives because they share a greater proportion of genes and so, by helping, an altruist should

increase the proportion of its genes in the next generation, thereby increasing its own inclusive fitness.

A corollary of the development and subsequent refinement of kin selection theory has been considerable research emphasis on determining patterns of genetic relatedness and social structure in natural populations to identify situations where altruism may evolve (Hoglund *et al.* 1999) or explain observed behaviour among conspecifics (Griffin & West 2003). Hypervariable molecular-marker systems, such as microsatellite DNA polymorphisms, facilitate such effort by providing an ability to identify relatives in natural populations, even in the absence of any behavioural or

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observational information that may indicate putative pedigrees (Piertney *et al.* 1999; Shorey *et al.* 2000).

There are, however, very few studies that have documented temporal variation in localized kin structure to examine the extent to which kin selection can vary over time, or any consequences for behaviour and population dynamics (Coltman *et al.* 2003; Nussey *et al.* 2005). This is somewhat surprising as temporal changes in kin structure have been proposed as an important, yet often overlooked, process that can drive population dynamics (Krebs 1996). In principle, changes in kin structure may affect spacing behaviour and social tolerance, which themselves may influence reproduction, mortality or dispersal (Cote *et al.* 2007) to an extent that can cause population regulation or fluctuations in density (Krebs 1985). Such ideas have been reinforced by recent theoretical and empirical studies on how patterns of altruistic behaviour, determined by kin selection, may be mediated by population level parameters such as density and competition. If altruistic behaviour among relatives subsequently leads to increased competition among them, there should be a reduction in any net selective advantage of altruism, so removing any incentive to act altruistically (West *et al.* 2001, 2002). Hence, the consequences of altruism may change over time as patterns of density and relatedness vary, and if altruism affects recruitment it may regulate overall population size. In particular, if the kin structures that mediate altruism or social tolerance take time to build up and decay, the resulting lag between population density and recruitment can cause population cycles.

A species in which intrinsic population processes mediated through kin selection have been considered as fundamental for driving population dynamics is the red grouse (*Lagopus lagopus scoticus*). This game bird species is locally common in heather-dominated regions of northern and western UK. Populations undergo regular cyclical fluctuations in abundance with periods of between 4 and 10 years (Moss & Watson 2001). Several hypotheses have been proposed to account for such cyclical dynamics, and the effects of food availability, predation and fluctuating genotypic selection have been refuted outright (see Moss & Watson 2001 and references therein). The prevailing view has been that cycles are caused by delayed density-dependent interactions with a caecal nematode parasite, *Trichostrongylus tenuis*, primarily by influencing female breeding success and hence the number of young available for recruitment to the breeding population (Hudson 1986; Hudson *et al.* 1992, 1998, 2002). However, recent experimental studies have concluded that interactions between parasite and host do not explain cyclic dynamics in red grouse, and that other processes must operate to cause cyclic population declines (Redpath *et al.* 2006).

An alternative explanation for cyclic population dynamics in red grouse is the kinship hypothesis (Mountford *et al.*

1990; Moss *et al.* 1994, 1996; Watson *et al.* 1994; Moss & Watson 2001). This posits that changes in kin structure through the course of a population cycle determine levels of aggressiveness and that these, in turn, regulate density. Male red grouse are monogamous and territorial, and the number of territory-holding males determines the male and female breeding population size (Moss *et al.* 1994; Mougeot *et al.* 2003a, b). Males obtain territories in autumn, retain these over winter, pair with a female by spring, father a brood of chicks and help to rear them in summer. Young males from these broods compete among themselves and with established males to obtain a territory the following autumn. The recruitment of males to the local adult population is contingent on an individual successfully gaining a territory. Territorial males are less aggressive towards kin than to non-kin and, at low population density, established males help young relatives to recruit into the population by relinquishing ground or helping in territorial contests with other, unrelated males (MacColl *et al.* 2000). This increases density and leads to the formation of clusters of territories held by related males (Watson *et al.* 1994; Piertney *et al.* 1999). Positive feedback between kin selection and recruitment is thought to cause these kin clusters to proliferate and density to increase in subsequent years until space becomes limiting, and kin selection is curtailed because the net gain for an individual being altruistic no longer matches the loss in direct fitness caused by increased competition. At this point all individuals behave aggressively toward each other and recruitment will be depressed to a level that cannot compensate for natural mortality and the population will go into decline. Recruitment should remain low as kin clusters break up because, whilst kin competition may be curtailed as density falls, kin structure is now minimal and so kin-selected behaviour is also minimal. Hence population-level aggressiveness continues to increase. As a result, there is more than one year of population decline. Only when density and competition among kin and non-kin is sufficiently low for the process of cluster formation and kin-selected recruitment to recommence does the cycle start again.

A succession of studies using different modelling approaches confirm that interactions between kin selection, aggressiveness and density can produce cyclic population dynamics that mirror the period and amplitude of cycles seen in natural populations (Hendry *et al.* 1997, 1998, 2000, 2002, 2003, 2005). Models of interactions between and aggressiveness alone, without the delayed density-dependence in aggressiveness induced by kin selection lead to stable dynamics. Moreover, recent experiments have shown that aggressiveness does regulate red grouse populations (Mougeot *et al.* 2003a, b; 2005a, b): experimental implants of testosterone into adult male grouse during autumn increased their aggressiveness and territory size, reduced recruitment and breeding density in at least two subsequent springs, and so

changed population growth rates from positive to negative (Mougeot *et al.* 2003a). None of these studies however, demonstrated that, in accordance with the kinship hypothesis, changes in aggressiveness are a consequence of varying patterns of kin structure and kin selection.

Here we document levels of kin structure annually over a 10-year period encompassing a full, 8-year population cycle in a natural population of red grouse in northeast Scotland. We examine whether the changing patterns of kin structure are consistent with detailed predictions of the kinship hypothesis, and determine the relationships between levels of kin structure, aggressiveness and recruitment within the population. The conceptual relationships between density, aggressiveness and kin structure as envisaged by the kinship hypothesis are illustrated in Fig. 1A, and these define the following specific predictions:

- 1 Kin structure will build up during the increase phase of a cycle, but breaks down prior to maximum density with birds becoming more aggressive as space becomes limiting. Thus, at equivalent population density, kin structure should be higher during the incline phase than during the decline phase of a cycle.
- 2 Because of the way in which kin structure influences aggressiveness, there will be a negative relationship between kin structure in spring of year t and aggressiveness in the autumn of the same year.
- 3 Because aggressiveness regulates density, there will be a negative relationship between aggressiveness in autumn t and density in spring $t + 1$, and between aggressiveness in autumn t and population change between springs t and $t + 1$.
- 4 Because kin structure influences population density via recruitment and aggressiveness, there will be a positive relationship between kinship in spring t and the recruitment of young males between springs of year t and $t + 1$.

We determine kin structure by mapping all territories and then genotyping all territory-holding males at multiple hypervariable microsatellite DNA loci to identify related individuals (Piertney *et al.* 1999). Levels of aggressiveness are indexed as supra-orbital comb height, which is a proxy for aggressiveness as it correlates positively with circulating plasma testosterone levels (Moss *et al.* 1979; Mougeot *et al.* 2005b).

Materials and methods

Study site and sampling

Changes in male population density, kin structure and aggressiveness were monitored annually between 1994 and 2003 at Glas Choille (57°07'N, 3°19'W) northeast Scotland. Individuals were located and captured by

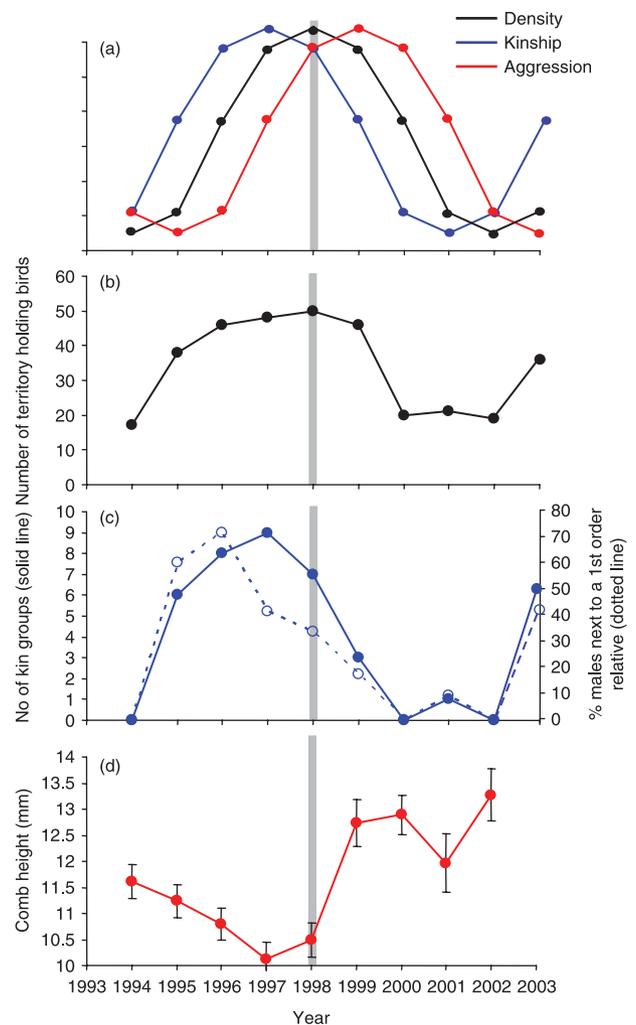


Fig. 1 Predicted and observed (1994–2003) temporal changes in population density, aggressiveness and kin structure for male red grouse: (a) predicted changes in density, kin structure and aggressiveness according to the kinship hypothesis, whereby changes in density lag behind kin structure and changes in aggressiveness lag behind density; (b) observed population size (number of males holding a territory in spring); (c) kin structure as measured by the number of kin groups (solid line and closed symbols) and the proportion of individuals next to a relative (dotted line and open symbols); (d) comb height (mm) in autumn (\pm SE). The grey line in each graph indicates the year of peak density.

dazzling and netting them at night (Hudson 1986). Grouse were sampled across a 140-hectare area of Glas Choille, but density and kin structure estimates are presented for a central 52-hectare area. This core area is therefore bordered by a buffer zone, which minimizes edge effects when calculating the number of kin groups in the population. Males were individually ringed and marked with a unique combination of coloured wing streamers that allowed identification at distance (Boag *et al.* 1975). The number and approximate boundaries of individual male territories

were established in spring (March through to May) from early morning watches of instances of territorial behaviour of identifiable birds. As grouse are monogamous and males only recruit to the breeding population once they have acquired a territory, overall population size was determined from the number of territory-holding males present. Per capita recruitment rate was measured as the number of young territorial males in the spring of year $t + 1$, divided by the total number of males holding territories in the spring of year t . Overall population change was measured as the difference in the total number of territory-holding males between springs t and $t + 1$ divided by the number of territory-holding males in spring t .

The maximum height (in mm) of the supra-orbital combs of males during autumn (September–December) was measured as a proxy for aggressiveness (Moss *et al.* 1979; Mougeot *et al.* 2005a). Given that measurements were unevenly distributed between months within autumn, and that measurements varied among months for a given year, comb height was modelled via a mixed model (MIXED procedure; SAS 2001) with year and male age as fixed effects, and individual male and month-nested-in-year as random effects. Unequal group variances were adjusted for by using Satterthwaite's approximation (SAS 2001) to determine the degrees of freedom. Fitted values from these models thus provided average comb height values for each autumn, standardized for sampling date and age.

DNA extraction and microsatellite genotyping

Blood samples were taken from the brachial vein of each individual and stored in sterile isotonic SSC buffer. DNA was extracted using a DNeasy DNA extraction kit (Qiagen Ltd) according to the manufacturer's instructions, with elution into 200 μ L of storage buffer. Individuals were genotyped at between 15 and 17 di-, tri- and tetranucleotide microsatellite loci according to Piertney & Dallas (1997) and Piertney *et al.* (1998).

Related individuals were identified among genotyped individuals using a combination of approaches according to Piertney *et al.* (1998). In brief, parent/offspring relationships were identified using CERVUS (Marshall *et al.* 1998), which by inference also identified some full-sibling relationships when a father had more than one offspring. Full-sibling pairs that were present but whose father was not a territory holder and hence potentially not sampled were identified from relatedness estimates (Queller & Goodnight 1989). Non-overlapping distributions of relatedness for non-relatives and first-order relatives allow correct inference of relationship from relatedness (Piertney *et al.* 1999). Likelihood-ratio tests, implemented within KINSHIP version 1.3.1 (Queller & Goodnight 1989) were used to confirm that putative brothers were significantly more likely to be actual brothers than unrelated. Kin

clusters were defined as groups of relatives holding neighbouring territories with a common boundary between two or more relatives and no other intervening territory.

Results

Ninety-seven percent of birds that held territories between 1994 and 2003 were captured, sampled and included in analyses ($n = 464$). Changes in male density at Glas Choille showed an eight-year population cycle (Fig. 1b). The number of territory-holding males in the 52-ha core area increased yearly from 17 in 1994 to 50 birds in 1998 and 49 in 1999. Numbers of birds then crashed to 19 birds in 2000, and began to rise again in 2003.

Kin structure was dynamic through the course of the population cycle (Figs 1c and 2). In the first year of the cycle (1994), the 17 territory-holding males were all unrelated. The following year (1995), the number of territorial males increased to 38, and 61% of them were adjacent to a relative. This defined six kin clusters of mean size 3.83 ± 1.14 (SE) individuals. The number of kin clusters increased for a further two years (eight clusters of mean size 4.13 ± 1.13 (SE) involving 72% of the population in 1996 and nine clusters of mean size 2.22 ± 0.15 (SE) individuals involving 42% of the population in 1997). In 1998, the number of kin clusters declined to seven, involving 34% of individuals, and there were further reductions in subsequent years (three clusters in 1999 involving 17% of birds, and zero clusters in 2000). Thus, kinship peaked before the peak in density, and at equivalent density the prevailing kinship was greater during the incline phase than during the decline phase of the cycle (compare Fig. 2c, f).

Comb height decreased during the incline phase of the cycle, reached a minimum in autumn 1997, increased slightly in 1998, and then increased greatly in 1999, whereupon the population crashed (Fig. 1c). Hence, the population decline was associated with an increase in aggressiveness. Maximum aggressiveness was reached after the peak in density.

Overall, the time lags between density and kinship, and between density and aggressiveness, are consistent with the predictions in Fig. 1a. These time lags are further illustrated by phase plots (Fig. 3). The clockwise spiral-phase plot of the number of kin groups against the number of territory-holding males (Fig. 3a) indicates a time lag with peak kinship occurring prior to peak density. A similar pattern is seen if the proportion of individuals next to a relative is substituted for the number of kin groups (data not shown). Conversely, the anticlockwise, spiral configuration resolved when comb height is plotted against the number of territory-holding males (Fig. 3b) indicates a delayed density-dependent relationship in comb height, a surrogate for aggressiveness.

Across all years there was a significant negative relationship between kinship and comb height in year t (number of

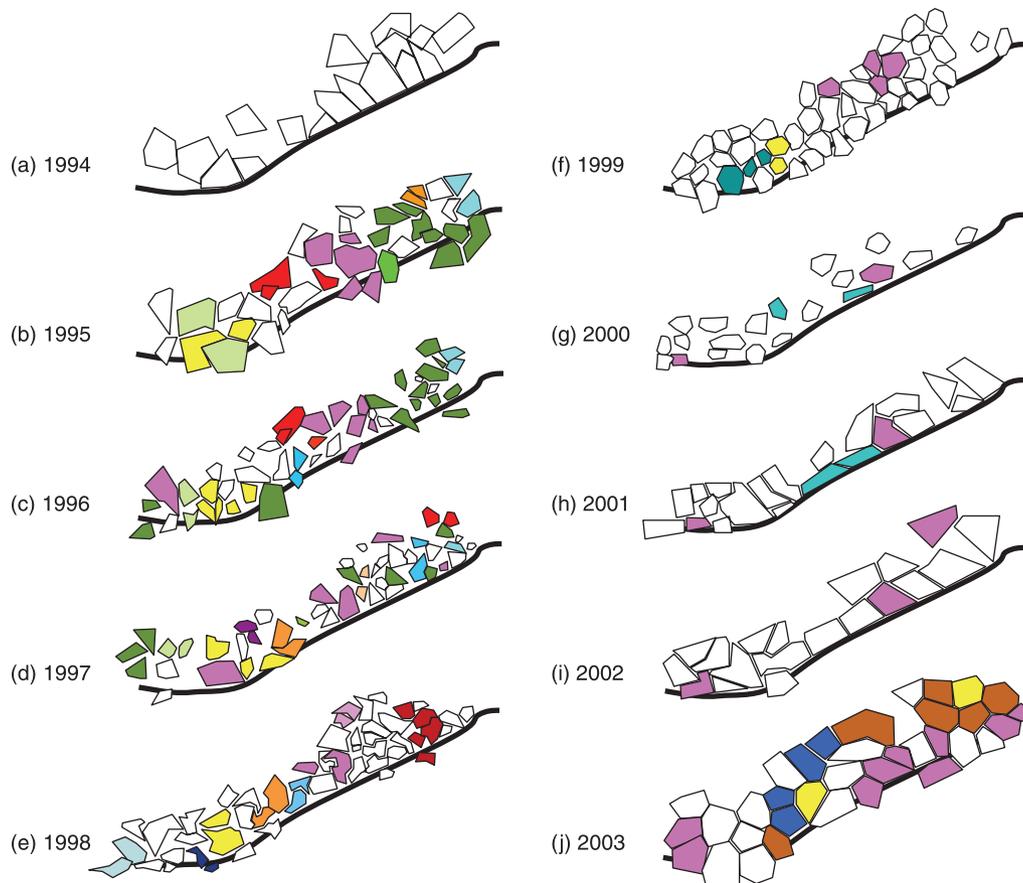


Fig. 2 Patterns of kin structure in the core area at Glas Choille for each spring between 1994 and 2003. Each polygon represents an individual male's territory, and polygons of identical colour are occupied by related individuals. Colours of different patriline are consistent between years. Individuals occupying uncoloured territories are unrelated to any of the other territorial males in the study zone. The black line running through the population is the road that delimits one edge of the study area.

kin groups: Pearson's $r = -0.82$, $P = 0.007$; proportion of individuals next to a relative: $r = -0.68$, $P = 0.044$); a highly significant positive relationship between kinship in spring t and per capita recruitment from spring t to $t + 1$ (number of kin groups: partial $r = 0.95$; $P = 0.004$), and a significant negative relationship between the height of supra-orbital combs in autumn t and density in spring $t + 1$ ($r = -0.89$; $P = 0.001$), and with population change between springs t and $t + 1$ ($r = -0.80$; $P = 0.031$).

Discussion

Our data have highlighted that (i) kin structure was dynamic through the course of an 8-year cycle in a natural population of red grouse; and (ii) the changing pattern of kin structure was entirely consistent with the predictions of the kinship hypothesis that posits that changes in kin structure can generate lagged changes in aggressiveness, and that these can regulate density, so generating cyclic population dynamics.

The kinship hypothesis states that lower levels of aggressiveness between kin than between non-kin will produce kin-biased recruitment and the formation of kin clusters within populations. These processes have been confirmed previously (Watson *et al.* 1994; Piertney *et al.* 1999; MacColl *et al.* 2000). As density increases, positive feedback between kinship and recruitment is posited to increase kin structure, until space becomes limiting and the benefit of altruism is small, whereupon individuals switch from being kin-tolerant to intolerant. Our data are consistent with this prediction, showing a build up of kin structure through the incline phase of the population cycle and low levels of aggressiveness when there were high levels of kinship. We also showed a switch in aggressiveness as the population approached peak density—comb height showed year-on-year reductions until 1997, whereupon it increased to a maximum in 1999.

The kinship hypothesis also states that once kin-tolerant behaviour is curtailed, recruitment is reduced to a point that cannot compensate for mortality and the population

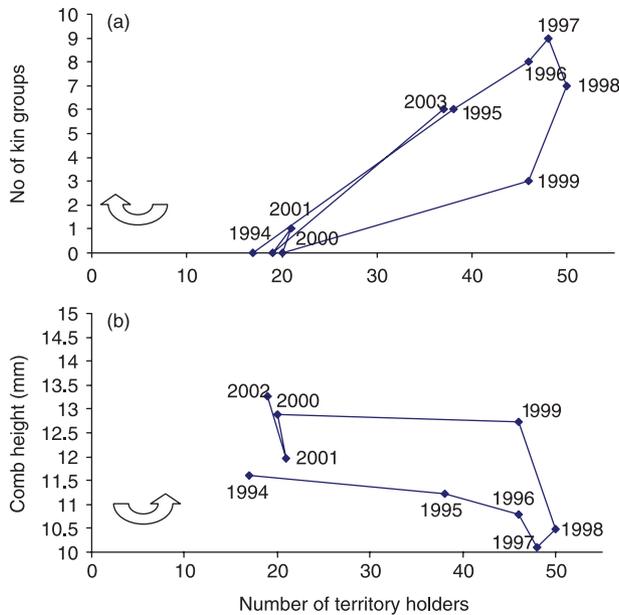


Fig. 3 Phase plots between the number of territory-holding males and (a) number of kin groups and (b) comb height. In (a), the clockwise spiral configuration indicates a time lag with the peak in kinship occurring prior to the peak in density, whereas in (b) the anticlockwise spiral configuration indicates delayed density-dependence in comb height (aggressiveness).

goes into decline. Again we show that the patterns observed are consistent with these predictions, with density declining slightly between 1998 and 1999, then crashing between 1999 and 2000. If a decline is to last more than a single year, aggressiveness must remain high following the initial decline in density. This would be caused by further increases in aggressiveness following the initial break-up of kin groups, in spite of declining density. The observation that comb height remained high at least until 2001 is consistent with this prediction.

Over the course of the cycle, comb height in autumn t was closely related to density in spring $t + 1$, so confirming that aggressive behaviour regulates density (Mougeot *et al.* 2003a, b, 2005a, b). The expected relationships between kinship, aggressiveness and density were also confirmed. Kinship in spring t was negatively related to aggressiveness in autumn t and also to per capita recruitment rate between year t and year $t + 1$, consistent with the idea that kinship regulates recruitment and population change by mediating changes in aggressiveness.

Logistical constraints prevented us replicating this study across multiple sites or over multiple cycles. Nevertheless, the 10-year study included an 8-year cycle and the early increase phases of two consecutive cycles, with a consistent signature of kin cluster formation with increasing density. Moreover, the main predictions of the kinship hypothesis

could each have been refuted in each year of the study, giving many opportunities for rejection of the hypothesis as a potential cause of cyclic dynamics in red grouse. The challenge now is to experimentally test whether manipulation of kin structure in natural populations produces the predicted changes in aggressiveness, sufficient to change levels of recruitment and density.

An enduring issue in ecology has been understanding the relative importance of extrinsic processes, such as host-parasite or predator-prey interactions, and intrinsic processes, such as behaviour, in the regulation of animal numbers (May 1973; Stenseth & Ims 1993; Berryman 2002; Turchin 2003). Much of the focus of such work has been on cyclic population dynamics of northern temperate vertebrate species, and the prevailing view has developed that extrinsic processes are the more likely drivers of cyclic dynamics, with intrinsic processes being deemed insufficient to destabilize populations (Berryman 2002; Turchin 2003). However, this view appears to have been reached through a lack of theoretical models and empirical evidence to show how proposed intrinsic mechanisms could operate in natural populations, rather than any direct refutation that they do not (Matthiopoulos *et al.* 2003, 2005). The findings of the current study highlight how intrinsic processes can operate in cyclic populations, and as such should stimulate examination of similar processes that may operate in other species (Charnov & Finerty 1980; Lambin & Krebs 1991; Lambin & Yoccoz 1998; Sutherland *et al.* 2005).

From a broader perspective, the current study highlights the dynamic nature of local genetic structure in natural populations. Non-random distribution of individual genotypes is known to influence local selection, inbreeding and dispersal, and also to play a confounding role in allelic association and quantitative genetic analyses (Ewens & Spielman 1995; Coltman *et al.* 2003; Nussey *et al.* 2005). The demonstration that local structure can be transient, or at least varies temporally, will complicate attempts to understand the longer term evolutionary and ecological consequences of such processes. Moreover, temporal variation in genetic structure violates a central assumption of many population genetic studies that aim to determine the spatial distribution of genetic diversity from single samples, and from this to infer patterns of dispersal, connectivity and isolation among populations. Local temporal variance may have important consequences, especially for conservation and management.

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