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Anglia HadCRUT temperature data set, based on land station and ship reports[28]. The trends for each $5° \times 5°$ grid cell were evaluated by a least-squares fit for the period 1965–2000. The gridded trend values were then smoothed spatially using a Cressman analysis, which effectively determines a pixel value as a weighted sum of contributions from surrounding grid points for which data are available. Weights vary as the inverse fourth power of the distance from the pixel in question. The radius of influence is 500 pixels, or approximately one-quarter the maximum width of the image.

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Correspondence and requests for materials should be addressed to P.T.D. (e-mail: pdoran@uic.edu).

DNA reveals high dispersal synchronizing the population dynamics of Canada lynx

Michael K. Schwartz*†, L. Scott Mills*, Kevin S. McKelvey†, Leonard F. Ruggiero† & Fred W. Allendorf‡

* Wildlife Biology Program, School of Forestry, University of Montana, Missoula, Montana 59812, USA
† USDA/USFS Rocky Mountain Research Station, 800 E. Beckwith, Missoula, Montana 59801, USA
‡ Division of Biological Sciences, University of Montana, Missoula, Montana 59812, USA

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Population dynamics of Canada lynx (*Lynx canadensis*) have been of interest to ecologists for nearly sixty years[1–4]. Two competing hypotheses concerning lynx population dynamics and large-scale spatial synchrony are currently debated. The first suggests that dispersal is substantial among lynx populations[5], and the second proposes that lynx at the periphery of their range exist in small, isolated patches that maintain cycle synchrony via correlation with extrinsic environmental factors[2]. Resolving the nature of lynx population dynamics and dispersal is important both to ecological theory and to the conservation of threatened lynx populations: the lack of knowledge about connectivity between populations at the southern periphery of the lynx's geographic range delayed their legal listing in the United States[6]. We test these competing hypotheses using microsatellite DNA markers and lynx samples from 17 collection sites in the core and periphery of the lynx's geographic range. Here we show high gene flow despite separation by distances greater than 3,100 km, supporting the dispersal hypothesis. We therefore suggest that management actions in the contiguous United States should focus on maintaining connectivity with the core of the lynx's geographic range.

Trapping records show that twentieth-century lynx population dynamics in parts of North America exhibit patterns of lagged synchrony, with irruptions occurring in the centre of the continent 2–3 years before they occur at the periphery of the range[5]. One potential mechanism for this phenomenon is a travelling wave of lynx emanating from the centre of the continent, which synchronizes the lynx populations[4]. If this 'dispersal hypothesis' is correct, then populations at the periphery of their range should be highly influenced by lynx periodically diffusing outwards from the core.

Alternatively, lynx populations at the periphery of their geographic range may be self-sustaining, and largely isolated[7]. Under this 'peripheral isolation hypothesis' there would be few dispersers and the number of dispersers would decline exponentially with distance, leading to lower connectivity at the edge of the geographic range[3]. To support the peripheral isolation hypothesis there are weak correlations between lynx irruptions in Alberta and British Columbia and lynx abundance indices in some southern, peripheral populations, as well as the patchy nature of lynx habitat in southern Canada, Montana, and Washington[5,7]. If populations are relatively isolated, synchrony between peripheral lynx populations could be generated by exogenous density-independent events such as weather[2] (that is, the Moran effect[8]).

We used nine microsatellite loci to estimate gene flow among lynx populations (see Methods). We analysed lynx samples from 17 collection sites in the periphery and core of the lynx's geographic range (Fig. 1). If the dispersal hypothesis is correct, gene flow should be high among populations, including central Canadian populations and the populations on the periphery of the geographic range. Alternatively, if the peripheral isolation hypothesis is correct, then gene flow should be low between peripheral lynx populations and

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central Canadian and Alaskan populations, and negligible among populations that are far apart.

The global F_{st}, a measure of population subdivision, was 0.033 (standard error of the mean, s.e.m. ± 0.002). This degree of subdivision is expected if there are on average approximately six dispersers ('migrants' in the genetic sense) entering each population each generation, assuming an island model of migration[9,10]. Furthermore, substantial gene flow was apparent among all populations. The Kenai Peninsula population was genetically most divergent from other populations with a mean pairwise F_{st} of 0.051 (s.e.m. ± 0.003). However, this amount of subdivision still represents approximately four dispersers entering each population per generation, and so the Kenai Peninsula population is probably not biologically different. Despite sampling lynx populations more than 3,100 km apart, we found no evidence for decreased gene flow with increasing geographical distance across western North America (Fig. 2; Mantel's test, $g = 0.117$, $P = 0.42$).

Small F_{st} values can be indicative of high current gene flow between populations or can be caused by populations sharing recent common ancestry[9]. We attribute our results to high current gene flow because many peripheral populations in our study have had small population sizes for long periods. Lynx are known to have low population densities[5,7], especially at cyclic lows that would reduce effective population size (N_e). On the Kenai Peninsula, our estimate of N_e was less than 30 (see Methods). For ideal isolated populations with $N_e = 30$, substantial values of F_{st} would accumulate in only a few generations (t). For example, F_{st} is expected to be greater than the global F_{st} of 0.033 in just two generations for populations with an $N_e = 30$, and in four generations for populations with $N_e = 50$ ($F_{st} = 1 - (1 - 1/(2N_e))^t$ [9–11].

Our F_{st} results are corroborated by assignment test results (see Methods)[12]. Only 40.8% of lynx assigned to the population from which they were captured. Low assignment rates may indicate either

high gene flow or low power to assign because of too few markers or too little genetic variation per marker. However, other studies with less overall genetic variation and equal numbers of microsatellites have produced much higher assignment rates[13], so we attribute our low assignment rates to high gene flow.

Radiotelemetry data have shown that lynx regularly travel distances greater than 100 km, and can travel distances up to 1,100 km (refs 14, 15). However, it is unknown whether these movements led to gene flow. Our genetic data suggest that long distance movements are probably common and result in very high levels of gene flow, among the highest yet found for any carnivore. Wolves and coyotes show high levels of gene flow[16], yet wolves still follow an isolation by distance model[17]. North American brown bears also display high gene flow, but have F_{st} values much higher (implying gene flow levels much lower) than are reported here for lynx[18].

Our results for lynx strongly support the dispersal hypothesis rather than the peripheral isolation hypothesis. Peripheral populations in the south, north and west appear to readily exchange dispersers with the core populations. Even the peninsular Kenai population shows high gene flow.

Gene flow has implications for synchrony in lynx cycles across large landscapes. Stenseth et al.[2] used lynx fur trade records from Canada's Hudson Bay Company along with time-series data from Statistics Canada to show that density-independent factors (that is, weather) synchronize isolated lynx populations with similar density-dependent structures. Specifically, their models based on climatic regions (Pacific maritime, Continental, and Atlantic maritime) had more support than models subdividing lynx populations based on ecological groupings (western, northern, southern and eastern), provincial boundaries, or Hudson Bay Company administrative regions. Stenseth et al.[2] concluded that region-specific variation in climate, probably produced by the North Atlantic Oscillation, coupled with similar density-dependent structures in lynx populations, caused lynx cycling synchrony within climatic regions. A different model[3] explained large-scale spatial synchrony by assuming that dispersal between patches declined exponentially with distance.

We suggest that immediately after the peak of the lynx cycle in the centre of their range, large numbers of lynx disperse long distances creating a wave of immigrants that drive cycle-like synchrony in the western lynx populations. This suggestion is supported by both trapping records[5] and our gene flow results. A dispersal hypothesis is also a more parsimonious explanation of lynx cycle synchrony, negating the reliance on large-scale density-independent events coupled with similar density-dependent population structures[19–22]. Dispersal may also be significant in synchronizing population cycles in other species. For example, initial research on collared lemmings showed that synchrony occurred only in populations separated by as much as 6 km (ref. 23). Because this distance was greater than the
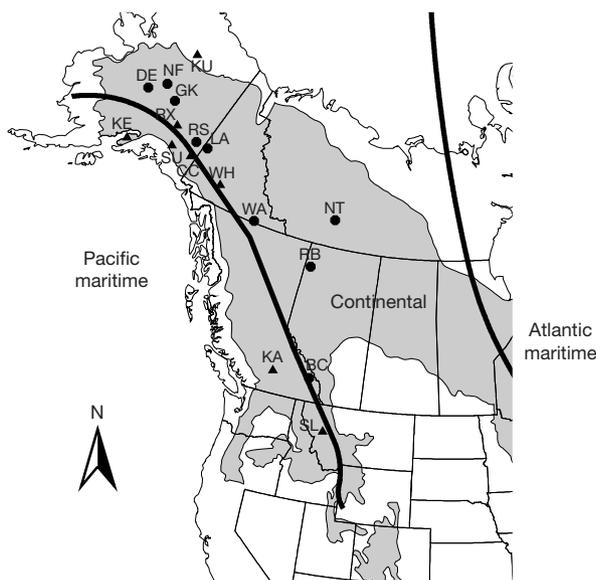
Figure 1 The geographic distribution of lynx (in grey). Each triangle represents a location of a 'peripheral' lynx population and each circle represents a 'core' lynx population. The population abbreviations and sample sizes are as follows: Seeley Lake, Montana (SL, 32); Kuyuktuvuk Creek, Alaska (KU, 7); Kenai Peninsula, Alaska (KE, 115); Ladue River, Yukon/Alaska (LA, 10); Cooper Center, Alaska (CC, 19); North of Fairbanks, Alaska (NF, 19), Fort Province, Northwest Territories (NT, 84); Riverside, Alaska (RS 43); West of Denali, Alaska (DE, 16); Rainbow Lake, Alberta (RB, 18); Watson Lake, Yukon (WA, 27); Whitehorse, Yukon (WH, 52); Kootnay−Banff, British Columbia (BC, 20); Gold King Creek, Alaska (GK, 32); North of Kamloops, British Columbia (BC, 20); Paxson, Alaska (PX, 45); and Susitna Lake, Alaska (SU, 35). The regions Atlantic, Continental and Pacific represent the climatic regions of ref. 2.
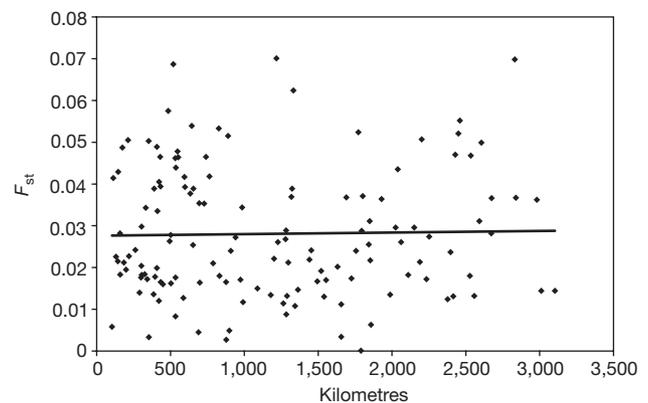
Figure 2 Regression of F_{st} on geographic distance between all pairs of the 17 populations.

maximum observed lemming dispersal distance (3 km) (ref. 24), dispersal was discounted as a synchronizing mechanism. However, recent genetic data revealed that collared lemming disperse distances up to 20 km (ref. 24), suggesting that dispersal may indeed synchronize these populations.

Our results have important implications for lynx conservation. Our data imply that persistence in the contiguous United States depends upon dispersal from larger populations; therefore joint international efforts should be initiated to ensure that connectivity between northern and southern populations is sustained. □

Method

Genetic analysis

We genotyped 599 lynx samples from 17 populations using nine microsatellite DNA markers developed from domestic cats[25,26]. DNA extraction methods, microsatellite DNA amplification conditions, and Hardy–Weinberg (HW) proportions and gametic disequilibrium analyses can be found in ref. 27. Average heterozygosity across all populations and loci was 0.66 (s.e.m. = 0.074). Several populations had one locus out of HW proportions ($P < 0.05$); however, there was no consistency as to which locus. The only population with more than one locus out of HW proportions was the Kenai population that had three of nine loci deviating from HW proportions.

Effective population size

We estimated N_e of the Kenai lynx population using the temporal change in allele frequency method[28]. Our samples were collected 10 years apart, a period representing between two and three lynx generations. Assuming the samples were separated by two generations produced an N_e estimate of 22.1 (s.e.m. = 11.5–49.1); assuming the samples were separated by three generations resulted in an N_e estimate of 28.8 (s.e.m. = 17.6–62.0).

Assignment tests

An assignment test classified an individual to a population where it most probably was born, on the basis of the expected frequency of an individual's genotype in each population[12]. We used the partially bayesian exclusion test of ref. 12, which has been shown to be effective over a wide range of F_{st} values and is robust to slight deviations from Hardy–Weinberg proportions[12,13]. We used the 'leave one out' method when conducting this analysis, which means that each individual was removed from the data set, the allele frequencies were recalculated, and then the individual was assigned to the population.

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Identification of diploid endosperm in an early angiosperm lineage

Joseph H. Williams*† & **William E. Friedman***†

* *Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA*
† *These authors contributed equally to the work*

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In flowering plants, the developmental and genetic basis for the establishment of an embryo-nourishing tissue differs from all other lineages of seed plants. Among extant nonflowering seed plants (conifers, cycads, *Ginkgo*, Gnetales), a maternally derived haploid tissue (female gametophyte) is responsible for the acquisition of nutrients from the maternal diploid plant, and the ultimate provisioning of the embryo. In flowering plants, a second fertilization event, contemporaneous with the fusion of sperm and egg to yield a zygote, initiates a genetically biparental and typically triploid embryo-nourishing tissue called endosperm. For over a century, triploid biparental endosperm has been viewed as the ancestral condition in extant flowering plants[1–3]. Here we report diploid biparental endosperm in *Nuphar polysepalum*, a basal angiosperm. We show that diploid endosperms are common among early angiosperm lineages and may represent the ancestral condition among flowering plants. If diploid endosperm is plesiomorphic, the triploid endosperms of the vast majority of flowering plants must have evolved from a diploid condition through the developmental modification of the unique fertilization process that initiates endosperm.

In 1999, a series of phylogenetic analyses[4–6] identified a set of