Spatio-temporal dynamics of the grey-sided vole in Hokkaido: identifying coupling using state-based Markov-chain modelling

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Explaining synchronization of cyclical or fluctuating populations over geographical regions presents ecologists with novel analytical challenges. We have developed a method to measure synchrony within spatial-temporal datasets of population densities applicable to both periodic and irregularly fluctuating populations. The dynamics of each constituent population is represented by a discrete Markov model. The state of a population trajectory at each time-point is classified as one of 'increase', 'decrease', 'peak' or 'trough'. The set of populations at any time-point is characterized by the frequency distribution of these different states, and the time-evolution of this frequency distribution used to test the hypothesis that the dynamics of each population proceeds independently of the others. The analysis identifies years in which population coupling results in synchronous states and onto which states the system converges, and identifies those years in which synchrony remains high but is accounted for by coupling observed in previous years. It also enables identification of which pairs of sites show the highest levels of coupling. Applying these methods to populations of the grey-sided vole on Hokkaido reveals them to be fluctuating in greater synchrony than would be expected from independent dynamics, and that this level of synchrony is maintained through intermittent coupling acting in *ca.* 1 year in four or five. High synchrony occurs between sites with similar vegetation and of similar altitude indicating that coupling may be mediated through shared environmental stimuli. When coupling is indicated, convergence is equally likely to occur on a peak state as a trough, indicating that synchronization may be brought about by the response of populations to a combination of different stimuli rather than by the action of any single process.

Keywords: Markov chain; population cycles; synchrony; grey-sided vole, *Clethrionomys rufocanus*; Hokkaido; Moran effect

1. INTRODUCTION

Synchrony must arise as the result of some form of general coupling of populations. The mechanism of this coupling could be the result of a dispersal process (Zweigler 1977; de Roos *et al.* 1991; Ranta *et al.* 1995; Haydon & Steen 1997), or as a result of a common demographic reaction to regional-scale environmental (e.g. climate (Moran 1953)) or trophic stimuli (e.g. nomadic predators (see Ydenberg, 1987; Norrdahl & Korpimäki 1996)) or a mixture of all or some of these mechanisms. When population densities exhibit some inherently periodic behaviour, synchrony may be maintained as a consequence of only intermittent coupling of populations so long as the rate at which phase is 'forgotten' is low relative to the frequency of coupling that brings populations back into the same phase (e.g. Ranta *et al.* 1995; Haydon & Greenwood 2000; Haydon *et al.* 2001). If the dynamics are less periodic, coupling must be more frequent to generate the same levels of synchrony. Identifying the frequency, magnitude and means of population coupling remains a largely

unsolved problem in population ecology (Ranta *et al.* 1999; Bjørnstad & Grenfell 2001; Jonzen *et al.* 2002).

Distilling the large amounts of information contained within data concerning spatial-temporal variation in population density may be awkward for several reasons (Buonaccorsi *et al.* 2001). Data may exist from many locations but only for short time-periods (e.g. fur returns for muskrat and mink across Canada (Erb *et al.* 2000)), or for long time periods but from few locations (e.g. fur returns for lynx across Canada (Elton & Nicholson 1942)). The data may exhibit quite different dynamics at each location, or exhibit dynamic irregularities or heterogeneities at different times at the same location, and/or be complicated by long-term trends that are not easily dealt with (e.g. shooting records for red grouse in the UK (Haydon *et al.* 2002)). Often the most extensive datasets use quantities like fur returns or shooting records that may be nonlinearly related to population density, or may be riddled with substantial observation error. Only on somewhat serendipitous occasions are spatio-temporal datasets extensive enough to allow unleashing of the full power of modern analytical methods (e.g. wavelet analysis (Grenfell *et al.* 2001)).

The extensive dataset describing the population densities of the grey-sided vole (*Clethrionomys rufocanus*)

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Figure 1. (a)(i) Map of Hokkaido indicating the location of 225 sampling stations for time-series included in this study. Also two typical time-series from (ii) group 2 and (iii) group 6. (b) Diagram of the Markov chain underlying the population dynamics. In strictly 4-year periodic populations, the Markov chain will be traversed by the thicker arrows in a clockwise manner. Where the dynamics are less predictable the state transitions will assume greater use of the transitions indicated by the thinner arrows.

through time across the entire island of Hokkaido exhibits several of these properties (Stenseth & Saitoh 1998). The time-series are short, no longer than 31 years' duration, densities were sampled at over 225 different spatial locations from 11 topographically distinguishable groups (figure 1a; Saitoh *et al.* 1998), but the dynamics are various. In northeastern and central mountainous locations

the populations appear cyclical, with somewhat noisy periods of 2–4 years, whereas southwestern populations show only seasonal fluctuations (Saitoh 1987; Bjørnstad *et al.* 1996, 1998). Attention has been directed at an explicit description of the patterns of population synchrony across the island (Saitoh 1987; Bjørnstad *et al.* 1999), but much less at examining the temporal flux in synchrony; which

may provide important clues about the mechanisms underlying the generation of synchrony.

Our objective here is to develop a methodology that allows quantification of the degree of dynamic cohesion or state-synchrony between vole populations through time at different locations across Hokkaido. We estimate the fraction of years when this level of synchrony is unusually high, and the frequency of years in which coupling must have occurred to give rise to these elevated levels of synchrony. We are also interested in establishing the state of the populations immediately before and after coupling events as this might suggest possible mechanisms underlying synchronization. We seek to establish between which population coupling is strongest, and to identify environmental features of sites that correlate with a propensity for sites to exhibit coupled dynamics. This we use to analyse the extent of synchronization—and probable underlying mechanisms—in the Hokkaido vole system (e.g. Stenseth & Saitoh 1998).

2. METHODS

The data we consider are a family of time-series $\{X_{i,t}\}$, where i ($i = 1 \dots n$) denotes a site and t denotes discrete time ($t = 1 \dots z$). The value of $X_{i,t}$ is proportional to the population density at site i in year t . We are interested in the periodicities of the time-series and the degree of synchrony. By synchrony we mean the extent to which population fluctuations are aligned. Note that this is a different question from correlation because amplitude is not taken into account (Buonaccorsi *et al.* 2001).

We regard the data $\{X_{i,t}\}$ as having arisen from an evolving random field, that is, the time-series at the various locations evolve according to some space-time dynamics. The evolutions at different sites are related by some additional dynamics which may work in the direction of causing synchrony among the sites. We construct a model with the aim of statistical detection of this synchrony. Inferences will be made about questions of interest which are framed in terms of a number of stochastic models.

(a) The Markov model

From each time-series $\{X_i\}$ corresponding to a fixed location, let us define a new time-series $\{Y_i\}$ ($t = 2 \dots z - 1$) with four states, namely

- $Y_t = 1$ if $X_{t-1} > X_t \leq X_{t+1}$ (X_t is a trough),
- $Y_t = 2$ if $X_{t-1} \leq X_t \leq X_{t+1}$ (X_t is the intermediate value of two consecutive increase years),
- $Y_t = 3$ if $X_{t-1} \leq X_t > X_{t+1}$ (X_t is a peak),
- $Y_t = 4$ if $X_{t-1} > X_t > X_{t+1}$ (X_t is the intermediate value of two consecutive decrease years).

Note that we have classified the (infrequent) years of no change as 'increasing' events. Suppose the time-series $\{Y_i\}$ is defined as Markov. Then there is a 4×4 transition matrix for $\{Y_i\}$ which we denote $\mathbf{T}$, with entries $t(a,b)$, a and b taking values 1,2,3,4. Populations will visit these states in some restricted order but may spend varying times in the increase and decrease states. Of course, the populations will not by definition exist in peak or trough states for consecutive years. Because each row of $\mathbf{T}$ sums to one, there are potentially four independent parameters in the transition matrix $\mathbf{T}$: $t(1,2)$, $t(2,2)$, $t(3,1)$ and $t(4,1)$ (see figure 1b).

The form of the matrix $\mathbf{T}$ is

$$\mathbf{T} = \begin{bmatrix} 0 & t(1,2) & 1 - t(1,2) & 0 \\ 0 & t(2,2) & 1 - t(2,2) & 0 \\ t(3,1) & 0 & 0 & 1 - t(3,1) \\ t(4,1) & 0 & 0 & 1 - t(4,1) \end{bmatrix}.$$

If transitions to states occur independently of preceding states (i.e. the probability of density going up or down is independent of the state at all previous time intervals) then these parameters may all be written simply in terms of the probability that the population will either go up (denoted p) or down ($1 - p$). Specifically $t(1,2) = t(2,2) = t(3,1) = t(4,1) = p$ and $t(1,3) = t(2,3) = t(3,4) = t(4,4) = 1 - p$.

By adding constraints we may define several special cases. For example, it might be that transition probabilities from all states accord with the overall probability of going up or down (i.e. are state independent), except if the system is in the trough state, in which case the proceeding state is more likely to be an increase state than the simple probability of going up would suggest (i.e. trough states are disproportionately more likely to be followed by multiple years of increase than by a single year). In this case we would identify transition from the trough state to be state-dependent. There are four possible models with only one state-dependent transition probability, six models with two state-dependent transition probabilities, four models with three state-dependent transition probabilities, and (the full 'saturated' model) with four state-dependent transition probabilities. Which of these models, if any, is appropriate for use in the case of the Hokkaido vole system? We can decide by estimating the components of the matrix $\mathbf{T}$, both unconstrained and under the various constraints corresponding to the different models and computing likelihoods in each case (e.g. Menard *et al.* 1993).

We estimate p , as the observed proportion of occasions where the population density increases between two time-points:

$$\hat{p} = 1/n(z-1) \sum_{i=1}^n \sum_{t=1}^{z-1} \delta_{i,t,p}$$

where $\delta_{i,t} = 1$ if $X_{i,t} \leq X_{i,t+1}$ and $\delta_{i,t} = 0$ otherwise. Similarly, $t(a,b)$ is estimated as the observed proportion of occasions when the time-series changes to state b at time $t+1$, given that it was in state a at time t :

$$\hat{t}(a,b) = 1/n(z-2) \sum_{i=1}^n \sum_{t=2}^{z-2} \delta_{i,t,p}$$

where $\delta_{i,t} = 1$ if time-series i is in state a at time t .

(b) Model selection

The estimated log-likelihood of the data $\{Y_{i,t}\}$, corresponding to the estimated transition matrix $\hat{\mathbf{T}}$ is

$$\text{LL}(\{Y_i\}|\mathbf{T}) = \sum_{i=1}^n \sum_{t=2}^{z-2} \ln \hat{\mathbf{T}}(Y_{i,t}, Y_{i,t+1}).$$

The likelihoods of the constrained models mentioned above can be computed by estimating the components of $\mathbf{T}$ under the corresponding restrictions. Likelihood ratio tests then select the most appropriate of the 16 possible models. Because the time-series are short it is necessary to estimate model parameters from multiple time-series. However, because we know that different dynamics characterize different groups of populations across the island (figure 1a; Saitoh 1987; Bjørnstad *et al.* 1996, 1998) we

only combine time-series within groups and do not attempt to fit one single model to more than one group of time-series.

The adequacy of the resulting selected model $\hat{T}$ as a representation of the dynamics of each time-series may be assessed by examining the distribution of likelihoods computed by simulation from a large number of time-series of length $z-2$, from the saturated four parameter model. If $LL(\{Y_i\}|\hat{T})$ lies inside the 95% confidence intervals (CI) for the likelihoods calculated from these simulated datasets then $\hat{T}$ may be judged a reasonable fit to the data.

(c) Comparing properties of the model and data

From the Markov model it follows that the numbers of consecutive times of increase or of decrease are geometrically distributed, specifically that the probability of spending i ($i > 0$) consecutive years increasing is $\tau(2,2)^{i-1}\{1-\tau(2,2)\}$ and that the probability of spending i years decreasing is $\tau(4,4)^{i-1}\{1-\tau(4,4)\}$. This assumption can be checked against the observed frequency distribution of consecutive times in states 2 and 4 using a χ^2 goodness-of-fit test.

We compute the distribution of the first return times of a Markov chain with transition matrix $\hat{T}$ to each of the four states (although we note this distribution could be recovered from $\hat{T}$ analytically (Kemeny & Snell 1976)). From the distribution of return times, say to state 1, the trough state, we can evaluate the extent to which the time-series is periodic, and obtain a rough estimate of the period. This is compared with periodicity information obtained (by others) using the periodogram of the data. It is also interesting to compare the distributions based on simulation of $\hat{T}$ of return times to the various states, to the empirical return time distributions obtained directly from inspection of the data.

We measure synchronization in the model and data as follows. Let the elements, $s(j)_t$, of the row vector s_t be the proportion of populations in each state at time t ($j=1\ldots 4$). As a measure of state synchronization, we adopt the entropy (this is also the Shannon-Weaver diversity index (e.g. Ricklefs 1990)) of this empirical distribution at time t , estimated as

$$H_t = -\sum_{j=1}^4 s(j)_t \ln(s(j)_t).$$

Let H_{null} denote possible values of H_t under the hypothesis that the n time-series are stationary, independent Markov chains, all associated with transition matrix $\hat{T}$. We approximate the distribution of H_{null} by simulation, noting that $s_{t+1} = s_t \hat{T}$, and using $\hat{T}$ as the estimate of the transition matrix T to simulate the dynamics of each of the n populations treated as separate and independent. If

$$1/(z-2) \sum_{t=2}^{z-1} H_t$$

lies outside the 95% CI for H_{null} , the collection of time-series $\{Y_{i,t}\}$ ($i=1\ldots n$) can be regarded as significantly synchronized (and therefore not independent of each other).

A useful measure of degree of synchronization is then the quantity $\Phi_t = 1 - H_t/\bar{H}_{null}$ (where $\bar{H}_{null}$ is the expected value of H_{null}) which will be close to zero when the observed time-series are independent and close to one if the time-series are always all in the same state at the same time (i.e. fully synchronized). Exploratory simulation analysis shows that the synchrony index Φ_t falls off exponentially in an initially synchronized but uncoupled set of populations. Using simulation we estimate the

half-life, t_ϕ , of the synchrony index as it decays from a value of one in sets of populations equal to the number of populations in each group. We also compute 'one-step' CIs about the expected entropy at time $t+1$, conditional on the observed state of the whole system at time t . Comparing the profile of H_t with these one-step conditional CIs indicates over which time-intervals the dynamics of the n time-series are significantly at odds with the assumption of dynamical independence.

(d) Pairwise synchrony analysis

Consider two time-series, $\{Y_{1,t}\}$ and $\{Y_{2,t}\}$, undergoing independent state transitions according to model $\hat{T}$. Let $q(i,j,k,l)$ indicate the probability that $Y_{1,t+1}=k$ and $Y_{2,t+1}=l$, given that $Y_{1,t}=i$ and $Y_{2,t}=j$. This 16×16 matrix of probabilities may be estimated as the Kronecker product of $\hat{T}$ with itself: $Q = \hat{T} \otimes \hat{T}$. We say that a pair of state transitions is a synchronized pairwise transition if they convey two time-series in identical states at time t to identical (but not necessarily alternative) states at time $t+1$.

Define $PLL\{Y_i, Y_j|\hat{T}\}$ to be the following partial pairwise likelihood:

$$PLL\{Y_i, Y_j|\hat{T}\} = \sum_{t=2}^{z-2} \delta_t \ln q(Y_{i,t}, Y_{j,t}, Y_{i,t+1}, Y_{j,t+1}),$$

where $\delta_t = 1$ if $(Y_{i,t}, Y_{j,t}, Y_{i,t+1}, Y_{j,t+1})$ is a synchronized pairwise transition, and zero otherwise; $PLL\{Y_i, Y_j|\hat{T}\} = 0$ when $i=j$.

Note that $PLL\{Y_i, Y_j|\hat{T}\}$ takes on its maximum value (zero) if time-series i and j never undergo a synchronized pairwise transition, and will be smallest (most negative) when i and j undergo many such transitions. We interpret this latter state of affairs as evidence of non-independent pairwise coupling. Values of $PLL\{Y_i, Y_j|\hat{T}\}$ may be assembled as elements of an $n \times n$ dissimilarity matrix, wherein zero entries indicate absence of synchronized transitions and very negative entries indicate many such transitions.

For each of the n sites, four different physical characteristics were available: geographical coordinates, average annual snow depth, height above sea-level, a vegetation index and (from the population data) the average population density. To compare the hypotheses that (i) sites that share similar physical characteristics would tend to be synchronous, and (ii) sites that are spatially proximate to each other would tend to be synchronous, we constructed $n \times n$ pairwise 'proximity matrices' that indicated similarity of sites for each characteristic (Euclidian distance, absolute difference in average annual snow depth, absolute difference in elevation, absolute difference in vegetation index and absolute difference in average population density). We tested the significance of the correlation coefficient between all pairs of these five matrices, and between these matrices and the matrix of partial likelihoods (indicating the pairwise synchrony) using a Mantel randomization test.

3. RESULTS

The number and length of time-series in each group are given in table 1 (columns 2 and 3). For time-series from groups 1 and 6 all transitions were state-dependent. Other groups required between one and three of the possible possible transition probabilities to be state-dependent (table 1, columns 6–9). The likelihoods of models selected to fit the 11 groups of time-series all fell within the 95% limits of the distributions of likelihoods generated from

Table 1. Summary statistics for the models fitted to each group of time-series.

group	<i>n</i>	<i>z</i>	Φ_t^a	half-life <i>t</i> _θ ^b	$\hat{\imath}(1,2)^{c(\text{increase})}$	$\hat{\imath}(2,3)^{d(\text{decrease})}$	$\hat{\imath}(3,4)^{e(\text{decrease})}$	$\hat{\imath}(4,1)^{f(\text{increase})}$	proportion of time spent in states 1, 2 and 3 ^g	mean RT ^h	CV RT ⁱ	
1	31	31	0.178 ^{0.009}	7.14	0.405	0.678	0.329	0.736	0.329	0.196	0.329	3.107
2	31	31	0.342 ^{0.001}	7.15	0.539*	0.762	0.401	0.853	0.315	0.222	0.315	3.10
3	20	27	0.350 ^{0.001}	4.68	0.560*	0.688	0.319	0.810	0.312	0.254	0.312	3.12
4	8	23	0.131 ^{n.s.}	1.87	0.614*	0.386 [†]	0.386 [†]	0.864	0.248	0.394	0.248	3.71
5	27	31	0.320 ^{0.001}	7.11	0.517*	0.721	0.483 [†]	0.793	0.301	0.216	0.301	3.14
6	27	23	0.188 ^{0.015}	7.21	0.458	0.670	0.316	0.808	0.325	0.222	0.325	2.94
7	20	23	0.165 ^{0.046}	4.91	0.561*	0.670	0.317	0.827	0.310	0.206	0.310	3.12
8	30	23	0.065 ^{n.s.}	7.19	0.552*	0.583	0.448 [†]	0.728	0.281	0.265	0.281	3.36
9	10	12	0.317 ^{0.019}	2.54	0.545*	0.857	0.455 [†]	0.545*	0.288	0.183	0.288	2.81
10	13	12	0.283 ^{0.023}	3.02	0.601*	0.767	0.399 [†]	1.000	0.314	0.246	0.314	2.87
11	8	12	0.148 ^{n.s.}	1.97	0.466*	0.534 [†]	0.534 [†]	0.722	0.249	0.217	0.249	2.89
all ^j	225	31	0.118 ^{0.001}									—

^a The relative synchronization of the various population groupings on Hokkaido with significance (*p*-value less than or equal to superscripted value) determined from bootstrapping (see text).
^b The half-life of the entropy, determined numerically, in sets of *n* independent Markov chains, initiated in perfect synchrony.
^{c–f} The estimated transition probabilities of optimal models selected using likelihood ratio tests: an asterisk indicates when the probability is the state independent probability of an increase (*p*); a dagger indicates when the probability is the state independent probability of a decrease ($1 - p$).
^g The stable-state structure predicted from the transition matrix $\hat{T}$.
^h The mean observed return time to the trough state of time-series starting out in the trough state.
ⁱ The average coefficient of variation of this return time for each series (this could not be calculated for groups 9–11 owing to the short length of each time-series).
^j We do not attempt to describe all 225 populations in the 11 groups by a single model because of the well-known dynamic differences that exist between them.

Figure 2. The observed (solid black) and predicted (grey stippled) frequency distributions of return times to state 1 (the trough state). (a) Group 1, (b) group 2, (c) group 3, (d) group 4, (e) group 5, (f) group 6, (g) group 7 and (h) group 8. Predicted frequencies are those associated with the transition model selected for each group (see table 1). Groups 9–11 are omitted because of their shorter lengths.

fitting the estimated model to data simulated assuming the saturated model determined the dynamics of each time-series. For two of the 11 groups, resident-time distributions for the increase phase did differ significantly from that predicted by the model (with marginally more multi-year periods of increase than predicted). However, in the remaining nine of the 11 groups, resident times in the increase state did not differ significantly (at the 5% level)

from the geometric distribution assumed by the model. The assumption of geometric resident times in the decrease state was met in all 11 groups. We therefore proceeded assuming the models fit the data adequately.

The distribution of return times provides an interesting summary of the periodic behaviour of time-series in each group (figure 2) and provides results in general agreement with those obtained from spectral analyses (Bjørnstad *et*

Figure 3. The line (solid circles) indicates the observed entropy across the entire island. The lower panel indicates the proportion of populations across the entire island that are in: state 1 (trough state, black); 2 (increase state, white); 3 (peak state, hatched); and 4 (decrease state, grey stippled). For example, 1976 saw a large proportion of the vole populations on Hokkaido in a trough state.

al. 1998). Only three groups have distribution modes greater than 2 years (groups 2, 3 and 5). The coefficient of variation around the mean return time (table 1, column 14) should be an inverse measure of the constancy of periodicity. The probability of a time-series being in each of the four states (i.e. the 'stable state' structure) is provided in table 1 (columns 10–12).

Figure 3 shows how the entropy for all 225 populations across the island varies over time. Prominent trough years are 1964, 1967, 1976, 1985 and 1988, but other states may dominate at this spatial scale, for example, 1965, 1975, 1979 and 1987 were years where most populations were in the peak state. Figure 4 shows how the entropy for each group varies over time. For several groups entropy levels for many years fall within the 95% CI expected assuming independent dynamics. Whereas overall 8 of the 11 groups were significantly synchronized in the sense that average entropy lay outside of the 95% CIs expected if all time-series in groups proceeded fully independently of each other (table 1, column 4), in most groups this is due to only a limited number of years in which coupling reduced entropy below expected levels. Only in groups 2, 3 and 5 do dynamics appear persistently synchronous. One-step conditional confidence limits on changes in entropy are indicated in figure 4. Circles at the base of the diagram indicate when observed entropy changes in a way that is significantly contradictory to the assumption of one-step independence (we refer to these as 'synchronizing years'). There are only 6 years (1964, 1965, 1970, 1974, 1980 and 1983) in which coupling activity is not observed in any of the groups. At the 5% level, synchronizing years are frequent events, occurring on average about once every 4 years (and even at the 1% level they still occur on average every 5 years). Almost all groups (and certainly those containing the longer time-series) experience these shock years, indicating that these sets of time-series are not adequately modelled assuming their dynamics to be independent, but require coupling events to occur on a more or less regular basis.

The analysis shows different groups undergo state realignments in different years, and reveals little evidence

for 'island-wide' shock years. When all 225 populations are viewed together it appears that the years of greatest synchrony coincide with island-wide troughs (see figure 3); however, a different picture emerges when the time-series are viewed by group. In synchronizing years the populations within a group are almost equally likely to converge to any state except the decrease state (in such years 33% of all transitions are to the trough state, 21% to the increase state, 32% to the peak state, but only 14% to the decrease state). Figure 5 shows the distribution of states within groups for each of the 60 occasions that synchronizing years were detected, ranked in order of their significance. From this it is clear that convergence occurs almost equally often on the trough and peak states, and that this is equally true of the strongest most improbable synchronizing years in which entropy is at its lowest, as the weaker ones. The estimated half-life of the synchrony index, t_{ϕ} , (table 1, column 5) is highly dependent on the number of time-series in the group, but is over 4 years for seven of the 11 groups which explains how this relatively infrequent coupling activity can result in high average levels of synchrony over time. The least probable reductions in entropy do not always result in the most obvious system synchronization, but may actually precede these occasions. The dynamics of the transition model are such that reductions in entropy (system synchronization) might be expected (even in the absence of any coupled dynamics) given a previously apparently unremarkable system configuration.

The correlation coefficients between elements of the matrices containing measures of pairwise synchrony and pairwise site similarity measures are indicated in table 2. Sites at which dynamics are synchronized tend to be close to each other, characterized by similar vegetation indices, and occur at the same elevations, they also experience similar levels of snow coverage (but not significantly so). Sites that support similar population densities tend also to be synchronized. Unfortunately the interpretation of these results is confounded by the fact that sites located close to each other are also characterized by similar vegetation indices and average population densities.

Figure 4. The line (solid circles) indicates the observed entropy of each group. (a) Group 1, (b) group 2, (c) group 3, (d) group 4, (e) group 5, (f) group 6, (g) group 7 and (h) group 8. The horizontal dashed lines indicate 95% confidence limits on the expected entropy in comparable datasets simulated using $\hat{T}$ and assuming total dynamical independence between the time-series. The vertical black lines indicate the one-step 95% CIs on the entropy conditional on the precise state configuration of the system one step previous. The black circles at the base indicate at which time periods the combined dynamics fail the one-step independence assumption. Groups 9–11 are omitted because of their shorter lengths.

4. DISCUSSION

This analysis shows that the state dynamics of vole populations on Hokkaido fluctuate in greater synchrony than would be expected if the dynamics were independent at each site, and that the population ‘trajectories’ are endowed with sufficient intrinsic periodicity that this level

of synchrony can be obtained through coupling acting only in *ca.* 1 year in four or five. This analysis shows synchrony to be highest among cyclical populations in the northeast of Hokkaido, and least in more irregularly fluctuating populations in the south and west of the island. Pairwise measures of the extent to which populations at different sites are synchronized correlate with the simi-

Figure 5. The distribution of states in each group for all identified synchronizing years. The date of synchronization and the group in which it occurs is indicated on the x-axis, and corresponds to the years indicated by black circles at the bottom of the panels of figure 4. Synchronizing years are ranked (left to right) in descending order of their statistical deviancy from expectation under the hypothesis of independent dynamics (using the s.d. of the boot-strapped predictions and t -statistics). Black, trough state; forward hatching, increase state; bold backward hatching, peak state; backward hatching, decrease state. The upper panel shows the observed entropy corresponding to each of these groups in these years.

Table 2. Correlation coefficients between elements of the similarity matrices and their significance evaluated using a Mantel randomization test.

(* $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$. Δ should be read as 'absolute difference between two sites with respect to...'. Our measure of pairwise synchrony runs from negative (synchronized) to zero (never synchronized), thus a positive correlation between synchrony and Δ distance indicates that sites separated by large distances are less synchronous than those separated by small distances. Similarly, sites separated by larger distances tend also to differ with respect to their vegetation indices and average population densities.)

	Δ distance	Δ snow depth	Δ vegetation	Δ altitude	Δ population density
synchrony	0.142***	0.052	0.085***	0.059**	0.111***
Δ distance		0.007	0.084**	0.017	0.084*
Δ snow depth			-0.072**	-0.049	-0.062
Δ vegetation				0.0252	0.051
Δ altitude					0.170***

larity of vegetation indices and the altitude measured at the same pairs of sites indicating that state coupling may be mediated through shared environmental stimuli. However, the same pairwise measures of synchrony also decline with distance between sites and differences in average population density, consistent with possible dispersal and predator-oriented explanations for synchrony. When coupling is indicated by improbable state-convergences, convergence is as likely to occur on a peak state as a trough, indicating that synchronization may not be brought about by the action of nomadic predators: in which case it might be expected that convergence would occur more often on only a single state.

If nomadic predators are not responsible for synchronization of populations, two further possibilities remain. Populations may be synchronized by high dispersal rates between populations or different populations may be responding similarly to large-scale environmental stimuli. Bjørnstad *et al.* (1999) established that the correlation length (the distance at which the covariance between two population densities at two sites is equal to that between

two randomly chosen locations) for *C. rufocanus* is ca. 50 km. These authors concluded that this correlation length is longer than would be anticipated from what is known about the dispersal of this vole species (thought to be considerably less than 1 km per generation) but were unable to distinguish between predation and other sources of environmental covariance as explanations for the observed levels of synchrony. Perhaps the observation that state-convergences occur irregularly and with equal frequency on both peak and trough states is also inconsistent with a dispersal mechanism. If this low level of dispersal is really inconsistent with the high correlation length of these populations, and not caused by nomadic predators then levels of synchrony must be explained by Moran effects, and this conclusion is consistent with the fact that synchrony levels are highest between sites with similar vegetation, population densities and height above sea level, because climatic anomalies might impact ecologically similar populations in the same way. However, because convergences are equally likely to occur on the trough and peak states it is likely that different environ-

mental phenomena may be capable of forcing the dynamics into synchrony.

Bjørnstad *et al.* (1996, 1998) identified a trend from cyclical dynamics in the northeastern and central regions of Hokkaido (groups 2, 3 and 5) to less cyclical dynamics in the south and west of the island (groups 6 and 8). Our analysis is in broad agreement with these findings: only in groups 2, 3 and 5 do the distributions of return times possess modal values greater than 2 years, and we find these are also the three most synchronous groups. Paradoxically, these groups have distributions of return times with higher standard deviations and coefficients of variation than other groups, indicating that by this measure they are less predictably periodic than other groups. Groups 4, 7 and 8 in the south and west of the island are among the least synchronous groups examined.

The approach proposed and applied here has several advantages: it makes minimal assumptions; it is particularly suited to the analysis of relatively short time-series with irregular higher frequency dynamics; it avoids the need to de-trend the time-series; it requires only knowledge of whether population density increased or decreased at each time interval; and it is simple, robust and intuitive to interpret. The analysis developed by Haydon & Greenwood (2000) generated similar insights about the potential coupling underlying synchronous population dynamics but that analysis required dynamics be clearly cyclical, and that the period of the cycles be relatively long so that phase increments at each time-point were modest. This current analysis, using just a four-state approach, is suited to data that fluctuate irregularly rather than cycles, specifically for fluctuations in which the distributions of times spent in increasing and decreasing phases is geometrically distributed, and is therefore particularly suited to high frequency fluctuations, often characteristic of small mammal dynamics. This method can be extended to work with more or less complex states than defined in this analysis. We analysed these data using states defined by a four-point, eight-state pattern (rather than the three-point, four-state pattern adopted here), but found the level of support for these more complex models only marginally increased, and the results to be almost identical (in fact the adoption of an eight-state Markov model overcomes the slight discrepancy in the distribution of consecutive 'increase' years we encountered in two groups but actually reinforces the conclusion that synchronizing years are as likely to occur on the peak state as the trough). Populations that fluctuate with longer and more regular periods would require a higher number of states based on more points than adopted here in order to capture the dynamics. The methods described in this paper are suited to time-series in which the demographic trends are large compared with any possible count error, however, so long as this is the case, the magnitude of any count error is unimportant. In the event that count error confuses the demographic trends some form of data smoothing would be appropriate.

In its application to the current data, the effectiveness, simplicity and intuitive appeal of this method is bought through the audacity of disregarding the quantitative estimates of the actual population densities at each site, in favour of the four states or 'phases' of our Markov chain. In phase-based analysis of population dynamics amplitude

of population fluctuation is not informative and may even be regarded as a statistical nuisance. An advantage of simplifying the time-series to one containing only a few unambiguous states is that considerable statistical power is left to estimate transition probabilities, and the time-evolution of the distribution of states can be reliably characterized. However, the value of this exchange obviously depends on the information content of the discarded data. Of course, when quantitative data are absent, as when resources are allocated in an attempt to acquire broad-scale information about population trends at the expense of detailed estimates at each site (an obvious historical example being Charles Elton's snowshoe rabbit enquiry (Chitty 1950)), then these sorts of non-metric methods might be particularly useful (see also Legendre *et al.* 1981; Menard *et al.* 1993).

In summary, eight out of 11 groups of vole populations on Hokkaido are significantly synchronized, and the most synchronous populations are also the most regularly cyclical. However, synchrony is not maintained uniformly over time, rather it is generated intermittently and irregularly on *ca.* 1 year in four or five, after which it wanes, often rapidly. Because these populations tend to synchronize with equal frequency on population peaks and troughs, and dispersal rates are considered to be low, we suggest the available evidence supports the idea that synchrony is most likely to arise in these populations as a result of a shared response to common climatic stimuli.

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