

Distinguishing causes of intraspecific synchrony in population dynamics

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We examined the degree and cause of intraspecific synchrony in population dynamics between 29–42 populations for each of seven mammalian species. Regions containing multiple populations with similar dynamics were identified using cluster analysis. Two explanations for the observed synchrony were evaluated, dispersal and the “Moran effect”, a spatially correlated density independent perturbation, such as weather, which occurs across populations. Populations synchronized by dispersal are expected to exhibit a negative relationship between synchrony and distance, while populations synchronized by a Moran effect must have a similar density-dependent structure (DDS). To distinguish between these hypotheses we used autoregressive modeling to determine the DDS of each population, and cross-correlation to estimate the degree of synchrony between populations. Dispersal alone was assumed to be responsible for synchrony in populations with a significant negative synchrony-distance (S-D) relationship and heterogeneous DDS. We assumed that a Moran effect could have produced synchrony in populations with homogeneous DDS and a non-significant S-D relationship. It was not possible to assign synchrony to a single factor in regions with a homogeneous DDS and a significant S-D relationship, and we excluded the possibility of a Moran effect in regions with heterogeneous DDS and a non-significant S-D relationship. Using these criteria, we identified dispersal as synchronizing populations within one region each of ermine, lynx, mink and red fox and in two regions of muskrat. A Moran effect may have synchronized one region of ermine, fisher, lynx, and mink, although we were unable to identify a causative factor. One lynx and one mink region showed characteristics of both dispersal and Moran-based synchrony, and 9 regions of synchrony could not be assigned to either factor. These results show that by examining the DDS and the S-D relationship we were able to determine the factors most likely responsible for synchronized population dynamics in 10 of 21 cases. Possible cases of Moran-based synchrony do not appear to be common, occurring in only 18.2% of these regions. It should also be noted that just as correlation does not imply causation, presence of homogeneous DDS does not indicate a Moran effect, only its possible occurrence.

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Large-scale synchronous dynamics were first described over 600 years ago for cyclic pest species such as lemmings and insects (as cited in Elton 1942). Two features were quickly recognized in these species, their dramatic fluctuations in population size and the large scale synchrony of the fluctuations (Elton 1924, 1942, Elton and Nicholson 1942, Keith 1963). Most work in

this area has concentrated on understanding what factors control cyclicity (Hansson 1984, 1987, Krebs et al. 1986a, b, Hanski 1987, Hanski et al. 1991, 1996, Berryman 1995, Reid et al. 1995, Hanski and Henttonen 1996) rather than synchrony because researchers have been interested in trying to predict or reduce outbreaks (e.g. Berryman 1978). It was also usually assumed that

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a single factor was responsible for both cyclicity and synchrony.

Synchronous dynamics are interesting in their own right and work on synchrony, divorced from cyclicity, has increased recently (Myers 1988, Pollard 1991, Thomas 1991, Royama 1992, Hanski and Woiwood 1993, Ranta et al. 1995a, b, 1997a, b, Kaitala et al. 1996a, b, Stacy et al. 1997). Current interest derives from a new appreciation of the Moran effect (Moran 1953), its ability to synchronize dynamics, and its relationship to decades-old debates about the influence of density-dependent and density-independent factors and their scale of operation (Elton 1942, Andrewartha and Birch 1954, Lack 1954).

Two main hypotheses are used to explain synchronous dynamics. Interpopulation dispersal can correlate population dynamics especially when dispersal rates are related to density (Finerty 1980, Sutcliffe et al. 1996). As animals disperse from regions of high density they increase local population size in adjacent areas, synchronizing regional dynamics. Alternatively, density independent factors (e.g. weather) which are correlated across populations can synchronize density changes in populations that have a similar density-dependent structure (DDS), what is termed a Moran effect (Royama 1992). The DDS of a population is represented by the values of its density-dependent terms (Moran 1953). For example, population size at time t ($X_t = \ln N_t$) in a population whose dynamics are described by the Gompertz equation, $X_t = \alpha_0 + \alpha_1 X_{t-1} + \alpha_2 X_{t-2} + \varepsilon_t$, is determined by a constant (α_0), environmental noise (ε_t), and the DDS as indexed by the coefficients of the direct (α_1) and delayed (α_2) density-dependent terms. Moran showed that if the density-dependent coefficients, α_1 and α_2 , are equal in two or more populations, the correlation between their dynamics is equal to the correlation between their environmental noise (ε_t) components. As the differences increase between the density-dependent terms of the two populations, the ability of the Moran effect to synchronize the populations decays (Moran 1953, Royama 1992).

Ranta and co-workers (Ranta et al. 1995a, b, 1997a, b, c, Kaitala et al. 1996a, 1997, Heino et al. 1997) have investigated synchronization through dispersal and the Moran effect using simulations and long-term data sets for vertebrates. Simulations show that dispersal produces a negative relationship between distance and

degree of synchrony, which the Moran effect alone cannot produce (Ranta et al. 1995a, b). Synchrony produced by a combination of dispersal and the Moran effect is indistinguishable from results produced by dispersal alone based on the synchrony-distance (S-D) relationship (Ranta et al. 1995a, b). Simulations further indicate that a Moran effect, modeled as a stochastic factor reducing reproductive success, can produce synchrony (Ranta et al. 1997b). These studies suggested dispersal as the major synchronizing factor in 10 of 11 vertebrate species examined (Ranta et al. 1995a, b, 1997b).

While Ranta and colleagues note the importance of the Moran effect in population synchrony, they did not explicitly examine the DDS of these populations. Similarly, Myers (1998) nicely illustrates that many species of forest Lepidoptera experienced synchronized outbreaks between 1932–1992. She relates this to above normal precipitation and cool temperatures, suggesting that a Moran effect may have occurred. While this is a possible explanation it must be remembered that Moran based synchrony is a special case that only occurs when populations have similar density-dependent structure, which Myers was not able to examine.

In this paper we extend Ranta and colleagues work by explicitly combining their S-D relationship with Moran's theory, producing a framework for testing the relative importance of dispersal and density-independent factors in synchronous populations. Populations synchronized only by dispersal are expected to show a significant negative S-D relationship (but see Bascompte et al. 1997, Ranta et al. 1997a, b) and local variation in DDS, whereas synchrony induced by the Moran effect is expected to have no significant S-D relationship and little variation in DDS (Table 1). Most populations are probably influenced by both factors and lie within the continuum between these two extremes. We used the S-D relationship and DDS to describe the spatial synchrony of 7 mammalian species and to identify either dispersal or the Moran effect as likely synchronizing agents. In cases where a Moran effect could be present, we attempt to find environmental factors responsible for the observed Moran effects. We limit our evaluation of the DDS to two components, direct and delayed density dependence (sensu Turchin 1990), recognizing that these only represent statistical density dependence.

Table 1. Criteria used to identify synchronizing agent.

		Synchrony-distance relationship	
		significant	non-significant
Density-dependent structure	Heterogeneous	Dispersal Confounded	No Moran effect
	Homogeneous		Possible Moran effect

Methods

Data sets

We analyzed harvest data from 42 Hudson's Bay Company posts in Manitoba (1915–1940), Ontario (1915–1935), and Quebec (1915–1940) to evaluate synchronous changes in population size of ermine (*Mustela erminea*), fisher (*Martes pennanti*), lynx (*Lynx canadensis*), marten (*Martes americana*), mink (*Mustela vison*), muskrat (*Ondatra zibethica*), and red fox (*Vulpes vulpes*).

Because pelt prices can influence trapping effort (Johnson and Swanson unpubl.), we used stepwise multiple regression with a first-order autoregressive (AR) term and price as predictor variables of harvest. We found no positive relationship between fur price (Monk 1981) and the harvest of these species in Ontario during 1919–1938 (Johnson and Swanson unpubl.). We assume that price had no effect on the fur harvest in other provinces. All data were ln-transformed before analysis and harvest records of 0 were recorded as 1.0 to facilitate ln-transformation.

Population dynamics

Autoregressive estimates at lags 1 and 2 provide insight into the density-dependent structure of a population (Box and Jenkins 1976, Berryman 1992, Royama 1992). In this paper we use direct density dependence and first-order feedback synonymously to describe the influence of population size at time $t-1$ on population growth at time t . We estimated direct density dependence as the first-order autoregressive term (AR(1)). Delayed density dependence, or second-order feedback, is the influence population size at time $t-2$ has on population growth at t , and was measured as the second-order autoregressive term (AR(2)).

We used the autoregressive modeling abilities of SAS PROC AUTOREG (SAS Institute 1990) to estimate the density dependence coefficients in the Gompertz model (Bjørnstad et al. 1995, Steen et al. 1996). While the Gompertz model assumes linearity between the change in r and log abundances ($\ln N_t$), and many populations do not exhibit true linear dynamics, linear models can closely approximate the non-linear dynamics of real populations (Subba and Gabr 1980, Royama 1992, Stenseth et al. 1997). As Bjørnstad et al. (1995) point out, using linear models allows comparison of dynamics across populations as linear models consist of a single class compared to the multiple incompatible nonlinear models. The use of more sophisticated techniques such as TAR (e.g. Tong and Lim 1980) or forecast performance (e.g. Turchin 1996) was inappropriate because of the short length of these time series (20–26 yr).

Because there is debate over the accuracy of density dependence estimators (Wolda and Dennis 1993, Dennis and Taper 1994, Wolda et al. 1994, Saitoh et al. 1997), we only use the qualitative strength (i.e. significance of the AR terms) to determine presence or absence of each density dependence term. An AR term was considered significant if zero was not included within two standard errors (Steen et al. 1996). Autocorrelation and autoregressive results are sensitive to temporal trends, so we used least squares regression to detrend series deviating from a zero slope with $p < 0.25$ (Priestley 1981, Brockwell and Davis 1991, Royama 1992, Hanski and Woiwood 1993, Bjørnstad et al. 1996, Sutcliffe et al. 1996, Saitoh et al. 1997). Detrending may also reduce the probability of detecting spurious delayed density dependence (Saitoh et al. 1997).

We evaluated the fit of two models, one with only direct density dependence (AR(1) models) and one incorporating both direct and delayed density dependence (AR(2) models) using Akaike Information Criteria (AIC) values. Models were evaluated sequentially, regardless of the significance of the results of the AR(1) model. AIC values allow evaluation of models differing in the number of terms by penalizing models for each additional term. We followed the general practice that a difference of 1 or more between AIC values is significant (Sakamoto et al. 1986, Saitoh et al. 1997).

Synchrony analysis

We estimated synchrony as the cross-correlation (lag = 0) between the ln-transformed harvest data of individual populations (Ranta et al. 1995a, b). Regions of synchrony were identified with the JOIN function based on Euclidean distance and Ward's method of joining (SYSTAT 1992). The similarity tree was based on a correlation matrix of the X_t values from each population.

We calculated two synchrony statistics: the correlation between synchrony and interpopulation distance (as indexed by the locations of the Hudson's Bay Company posts) and mean regional synchrony (average interpopulation correlation within regions). Because correlations between populations are not independent (Ranta et al. 1995a, b), we determined the significance of average regional synchrony at $\alpha = 0.05$ based on the distribution of 1000 bootstrapped correlation coefficients from n paired sites.

We examined if dispersal ability influenced the slope of the S-D relationship by regressing the slope of the S-D relationship on the median dispersal distance for each species (as summarized by Van Vuren 1998).

We assumed (1) that regional populations with a homogeneous DDS and non-significant S-D slopes could have been synchronized by a Moran effect, (2) that a significant negative S-D slope and heterogeneous



Fig. 1. Distribution of direct and delayed density dependence in ermine (a), fisher (b), lynx (c), mink (d), muskrat (e), and red fox (f) populations. Density dependence estimates were performed using PROC AUTOREG (SAS Institute 1990) with the best fit model determined by comparing AIC values. Regions with synchronous population dynamics are enclosed within the thin black lines. Regions of synchrony were based on similarity trees derived from population dynamic correlation matrices using SYSTAT's JOIN procedure (SYSTAT 1992). Populations neither connected nor contained within a boundary line clustered with a region that would require boundary lines to cross. Closed circle (●) = populations with direct density-dependent structure; open circles (○) = populations with a delayed density-dependent structure. AT = Attawapiskat, BAR = Barrier, BER = Bersimis, BR = Berens River, CL = Cross Lake, DL = Deer Lake, EM = Eastmain, ER = English River, FA = Fort Albany, FG = Fort George, FH = Fort Hope, FR = Fort Rupert, FS = Fort Severn, GL = Gods Lake, GN = Grassy Narrows, GO = Gogama, GR = Grand Rapids, GW = Great Whale River, IL = Island Lake, LA = La Sarre, LL = Long Lake, MA = Mattice, MF = Moose Factory, MI = Missanabie, MO = Moberg, MT = Mistassini, NE = Nelson House, NP = Nipigon, NO = Norway House, OB = Obedjiwan, OG = Ogoki, OS = Osnaburgh, OX = Oxford House, RO = Romaine, SI = Seven Island, SL = Split Lake, STA = St. Augustine, TG = Temagami, TL = Trout Lake, TRI = Lac Seul/Sioux Lookout/Hudson, WA = Woswanaby, WE = Winisk, YF = York Factory.

Table 2. Summary of criteria used to determine the synchronizing factor of each region. Columns indicate species, region of synchrony, average correlation within each region for each species, slope of the synchrony-distance (S-D) regressions, r^2 of that regression, variation in density-dependent structure (DDS) within each region, and factor responsible for the observed synchrony. Significance of the average correlation was determined by 1000 bootstraps of n paired sites. Slopes of the synchrony-distance (S-D) relationship were estimated by linear regression of the cross correlations against the square root of distance. a = $p < 0.05$, b = $p < 0.01$, c = $p < 0.001$.

Species	Regions of synchrony	Average corr.	S-D slope	r^2	DDS	Synchronizing factor
Ermine	1	0.732 ^c	-0.281 ^a	0.209	heterogeneous	Dispersal
	2	0.429 ^a	-0.024	0.005	homogeneous	Possible Moran
	3	0.484 ^b	-0.065	0.02	heterogeneous	No Moran
	4	0.380 ^a	-0.130	0.008	heterogeneous	No Moran
Fisher	1	0.580 ^b	0.009	0.070	heterogeneous	No Moran
	2	0.581 ^c	-0.171	0.050	heterogeneous	No Moran
	3	0.555 ^b	0.116	0.012	homogeneous	Possible Moran
Lynx	1	0.567 ^b	-0.275	0.021	homogeneous	Possible Moran
	2	0.691 ^c	-0.222 ^b	0.067	homogeneous	Confounded
	3	0.653 ^b	-0.299 ^c	0.318	heterogeneous	Dispersal
Marten	1	0.253	-0.147 ^c	0.043	heterogeneous	NA
Mink	1	0.621 ^c	0.031	0.03	homogeneous	Possible Moran
	2	0.682 ^b	-0.249 ^c	0.145	homogeneous	Confounded
	3	0.682 ^b	-0.149	0.051	heterogeneous	No Moran
	4	0.741 ^c	-0.164 ^a	0.213	heterogeneous	Dispersal
Muskrat	1	0.645 ^b	-0.089	0.005	heterogeneous	No Moran
	2	0.564	-0.481 ^c	0.308	heterogeneous	Dispersal
	3	0.695 ^b	-0.260	0.050	heterogeneous	No Moran
	4	0.576	-0.579 ^c	0.613	heterogeneous	Dispersal
Red fox	1	0.775 ^b	-0.268 ^a	0.107	heterogeneous	Dispersal
	2	0.714 ^a	-0.052	0.007	heterogeneous	No Moran
	3	0.764 ^a	-0.013	0.005	heterogeneous	No Moran

DDS indicated the operation of dispersal, (3) that homogeneous DDS and significant S-D slopes represent populations confounded by both dispersal and possible Moran effects, and (4) heterogeneous DDS and a non-significant S-D slope excluded the Moran effect (Table 1).

In an attempt to determine the climatic effects potentially responsible for any Moran-based regions of synchrony, we performed a JOIN analysis on all combinations of six climatic factors: mean January temperature, mean July temperature, mean annual total snow fall, mean annual total precipitation, mean annual frost free days, and mean annual length of growing season (Dept of Mines and Technical Surveys 1957). If regional synchrony was produced by one or more of these factors, similar clustering of populations were expected when analyzed with population dynamics or weather variables.

Results

Spatial synchrony

The JOINS analysis produced 3 or 4 regions of synchrony for each species except marten (Fig. 1a-f). The average regional correlation was significantly greater than expected by chance in all regions except muskrat

regions 1 and 3 (Table 2). Regional boundaries showed little or no relationship to latitude, broadly scaled habitat types, or meteorological variables (Fig. 2) such as temperature, total rainfall, total snow fall, and length of the growing season (Dept of Mines and Technical Surveys 1957). There were no consistent differences in synchrony statistics of detrended and non-detrended series.

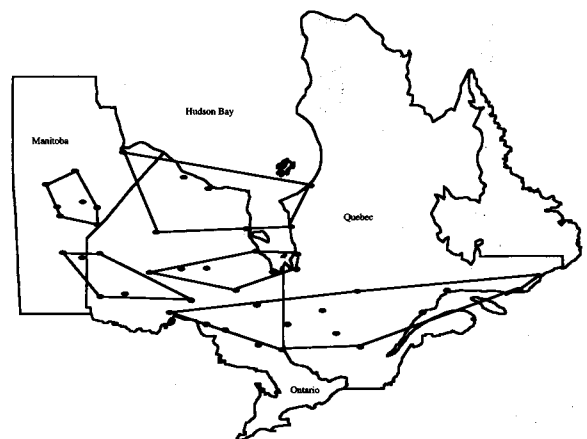


Fig. 2. Regions of climatic similarity based on the mean January temperature, mean July temperature, total precipitation, total snowfall, mean number of frost free days, and mean annual growing season. Regions are based on similarity trees based on SYSTAT's JOIN procedure (SYSTAT 1992).

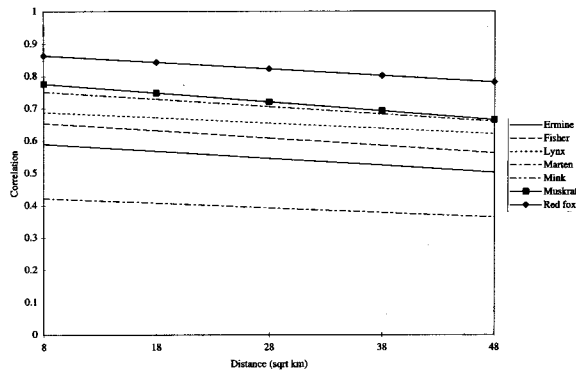


Fig. 3. Relationship between synchrony and distance (as indexed by $\sqrt{\text{km}}$). Interpopulation synchrony was measured as the cross-correlation at lag 0. Raw data have been left out to aid interpretability. Slopes and adjusted r^2 for each species; ermine ($\beta = -0.221$, adjusted $r^2 = 0.046$), fisher ($\beta = -0.231$, adjusted $r^2 = 0.099$), lynx ($\beta = -0.167$, adjusted $r^2 = 0.088$), marten ($\beta = -0.147$, adjusted $r^2 = 0.0463$), mink ($\beta = -0.230$, adjusted $r^2 = 0.158$), muskrat ($\beta = -0.279$, adjusted $r^2 = 0.110$), red fox ($\beta = -0.207$, adjusted $r^2 = 0.081$). All slopes are significant at $p < 0.001$.

A significant negative S-D relationship was found in 8 of the 21 regions (38.1%). The S-D relationship was highly significant in all species when examined across all populations (Fig. 3). A significant relationship existed between the slope of the S-D relationship and dispersal ability ($\beta = 0.018$, $r^2 = 0.712$, $F = 12.38$, $p < 0.02$).

Density-dependent structure

Distinct differences in DDS, as characterized by autoregressive modeling, were found at the local level in all species (Fig. 1a–f, Table 3). Direct density dependence was a better model for the majority of marten (83.3%, $\chi^2 = 14.30$, $p < 0.001$, Table 3), and mink (70%, $\chi^2 = 5.48$, $p < 0.025$, Fig. 1e) populations. There was no difference in the number of populations experiencing direct or delayed density dependence in ermine (61.4%, $\chi^2 = 1.88$, $p > 0.1$, Fig. 1a), fisher (63.0%, $\chi^2 = 1.81$, $p > 0.1$, Fig. 1b), lynx (62.5%, $\chi^2 = 2.45$, $p > 0.1$, Fig. 1c), muskrat (56.1%, $\chi^2 = 0.86$, $p > 0.25$, Fig. 1e) and red fox (62.2%, $\chi^2 = 2.63$, $p > 0.1$, Fig. 1f).

All regional series showed strong positive direct density dependence (90.9%), except ermine Region 1 and fisher Region 3 (Table 4). Significant delayed density dependence, AR(2), was found in at least 1 region of all species except for marten (Table 4). Sixteen of the 22 regions (72.7%) were best fit by a delayed density dependence model, although the delayed density dependence term in one of those regions was not significant.

Discussion

Synchrony

Using cross-correlation and JOIN analyses we identified distinct regions of spatial synchrony for six mammalian species in central and eastern Canada. Moreover, through the S-D relationship and DDS, our results suggest that different factors produced the synchrony we observed for various regions and species. These regions appear to represent biologically significant entities because (1) average synchrony within each region was greater than expected by chance (Table 2), and (2) clusters containing impossible combinations of populations were rare. Clusters produced by the joining method are based on similarity in population dynamics, thus it is possible for populations to cluster in geographically impossible patterns such as a population that clustered with one region being geographically located within another. However, only 27 of the 264 populations (10.2%) clustered in impossible patterns as shown by populations not contained within regional boundary lines (Fig. 1a–f). Twenty-five populations clustered with a non-adjacent region, and two populations were geographically located within a region in which they did not cluster. Populations that clustered with one region but were located within a different region were analyzed as belonging to the region they were geographically located in. The marten was the only species which showed no regional clusters of similar population dynamics. We attribute the lack of synchrony to disruption of its natural dynamics resulting from overharvest and habitat loss (de Vos 1952).

Using the criteria in Table 1, four regions (19.0%) could have been synchronized by a Moran effect (ermine region 2, fisher region 3, lynx region 1, and mink region 1), six regions (28.6%) could be attributed to dispersal (ermine region 1, lynx region 3, mink region 4, muskrat regions 2 and 4, and fox region 1), two regions (9.5%) showed characteristics of both (lynx region 2, and mink region 2), and we could not attribute synchrony to either factor in nine regions (42.8%). Factors producing synchrony probably varied between species because there was little congruity between species (Fig. 1a–f).

No single climatic variable could have produced the observed regions of synchrony. Unlike the regions of synchrony the climatic factors we examined changed with latitude, remaining relatively constant east to west, except near major bodies of water (Dept of Mines and Technical Surveys 1957). Combining climatic variables failed to improve the correspondence between climatic regions and population dynamic regions; all regions with a possible Moran effect contained at least 2 climatic regions (Fig. 2).

Our inability to determine a cause of synchrony in 42.8% of the regions could result from sampling at an

Table 3. Results for each population of autoregressive modeling comparing a direct density-dependent model (AR(1)) and a delayed density-dependent model (AR(2)). Estimates of the AR(1) term (first or only term) and AR(2) term (second term) were estimated using PROC AUTOREG as described in the text. The best fitting model was determined by comparing AIC values. Location and list of the population abbreviations are shown in Fig. 1. a = $p < 0.05$, b = $p < 0.01$, c = $p < 0.001$, d = $p < 0.0001$. -- = no data.

Population	Ermine	Fisher	Lynx	Marten	Mink	Muskrat	Red fox
AT	-0.43 ^a , 0.63 ^a	-0.91 ^a , 0.44 ^a	-0.83 ^a , 0.46 ^a	-0.58 ^a	-0.33, 0.23		-0.90 ^c , 0.48 ^a
BAR	-0.18	-0.59 ^a	--	-0.48 ^a	-0.50 ^a	-0.81 ^c , 0.33 ^a	-0.43 ^a
BER	-0.43 ^a	-0.46 ^a	-0.55 ^a , 0.19	--	-0.58 ^a	-0.58 ^a	--
BR	-0.30	-0.36	-0.41 ^a	--	-0.24	-0.60 ^a	-0.54 ^a
CL	-0.25, 0.37 ^a	--	-0.35	-0.60 ^a	-0.28	-0.65 ^b	-0.90 ^c , 0.43 ^a
DL	-0.27, 0.59 ^a	-0.62 ^a , 0.44	-0.49 ^a	-0.73 ^a	-0.58 ^a	-0.51 ^a	-0.48 ^a
EM	-0.53 ^a , 0.38 ^a	--	-0.96 ^a , 0.29	-0.48 ^a	-0.81 ^a , 0.40 ^a	-0.82 ^c , 0.34 ^a	-0.96 ^c , 0.47 ^a
ER	-0.05	-0.76 ^a , 0.30	-0.65 ^a	-0.42 ^a	-0.75 ^a , 0.20	-0.43 ^a	-0.61 ^b
FA	-0.41 ^a , 0.34 ^a	-0.21	-0.88 ^a , 0.4 ^a	-0.55 ^a	-0.24	-0.44 ^a	-0.59 ^b
FG	-0.30, 0.36 ^a	--	-0.48	-0.60 ^a	-0.81 ^a , 0.35	-0.61 ^a	-0.84 ^b , 0.42 ^a
FH	-0.52 ^a , 0.60 ^a	-0.38 ^a	-0.98 ^a , 0.58	-0.62 ^a	-0.57 ^a	-0.92 ^b , 0.27	-0.56 ^a
FR	-0.29	--	-0.85 ^a , 0.3 ^a	-0.62 ^a	-0.89 ^a , 0.47 ^a	-1.15 ^d , 0.55 ^b	-0.61 ^b
FS	-0.28, 0.46 ^a	--	--	-0.74 ^a , 0.35	-0.49 ^a	-0.62 ^a , 0.25	-0.47 ^a , 0.35
GL	-0.30, 0.55 ^a	-0.96 ^a , 0.50 ^a	-0.75, 0.34 ^a	-0.50 ^a , 0.18	0.30	-0.67 ^b , 0.38 ^a	-1.08 ^c , 0.43 ^a
GN	-0.16, 0.26	-0.26	--	--	-0.65 ^a	--	-0.72 ^b , 0.35
GO	-0.36 ^a	-0.01	--	-0.56 ^a	-0.70 ^a	-0.53 ^a	-0.66 ^a
GR	-0.16, 0.29	-0.52 ^a	-0.57 ^a	-0.60 ^a	-0.50 ^a	-0.83 ^c , 0.39 ^a	-0.94 ^c , -0.46 ^a
GW	-0.41 ^a	--	--	-0.50 ^a	-0.68 ^a , 0.31	-0.56 ^a , 0.47 ^a	-0.41 ^a , 0.46 ^a
IL	-0.23, 0.58 ^a	-0.71 ^a , 0.27	-0.56 ^a	-0.63 ^a , 0.21	-0.45 ^a	-0.70 ^a , 0.35	-0.85 ^a , 0.35
LA	-0.60 ^a	-0.48 ^a	-1.44 ^a , 0.53 ^a	-0.60 ^a	-0.69 ^a	-0.56 ^a , 0.38 ^a	-1.13 ^d , 0.53 ^b
LL		-0.73 ^a , 0.34	-1.01 ^c , 0.45 ^a	--	-0.83 ^b , 0.42 ^a	-0.25	-0.80 ^b , 0.31
MA	-0.58 ^a	-0.32	--	-0.60 ^a	-0.42 ^a	-0.60 ^b	-0.87 ^c , 0.37 ^a
MF	-0.10	-0.63 ^a , 0.30	-0.97 ^b , 0.42 ^a	-0.65 ^a	-0.94 ^c , 0.41 ^a	-0.15	-0.61 ^b
MI	--	-0.59 ^a	-0.95 ^b , 0.49 ^a	-0.51 ^a	--	--	-1.19 ^c , 0.69 ^b
MO	-0.41 ^a	-0.53 ^a	--	-0.60 ^a	-0.57 ^a	-0.98 ^c , 0.35 ^a	-0.78 ^b , 0.36 ^a
MT	-0.25	-0.53 ^a	-1.88 ^d , 0.64 ^a	-0.42 ^a	-0.63 ^b , 0.39 ^a	-0.42 ^a	-0.90 ^b , -0.49 ^a
NE	-0.17, 0.28	--	-0.49 ^a	-0.53 ^a	-0.82 ^c , 0.28	-0.66 ^b , 0.19	-0.56 ^a
NP	-0.17, 0.54 ^a	-0.30	-0.59 ^a	-0.48 ^a	-0.75 ^a	-0.27	-0.60 ^a , -0.01
NO	-0.26, 0.35	-0.81 ^a , 0.4	-0.64 ^a , 0.29	-0.02, -0.28	-0.64 ^b , 0.39 ^a	-0.60 ^a	-0.69 ^b , 0.37 ^a
OB	-0.31	-0.03	-0.63 ^a	-0.15, 0.43 ^a	-0.48 ^a	-0.58 ^a	-0.94 ^c , 0.48 ^a
OG	-0.48 ^a , 0.48 ^a	-0.66 ^a	-0.65 ^a	-0.46 ^a , 0.32	-0.52 ^a	-0.84 ^b , 0.39 ^a	-0.43
OS	-0.13, 0.70 ^a	-0.54 ^a	-1.01 ^c , 0.54 ^a	-0.61 ^a	-0.62 ^a	-0.48 ^a	-0.58 ^a , 0.13
OX	-0.21, 0.60 ^a	--	-0.23	-0.50 ^a	-0.42 ^a	-0.50 ^a	-0.54 ^b
RO	-0.65 ^a , 0.20	--	-0.63 ^a , 0.17	-0.38	-0.62 ^b	-0.88 ^b , 0.35	--
SI	-0.34	--	-0.50 ^a , 0.24	-0.60 ^a	-0.37 ^a	-0.51 ^a	--
SL	-0.13, 0.49 ^a	--	-0.78 ^b , 0.3	--	-0.85 ^b , 0.48 ^a	-0.60 ^a	0.15
STA	-0.51 ^a , 0.22	--	-0.63 ^a , 0.39 ^a	-0.49 ^a	-1.07 ^c , 0.47 ^a	-0.70 ^a , 0.38 ^a	--
TG	-0.05	-0.25	--	-0.30, 0.20	-0.78 ^b , 0.32	-1.07 ^c , 0.57 ^b	-0.87 ^b , 0.27
TL	-0.38 ^a , 0.58 ^a	-0.54 ^a	-0.79 ^b , 0.36 ^a	-0.43 ^a	-0.85 ^c , 0.48 ^a	-0.83 ^c , 0.36 ^a	-0.48 ^a
TRI	-0.27, 0.53 ^a	-1.03 ^a , 0.48 ^a	-0.86 ^b , 0.33 ^a	-0.52 ^a	-0.59 ^a	-0.49 ^a	-0.69 ^a , 0.20
WA	-0.64 ^a , 0.46 ^a	-0.60 ^a , 0.33	-1.04 ^c , 0.49 ^b	-0.51 ^a , 0.31	-0.51 ^a , 0.26	-0.66 ^a , 0.31	-0.79 ^b , 0.30
WE	-0.33, 0.58 ^a	--	--	-0.53 ^a	-0.59 ^a , 0.16	-0.31, 0.33 ^a	-0.54 ^a
YF	-0.31, 0.52 ^a	--	-1.17 ^c , 0.52 ^b	-0.21	-0.85 ^b , 0.48 ^a	-0.57 ^a	-0.69 ^b , 0.33 ^a

improper scale relative to the dispersal ability of the species examined. We found a significant relationship between the dispersal distance and the S-D slope that explained much of the variation ($r^2 = 0.712$), suggesting an interaction between dispersal ability and slope of the S-D relationship. However, there was surprisingly little variation between species despite their dispersal abilities differing by two orders of magnitude (e.g. muskrat 0.5 km, marten 50 km) and interpopulation distance ranging between 64 km and 2200 km. It appears that while dispersal ability influences the slope of the S-D relationship further research is required to determine if it plays more than a minor role.

Significant S-D relationships existed for all species when analyzed across all populations (Fig. 3) although the average interpopulation synchrony was not significantly greater than expected by chance in any case (Table 2). It is unlikely that dispersal is a major force in interprovincial synchrony given the great distance separating some populations (> 2200 km) and the small amount of variation in synchrony explained by distance (mean adjusted $r^2 = 0.107 \pm 0.148$, Table 2). A more plausible explanation is that both dispersal and environmental similarities produce highly synchronous populations across shorter distances (300–500 km), while the synchronizing strength of both of these factors decays with distance.

Table 4. Parameters of the best-fitting modified Gompertz model ($X_t = \alpha_0 + \alpha_1 N_{t-1} + \alpha_2 N_{t-2} + \varepsilon_t$) for regional time series of each species. Estimates of the strength of direct ($\alpha_1 \pm$ standard error) and delayed density dependence ($\alpha_2 \pm$ standard error) parameters were made by regressing X_t on N_{t-1} and N_{t-2} . α_0 is a constant which does not affect the density dependent structure and so is not shown here. ΔAIC = difference in AIC (Akaike information criteria) values. Positive values greater than 1 indicate that the more complex AR(2) model is a better fit (Sakamoto et al. 1986, Saitoh et al. 1997). NA = not applicable as the best model did not utilize this term. a = $p < 0.05$, b = $p < 0.01$, c = $p < 0.001$.

Species	Region	$\alpha_1 \pm$ S.E.	$\alpha_2 \pm$ S.E.	ΔAIC
Ermine	1	0.228 $\pm$ 0.199	-0.357 $\pm$ 0.199	2.86
	2	0.347 ^a $\pm$ 0.168	-0.741 ^b $\pm$ 0.168	16.99
	3	0.551 ^a $\pm$ 0.192	NA	-0.56
	4	0.060 $\pm$ 0.208	NA	-1.77
Fisher	1	0.865 ^c $\pm$ 0.198	-0.372 $\pm$ 0.198	2.86
	2	1.018 ^c $\pm$ 0.211	-0.535 ^a $\pm$ 0.211	7.68
	3	-0.006 $\pm$ 0.209	NA	-1.99
Lynx	1	1.00 ^c $\pm$ 0.179	-0.540 ^a $\pm$ 0.179	5.39
	2	1.327 ^c $\pm$ 0.156	-0.681 ^c $\pm$ 0.156	17.03
	3	1.143 ^c $\pm$ 0.169	-0.609 ^b $\pm$ 0.169	13.06
Marten	1	-0.565 ^b $\pm$ 0.172	NA	-1.87
	1	0.560 ^b $\pm$ 0.173	NA	-0.68
Mink	2	1.200 ^c $\pm$ 0.208	-0.553 ^a $\pm$ 0.208	4.68
	3	0.915 ^c $\pm$ 0.182	-0.518 ^a $\pm$ 0.182	6.31
	4	0.622 ^b $\pm$ 0.163	NA	0.78
	1	0.972 ^c $\pm$ 0.191	-0.483 ^a $\pm$ 0.191	7.67
Muskrat	2	0.828 ^b $\pm$ 0.231	-0.381 $\pm$ 0.231	4.67
	3	1.119 ^c $\pm$ 0.178	-0.580 ^a $\pm$ 0.178	11.76
	4	0.757 ^b $\pm$ 0.210	-0.270 $\pm$ 0.210	1.09
	1	1.030 ^c $\pm$ 0.181	-0.524 ^b $\pm$ 0.181	6.28
Red fox	2	0.973 ^c $\pm$ 0.188	-0.471 ^b $\pm$ 0.188	4.28
	3	1.213 ^c $\pm$ 0.202	-0.584 ^a $\pm$ 0.203	8.74

Population dynamics

In 22 of the 118 populations (18.6%) best fit by an AR(2) model (delayed density dependence) the second-order term was non-significant (Table 3). In these cases the fit of the AR(2) models was significantly better than the AR(1) models, implying that an AR(2) term is necessary to fit the data. This suggests that the duration of some of our time series was too short relative to the noise present to produce an accurate estimate of the second order term.

Population dynamics of many species in the boreal forest are tied to snowshoe hare dynamics (Boutin et al. 1995), allowing relatively simple models to accurately mimic population dynamics. For example, two-year and three-year lag models are sufficient to model lynx and snowshoe hare dynamics, respectively (Stenseth et al. 1997). This is in general agreement with our analysis at the regional level, where the majority of populations (72.7%) exhibit delayed density dependence. Results were more varied at the local level, as direct and delayed density dependence were equally common in fisher, ermine, lynx, and red fox series. This increased variability is probably due to local variation in biotic and abiotic conditions. Stenseth et al. (1997) found that a higher order model (third order) was needed to model

snowshoe hare dynamics. With respect to the one prey species analyzed, muskrat, a third order model (AR(3)) did not provide a better fit than the AR(1) or AR(2) models (data not shown).

Two weaknesses of these methods are the difficulty in identifying the factor(s) responsible for producing the Moran effect, and what can be concluded when populations exhibit homogeneous DDS; we have shown that it is relatively easy to exclude a Moran effect based on the heterogeneity of the DDS of a region's constituent populations. However, it must be emphasized that failing to reject the presence of a Moran effect does not equate with a Moran effect being present, just that the necessary conditions are present. Certainly it is no more appropriate to conclude a Moran effect is occurring without evidence of a synchronizing factor than it is to imply causation based on correlation. This leaves researchers in the unsatisfying place of not being able to answer perhaps the most interesting question, what is the synchronizing factor when DDS is homogeneous across populations within a region of synchrony? The ability to determine a causative factor is even more difficult because the synchronizing factor need not occur annually, nor does it have to be the same factor, as long as its effect is correlated across populations (Ranta et al. 1995b).

Conclusion

All of the species we examined here, except the marten, experienced synchronous changes in population density at some scale, and, within a single species, different factors were often responsible for the observed synchrony. Our results indicate that through the use of Ranta et al.'s (1995a, b) S-D relationship, Moran's theorem (1953), cluster analysis and estimation of density-dependence it is often possible to exclude dispersal or a Moran effect as a synchronizing agent, further illuminating the process of population synchronization. These techniques are valuable in pointing out possible causes of synchrony but further work is needed. Directions for future research should include more precise quantification of the density-dependent terms using methods such as Turchin's out of sample forecasting method (Turchin 1996) in longer time series. Accurate estimates of the strength of the density dependent components will allow predictions of the expected interpopulation synchrony. Perhaps more importantly long-term field work needs to be done to determine which environmental factors are responsible for the Moran effect when one could be present.

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