



# Density-dependent dispersal suggests a genetic measure of habitat suitability

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Recent research shows that density dependence should result in predictable movements between habitats of different suitability, depending on whether population densities are increasing or decreasing. When population densities are increasing, habitats become filled in order of their suitability, resulting in a net flow from high suitability to low suitability. When populations decrease in density, the reverse can happen. These patterns suggest that genetic information can be used to infer habitat suitability since individual-based genetic assignment tests permit high resolution assessments of migration. We used replicated landscapes to study fishers (*Martes pennanti*) during a population increase and predicted that there should be a net flow of individuals from areas of shallow to deep snow, since snow depth has previously been linked to fisher fitness. A total of 769 fishers were sampled from 35 different landscapes and profiled at 16 microsatellite loci. From assignment tests, we inferred five genetic populations. By assigning each of the 35 landscapes to one of these five populations, we were able to determine the proportion of immigrants to each. Consistent with our prediction, there was a positive relationship between the proportion of immigrants and snow depth. The best model of fisher habitat suitability was one with both snow depth and the proportion of coniferous forest in landscapes. Our findings suggest that where population trend is known, genetic information can be used to measure habitat suitability.

Theories of density-dependent habitat selection (Fretwell and Lucas 1970, Rosenzweig and Abramsky 1985, Morris 1994) provide a basis for understanding dispersal behavior. Density dependence should result in predictable movements of individuals between habitats of different suitability, depending on whether population densities are increasing or decreasing (Morris and Diffendorfer 2004, Morris et al. 2004). Here, habitat suitability is as defined by Fretwell, “a reflection of the average genetic contribution of resident adults to the next generation and must be closely related to the average lifetime production of reproducing offspring in the habitat” (Fretwell 1972; 106). In essence, this is equivalent to individual fitness. According to Morris et al. (2004), when population densities are increasing, habitats become filled in order of their suitability, resulting in a net flow of individuals from high suitability to low suitability habitats. When populations decrease in density, the reverse can happen, as indi-

viduals choose to move into higher suitability habitats as space becomes available. This has been termed reciprocating dispersal (Morris et al. 2004).

If patterns of migration can be linked to habitat suitability, it suggests that genetic information can be used to infer habitat suitability since individual-based genetic assignment tests permit high-resolution assessments of migration patterns (Pritchard et al. 2000, Berry et al. 2004). A genetic measure could be applied over large scales, and would be a benefit since it would make possible tests of migration patterns (and thus habitat suitability) at the scale of genetic structure.

We studied fishers (*Martes pennanti*) during a population increase to test predictions about habitat suitability using individual-based genetic assignment tests. The fisher is an endemic mustelid of North America. Krohn et al. (1995, 1997, 2004) and Raine (1983) have suggested that snow depth is limiting to fishers in winter and is thus an important component of

habitat suitability. According to this idea, where snow is deep and soft, fishers face energetic difficulties during winter and during the spring breeding period, resulting in poor body condition. Poor body condition may affect either survival or reproduction, or both (Krohn et al. 1995). Krohn et al. (1997) have also suggested a proximate mechanism for snow depth to affect the fisher's distribution. As most juvenile fishers disperse during the snow season, dispersers may assess relative snow depths as they settle in a territory.

Ongoing demographic research in our study area has provided information about fisher densities and population growth rates, and demonstrated that fisher populations were increasing for several years prior to and during our study (Bowman et al. 2006, Tully 2006, Koen et al. 2007b). Although no studies have explicitly tested for positive density-dependence in fisher dispersal, it appears likely given their intrasexually territorial social system (Powell 1979, Arthur et al. 1993, Matthysen 2005). Our approach was to assume we had correct knowledge of fisher habitat suitability (i.e. that it was related to snow depth). We then used this assumption to test whether, with an individual-based genetic assignment test, we could measure density-dependent habitat selection during a population increase. We predicted that there should be a net flow of migrants from areas of shallow snow to areas of deeper snow.

## Methods

### Sampling design

Geographic townships (average size about 300 km<sup>2</sup>) in southern Ontario, Canada, were the principal sampling unit for the study and the smallest resolution usually possible for individual fisher geographic locations. In a number of cases, two or more townships needed to be grouped together to obtain sufficient sample sizes of at least 20 individuals per sample. Township sample sites as well as telemetry study locations, and sampled areas around Gatineau (Québec) and Adirondack (New York), are hereafter referred to as landscapes. In the context of our study, landscapes were defined a priori as geographic sites of comparable size comprised of variable suitabilities. A systematic sampling lattice of 35 landscapes was established to encompass southern Ontario and its surroundings (Fig. 1). Sites were mostly rectangular in shape, and were separated by at least one township along vertical or horizontal (rook) axes, whereas they could be adjacent along diagonal (bishop) axes. These distances were chosen so that landscapes were not connected by fisher daily movements, but were connected by dispersers (Arthur et al. 1993, Bowman et al. 2002).

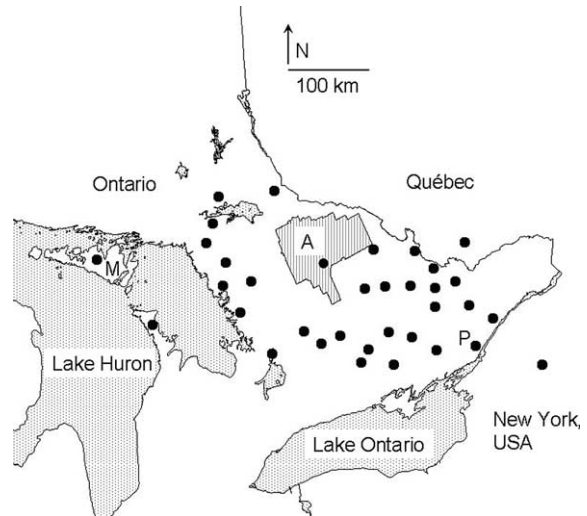


Fig. 1. Location of a fisher (*Martes pennanti*) genetics study area in the Great Lakes region of Ontario, Canada during 2000 to 2003. Geographic centroids of landscapes where fisher populations were sampled are depicted by black dots ( $n = 769$  fishers in 35 landscapes). Manitoulin Island (M), Prescott (P), and Algonquin Provincial Park (shaded area A) are identified separately.

Samples used in this study were those collected and genotyped in a previous study (Carr et al. 2007). Briefly, tissue samples from the 2001–2002 fisher harvest in Ontario were collected from Ontario Ministry of Natural Resources (OMNR) district offices. Manitoulin Island and Adirondack, New York samples from the 2000–2001 trapping season were those used previously by Kyle et al. (2001). Samples from the Gatineau, Québec area were from the 2001–2002 fur harvest. Algonquin Provincial Park and Prescott samples were obtained from ongoing fisher telemetry studies started in 2003 (landscapes A and P, respectively, in Fig. 1; Tully 2006, Koen et al. 2007b). Although all samples were obtained within a period of 3–4 years, the majority (83%) were from the winter of 2001–2002.

### Population assignment and identification of migrants

Assignment tests allow for the identification of immigrants to resident populations (Berry et al. 2004, Paetkau et al. 2004); therefore, in each sampled landscape we could calculate the proportion of immigrants if the resident population was known. We used a Bayesian assignment approach using the program Structure (ver. 2.1; Pritchard et al. 2000) to assign individuals in landscapes to inferred genetic populations a priori of geographic location. We then classified

each landscape as belonging to one of the five inferred populations on the basis of the greatest number of individuals with either high (probability  $\geq 80\%$ ) or moderate (probability 60–80%) ancestry to a population. This resulted in five “landscape clusters”, which were used to estimate migration in each landscape. This approach provided a conservative estimate of migration since the dominant cluster in any landscape was classified as the resident population.

Individuals were assigned to the inferred genetic population for which they had the highest membership value (estimated as a proportion). Immigrants were identified as those individuals that assigned to different inferred genetic populations than the landscape from which they were sampled. We used a threshold value of  $\geq 60\%$  assignment to an inferred genetic population to designate complete membership and individuals not meeting this criterion were considered to be of admixed membership. The 60% criterion identified fishers that were either currently migrating ( $F_0$ ) or were the first generation offspring ( $F_1$ ) of successful immigrants. The proportion of immigrants was calculated for each landscape by taking a ratio of the number of immigrants in a landscape over the sum of all individuals in that landscape. We used a Pearson correlation to compare the proportion of immigrants index based on a  $\geq 60\%$  assignment threshold to the same index based on a  $\geq 80\%$  threshold.

### Alternative components of habitat suitability

Snow depth records for the years 1993 through to 2002 (inclusive) were obtained from Ontario Ministry of Natural Resources monitoring stations and compiled as mean weekly snow depth from January to April. Snow depth values were then calculated for centroids of each landscape within Ontario. Proportion per landscape of deciduous, coniferous, mixed forest, and non-forested land cover were assessed within each landscape in Ontario using data from the 1996 Ontario 28-class Provincial Landcover Landsat TM Image (30-m resolution). Equivalent snow depth and forest cover data were not obtained for the Gatineau (Québec) or Adirondack (New York) landscapes so these two were excluded from analyses. Fur harvest information for registered and private trap lines, were obtained from OMNR trapping records for landscapes within Ontario and from New York State Dept of Environment and Conservation (unpubl.) for the New York samples. Fisher harvest density was calculated within each landscape as animals harvested  $\text{km}^{-2}$ , for both the 2000–2001 and 2001–2002 trapping seasons.

### Data analysis and regression model selection

We first assessed the statistical distribution of the proportion of immigrants to assess normality. We then used methods suggested by Legendre and Fortin (1989) to test for spatial structure in this metric across our study area. A spatially autocorrelated dependent variable would have to be accounted for in subsequent analyses because of the assumption of spatial independence in parametric tests. Sample locations were projected in metres using the Lambert Conical Conformic projection. Directional correlograms (Moran's  $I$ ) were used to test for spatial autocorrelation. Correlations were calculated for each distance class and a lag was selected that maximized point-pair homogeneity between distances classes. Correlations were analysed for significance using a Bonferroni correction for simultaneous inference (Legendre and Fortin 1989). Alternative components of habitat suitability were tested using least-squares linear regression to select a model that best explained the variation in the proportion of immigrants to landscapes.

### Results

We profiled 769 fishers from the 35 landscapes at 16 microsatellite loci. As discussed by Carr et al. (2007), we detected five inferred genetic populations using a Bayesian assignment approach. Each profiled fisher was assigned to one of these inferred populations or identified as an admixed individual. Landscapes were clustered into five different “landscape clusters” on the basis of the inferred population status of residents (i.e. the dominant group assignment of fishers in a landscape). There was a positive correlation between the proportion of immigrants per landscape estimated from a  $\geq 60\%$  assignment threshold and the same index estimated from a  $\geq 80\%$  threshold ( $r = 0.75$ ,  $n = 35$ ,  $p < 0.001$ ). For all subsequent analyses, we used the  $\geq 60\%$  assignment threshold. The number of migrants identified per landscape varied between 0 and 9, and the proportion of immigrants per landscape was approximately normally distributed (quantile plot not shown) with a mean of 0.18, a standard deviation of 0.11, and a median of 0.22.

The Bonferroni-corrected directional correlograms of the proportion of immigrants per landscape were not significant (Fig. 2). These correlograms were also not significant without a Bonferroni correction. We thus used parametric regressions to test alternative components of habitat suitability, such as snow depth, forest cover, and trapping pressure, where the proportion of immigrants per landscape was the dependent variable. The best fitting bivariate model was snow depth

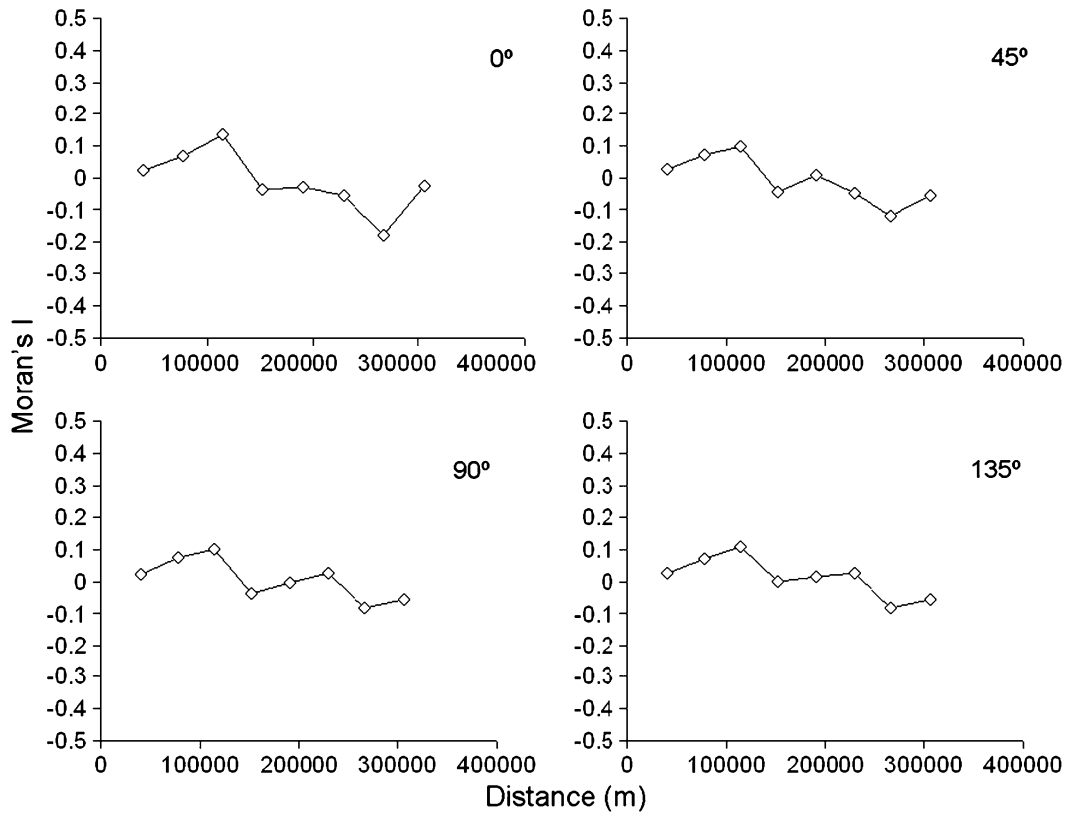


Fig. 2. Directional correlograms of proportion of immigrant fishers to 35 landscapes sampled in and around Ontario, Canada. Each panel represents an analysis at a different angular rotation (relative to north) to account for different possible directions in spatial trend. No correlations were significant.

averaged over 10 years for the period January to April, which was positively related to immigration (Table 1, Fig. 3). There was a negative relationship between immigration and the proportion of coniferous forest in landscapes. That is, there was more immigration to landscapes with less coniferous forest. This suggests that coniferous forest was of high suitability for fishers.

The correlation between snow depth and dense coniferous forest was not significant ( $r = -0.29$ ,  $n = 33$ ,  $p = 0.10$ ). We investigated these two variables further using Mallows's  $C_p$  (Venables and Ripley 1999). A model including the main effects of snow depth and coniferous forest ( $C_p = 0.337$ ) was better than a model including only snow depth ( $C_p = 0.352$ ).

Table 1. Linear regression outputs for alternative components of fisher (*Martes pennanti*) habitat suitability tested using migration inferred from genetic assignment tests of 769 fishers sampled in and around Ontario, Canada.

Model	Slope (SE)	Intercept (SE)	$F_{1,31}$	p	$R^2$
Snow depth <sup>A</sup>	0.008 (0.003)	-0.104 (0.108)	7.43	0.010	0.19
Conifer <sup>B</sup>	-0.999 (0.418)	0.244 (0.030)	5.70	0.023	0.16
Mixedwood	0.121 (0.122)	0.146 (0.046)	0.97	0.332	0.03
Non-forest	-0.105 (0.115)	0.200 (0.024)	0.83	0.370	0.03
Deciduous	-0.098 (0.216)	0.200 (0.036)	0.21	0.653	0.01
Harvest 2001 <sup>C</sup>	-0.339 (0.786)	0.210 (0.058)	0.19	0.669	0.01
Harvest 2000	0.078 (1.156)	0.183 (0.056)	0.00	0.947	0.00

<sup>A</sup>mean weekly snow depth for January to April, 1992 to 2002 inclusive

<sup>B</sup>all land cover types were estimated as a proportion for each landscape

<sup>C</sup>for harvest variables, the year stated is year in December (i.e. Harvest 2001 is the 2001–2002 winter trapping season)

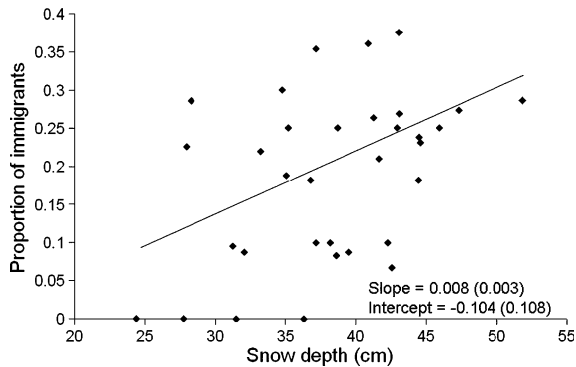


Fig. 3. The relationship between the proportion of fishers that were immigrants and mean weekly snow depth during January to April for 33 landscapes in Ontario, Canada. Snow depth was estimated using annual records compiled over 10 years (1993 to 2002). Tissue samples from 769 fishers were obtained during 2000 to 2003. Least-squares regression demonstrated a positive relationship between snow depth and the proportion of immigrants to each landscape ( $F = 7.43$ ,  $DF = 1, 31$ ,  $p = 0.010$ ,  $R^2 = 0.19$ ). Regression parameters (SE) are depicted on the graph.

or one including an interaction between snow depth and coniferous forest ( $C_p = 0.396$ ) ( $F = 5.53$ ,  $DF = 2,30$ ,  $p = 0.009$ ,  $R^2 = 0.27$ ; Table 2).

## Discussion

The pattern of fisher migration detected among our study landscapes was consistent with the prediction that deep snow reduces fisher fitness (Raine 1983, Krohn et al. 1995, 1997, 2004). We found that during a population increase, there was a net flow of migrant fishers from sites of relatively shallow snow to sites of deep snow. This finding suggests that individual-based genetic assignment tests might be used to measure habitat suitability at the scale of genetically structured populations. The best model of habitat suitability was one that included both snow depth and a negative relationship between immigration and the proportion of coniferous forest in landscapes. The most suitable landscapes had less snow and more coniferous forest.

Table 2. Multiple linear regression model explaining variation in the proportion of fishers that are migrants to landscapes in and around Ontario, Canada based on genetic assignment tests.

Model	Coefficient (SE)	p
(Intercept)	-0.005 (0.119)	0.968
Snow depth <sup>A</sup>	0.006 (0.003)	0.039
Conifer <sup>B</sup>	-0.732 (0.414)	0.088

<sup>A</sup>mean weekly snow depth for January to April, 1993 to 2002 inclusive

<sup>B</sup>proportion per landscape

The finding that coniferous forest is an important component of fisher habitat suitability is consistent with previous suggestions that fishers use coniferous forest cover in winter to avoid deep snow (Allen 1983).

Our study adds to the developing body of research often referred to as landscape genetics, which is defined as a combination of landscape ecology and population genetics (Manel et al. 2003). Landscape genetics uses genes to study the effects of landscape structure on movement patterns and demographic attributes of populations (Hale et al. 2001, Cushman et al. 2006). Many landscape genetics studies however, exhibit what Fahrig (2003) calls the patch-scale problem, which results from attempting to draw inference in a single, unreplicated landscape. Such unreplicated studies tend to assess movement and demography among patches within a single landscape ( $n = 1$ ) and therefore, can not draw landscape-scale inference (Delin and Andr en 1999, Fahrig 2003). Our study involved replicated landscapes and therefore enabled landscape-scale inference (Hurlburt 1984, Hargrove and Pickering 1992).

We have not explicitly tested for density-dependent dispersal by fishers. Relevant data however, were obtained using radio telemetry from two populations within our study area. In the deep snow landscape of Algonquin Provincial Park, female fisher mean annual home range size was estimated to be 29.9 km<sup>2</sup> ( $n = 9$ ) during 2003 to 2005 (Tully 2006). In the shallow snow landscape of Prescott in southern Ontario, mean female fisher home range was 3.6 km<sup>2</sup> ( $n = 15$ ) during the same years (Koen et al. 2007b; Fig. 1). Since density is inversely related to home range size for fishers (Fuller et al. 2001), it appears that density was higher in the shallow compared to the deep snow landscape. This is consistent with the hypothesis of density-dependent dispersal to lower quality (deep snow) habitats.

Since our study took place only during a population increase, we can not discriminate between reciprocating and alternative models of dispersal. Indeed, Morris et al. (2004) warned that movement data alone may not provide enough information to discriminate among all of the alternative dispersal systems, such as source-sink dynamics and balanced dispersal. For example, with our present data, it is not possible to determine whether the deeper snow landscapes are sinks or simply lower quality. An appropriate time series of demographic data is required to confirm the presence of a sink (Boughton 2000). However, historical patterns of occupancy by fishers in Ontario suggest that the deep snow landscapes are not necessarily sinks. For example, Algonquin Provincial Park had a high proportion of immigrants (0.25), but was an important refuge for fishers during population declines of the 1930s (de Vos 1952).

Our method is only relevant where sufficient genetic structure exists such that there are at least two inferred

genetic populations. Variation in demographic rates (and hence habitat suitability) within one inferred genetic population is not straightforward to detect using genetics. For example, by definition, source and sink populations should be functionally connected by dispersers and thus, many source–sink systems may not be structured genetically. This raises a question about the relationship between genetic and demographic definitions of a population. From a geneticist's perspective, there were five inferred populations in our study area (Carr et al. 2007). However, this does not necessitate five demographically distinct populations. Indeed, our results suggest a range of variability in immigration to landscapes even within genetic populations, perhaps due to local habitat conditions.

The recent fisher population increase appears to have been at least partly a response to increase food supply (Bowman et al. 2006). Certainly, food supply must be an important component of habitat suitability for predators such as fishers. In fact, the putative fitness effects of snow depth on fishers are largely a result of reduced access to food: snow depth (and snow quality) should affect a fisher's ability to capture prey, and would thus affect food supply (Krohn et al. 1995). There should be a negative correlation between snow depth and food supply for fishers, but not necessarily prey abundance. This suggests that snow depth is a superior metric of habitat suitability.

Trapping of fishers for fur occurred in most, but not all, of the study area. However, harvest of fishers per unit area was not related to patterns of migration (Table 1). Further, mortality rates of radio-collared populations suggest that harvest rates were low (Tully 2006, Koen et al. 2007a), as does an assessment of population trajectory in the study area (Bowman et al. 2006). It is likely that trapping had only a small effect on patterns of density-dependent dispersal. This would be especially true in the presence of density compensation.

## Summary

Where dispersal is density-dependent and populations are increasing in density, the proportion of immigrants should be greater in habitats with low habitat suitability. This suggests that in such cases, individual-based genetic assignment tests can be used to assess habitat suitability. We found a positive relationship between the proportion of immigrants and snow depth, a result consistent with suggestions that deep snow reduces fisher fitness. Our novel approach permitted landscape-scale inference about relationships between habitat suitability and demography of a vagile carnivore.

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