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Mammal Community Dynamics

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Coniferous Forests of
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Measuring and interpreting connectivity for mammals in coniferous forests

Introduction

Western coniferous forests have a history of natural disturbance due to fire, disease, and other factors (Agee 1993), but during the past century late-seral forests have been increasingly fragmented due to logging and development. For example, in the Pacific Northwest, less than half of pre-settlement, old-growth Douglas-fir (*Pseudotsuga menziesii*) forest remains, often in relatively small remnants of 100 ha or less in a matrix of clear-cuts and regenerating forest (Booth 1991, Garmon et al. 1999, Jules et al. 1999). Road building has also impacted wildlife habitat, with an average of 3.4 miles of road per square mile on United States Forest Service roaded-lands and approximately twice that on private lands (Federal Budget Consulting Group and Price-Waterhouse LLP 1997, Coghlan and Sowa 1998, Federal Register 2001, USDA 2001).

For certain species associated with late-seral forests, fragmentation due to human perturbations has two consequences: loss of habitat and changes in connectivity among remnants. Habitat loss, and the concomitant decrease in population size for some wildlife species, has garnered the most attention because such loss is painfully obvious both in its occurrence and its effects. The second consequence, the change in connectivity among populations, is more subtle and harder to measure.

Nevertheless, the importance of populations being connected versus isolated has been underscored in the scientific literature for at least 70 years. For example, biologists have long recognized that the interplay between population size, local adaptation, and gene flow (connectivity) will create a unique genetic structure across a landscape (Wright 1931). If populations on large forest tracts become small and isolated via

fragmentation, genetic variation can be decreased with subsequent effects on population persistence (*sensu* Mills and Tallmon 1999). Similarly, the demographic consequences of isolation versus connectivity have been emphasized at least since Nicholson and Bailey (1935) and Andrewartha and Birch (1954; see Fahrig and Merriam 1994, Hastings and Harrison 1994). In many cases, the stability of a collection of populations ("metapopulation"; Hanski and Gilpin 1997) may be very sensitive to connectivity. For example, Beier (1993) modeled connectivity for cougars in California and found that overall extinction probability is greatly reduced when connectivity is higher.

Connectivity is also demonstrably important at larger scales. The level of connectivity can affect the spread of geographic ranges and allow response to changing environmental conditions (Pease et al. 1989). Likewise, successful re-introduction can be facilitated by connectivity (Singer et al. 2000). Connectivity can also affect the synchrony across space and the amplitude of population size changes; the classic case is the "traveling-wave" dynamics of Canadian lynx (*Lynx canadensis*) populations emanating from the center of the taiga outward toward the periphery (Blasius et al. 1999, McKelvey et al. 2000, Mowat et al. 2000, Schwartz et al. 2002). Finally, the degree of connectivity has been proposed as a central criterion for determining taxonomy and population distinctiveness, thereby fundamentally affecting whether populations should be treated as distinct management units (Waples 1995, Crandall et al. 2000).

Clearly, the importance of connectivity for understanding population dynamics has implications for forest managers, ranging from evaluating population uniqueness to maintaining population persistence. In addition, re-introduction programs will be heavily weighted by whether or not a species is likely to re-colonize naturally (as in the case of wolf re-introduction and proposed grizzly bear re-introduction in Idaho and Montana). Similarly, decisions of whether supplementation is necessary for extant populations will hinge on the current degree of isolation.

In short, knowledge of connectivity across the landscape is essential to understand wildlife populations (Martin and McComb 2003), and yet connectivity has been enormously challenging to measure, with most of the successful examples of measuring connectivity being experimental studies of small spatial and short temporal scales (reviewed in Debinski and Holt 2000). We will provide an overview of new approaches to measuring connectivity, with examples from some of our own research on mammals in western coniferous forests. We will also consider "how much"

connectivity is desirable and some ways of achieving it in a fragmented landscape.

Some definitions

Connectivity is a broad and vague term that implies movement among populations, analogous to what has been described as "transfer" (Ims and Yoccoz 1997). Connectivity can be described more precisely with other terms, such as dispersal, emigration, immigration, colonization, and migration rates. The term "dispersal" addresses behavioral aspects, "constituting movements of individuals (or propagules) away from their home areas, excluding short-term exploratory movements" (Lidicker and Patton 1987:144). "Emigration" and "immigration" refer to dispersal out of and into a target population, respectively. These are demographically meaningful because abundance and population trend are a function of emigration plus deaths leaving the population versus immigration and births adding to it. In addition to dispersal among extant populations, dispersal can occur to areas currently unoccupied by the species ("colonization" if the species has never occupied the site and "re-colonization" if it has).

In population genetics, "migration rate" (m) is the proportion of individuals that move between populations, establish residence, and breed. Thus, migration is equal to "gene flow" in classic population genetics models. Although we will use "migration" in this sense, we recognize that it is different from the traditional ecological use of "migration" as a descriptor of seasonal movements across elevation or latitude (see Webster et al. 2002 for an excellent overview of measuring migratory connectivity). For example, although polar bears (*Ursus maritimus*) are known to have extremely large seasonal movements, gene flow between populations is restricted (Paetkau et al. 1995, 1999).

Measures of connectivity differ in both the timing of movements and whether or not reproduction (gene flow) occurred. Research or management questions may revolve around current movement rates, or around average movement during the recent past, or even in the historical past before widespread human-caused fragmentation. Reproduction is important because dispersal of individuals could have immediate demographic effects, but unless new arrivals breed (i.e., gene flow) they will not affect genetic structure (Ehrlich and Raven 1969) or directly increase long-term population size.

Approaches to measuring connectivity

Historically, connectivity among mammal populations has been evaluated through heroic efforts using radiotelemetry and capture-recapture techniques. Both have the advantages of directly measuring connectivity while also providing insights into natural history, habitat use, individual health, survival, age structure, and population size. In general, trapping grids and telemetry have underestimated dispersal rates and distances because the further an animal goes the less likely it is to be detected, and rare but important dispersal events tend to be missed (Koenig et al. 1996, Peacock 1997). Recent advances in telemetry have been assets for these direct measures of connectivity, and more species will be followed with satellite transmitters (e.g., Ferguson and Messier 2000) as transmitter size, weight, and cost decrease. However, for mammals in western forests, canopy cover may limit the use of satellite technology.

Like the technological advances, development of new analytical methods for capture-recapture (and telemetry) data are also important because they facilitate estimates of both survival and movement among populations (Spendelov et al. 1995, Burnham and Anderson 1998, Powell et al. 2000, Bennetts et al. 2001). However, capture-recapture and telemetry methods cannot readily quantify whether reproduction occurred. On the other hand, recent developments in molecular biology techniques and analyses of genetic data provide a new suite of tools with tremendous potential to monitor rates of gene flow, but the temporal scale of gene flow is typically less clearly defined.

To further explore the utility and limits of these new approaches, we next provide overviews of emerging tools to quantify connectivity based on capture-recapture and genetic analysis. We will focus on approaches most relevant to mammals.

Estimating connectivity with capture-mark-recapture (CMR) approaches

Capture-mark-recapture (CMR) models provide a statistical basis for separating the probability of capture from biologically interesting parameters such as abundance, mortality, and dispersal. Here, we discuss a subset of CMR methods referred to as multi-state or multi-strata models that provide the theoretical framework for estimating transition probabilities among geographic "states" (see Ims and Yoccoz 1997, Nichols and Coffman 1999, Hanski et al. 2000). Multi-state models are extensions of Cormack-Jolly-Seber models that have been used for decades to estimate

abundance and survival in open populations (not closed to births, deaths, emigration, and immigration). Following an information theoretic approach to analyzing multi-state CMR data (Lebreton et al. 1992, Burnham and Anderson 1998), a researcher first develops a candidate model set that identifies biologically realistic sources of variation (e.g., age, gender, time of year, population location, etc.) in the parameters of interest. This is accomplished by drawing upon knowledge of the system, previous studies, and biological intuition. Once the data have been obtained, an information criterion, such as Akaike's information criterion (AIC), is used to select the model(s) most consistent with the data.

This model-selection process accomplishes two important tasks. First, model selection tests biological hypotheses by determining which of the models in the candidate set best approximate the data. Second, by determining the candidate models most appropriate for the data, information theoretic approaches provide parameter estimates with minimized bias (given the candidate models and the quality of the data) and estimates of their precision (Lebreton et al. 1992, Burnham and Anderson 1998). Because the inferences that can be made about a system are limited to the validity of the candidate set of models, previous knowledge of a biological system and natural history is important in the development of realistic and valid candidate models (Burnham and Anderson 1998).

One reason why multi-state models have not been used more to estimate connectivity is because capture probabilities (and number of captures) must be high in order to obtain reasonably precise survival and movement estimates (Ims and Yoccoz 1997). High capture probabilities usually require a great deal of effort, and the effort increases as the number of populations (and parameters in the multi-state model) increases. Consequently, there is an implicit trade-off between the number of populations sampled and the precision of parameter estimates.

Estimating connectivity with genetic tools

Genetic tools for measuring connectivity have undergone astonishing developments in the last decade, with advances in both molecular techniques and analytical tools. The greatest leap in molecular techniques has been in applications of the polymerase chain reaction (PCR). Amplification of deoxyribonucleic acid (DNA) via PCR has led to analysis of bits of tissue collected in creative ways from hair, scats, saliva, and blood (Kohn and Wayne 1997, Schwartz et al. 1998, Taberlet et al. 1999). Thus, it is possible to sample non-invasively (Taberlet and Luikart 1999), so that no capture or restraint is necessary. PCR also allows the use of ancient

DNA to examine connectivity among historic populations. For example, a lack of connectivity currently and historically among pocket gophers was inferred from the fact that in Lamar Cave (Yellowstone National Park) gophers had unique *cytochrome b* sequences in samples spanning from the present to 2400 years ago, and these sequences were absent from adjacent localities (Hadley et al. 1998).

On the heels of breakthroughs in non-invasive sampling, there is now an impressive array of approaches for individual and species identification, phylogenetic analysis, and estimation of abundance (Haig 1998, Waits and Leberg 1999, 2000, Woods et al. 1999, Mills et al. 2000a, 2000b). For measuring connectivity, both nuclear and mitochondrial (mtDNA) markers may be used for complementary insights. Mitochondrial DNA is maternally inherited, so it will not detect connectivity by males alone (male-biased dispersal). In one sense this is a disadvantage of mtDNA. However, if female movement is of primary interest, then the signal movement from mtDNA will be preferred to that of nuclear DNA (Taylor et al. 2000). Furthermore, comparing the signals from mtDNA to nuclear DNA may elucidate sex-biased dispersal patterns of the species of interest.

The analytical and statistical tools to analyze DNA have developed as dramatically as the molecular advances (Rousset and Raymond 1997, Luikart and England 1999, Balding et al. 2001). Next we describe both equilibrium and non-equilibrium measures for estimating connectivity using genetic tools.

Equilibrium genetic measures

Although a number of different metrics have been developed to estimate gene flow from nuclear genetic data (e.g., Slatkin 1995), most derive from Sewall Wright's F_{st} (for history and derivation see Slatkin 1985) so that the mean number of migrants entering each population each generation is inversely related to the variance in gene frequencies among different populations. Specifically, under the assumptions of the island model (Wright 1931; see also Slatkin and Barton 1989, Mills and Allendorf 1996):

$$Nm \approx [1/(4F_{st})] - (1/4) \quad (1)$$

where F_{st} is the proportion of total gene diversity due to divergence among subpopulations, N is the effective population size of each subpopulation, and m is the proportion of migrants entering subpopulations. The product Nm is the number of migrants entering a subpopulation each generation.

These are considered "equilibrium" measures of gene flow because it is assumed that the variance in gene frequencies among populations (F_{st}) represents an equilibrium between genetic drift increasing divergence and gene flow decreasing it. Importantly, the time that it takes for F_{st} , and therefore Nm , to reach equilibrium can be extremely long (hundreds to thousands of generations) when the migration rate is small and/or the population size is large (Varvio et al. 1986, Steinberg and Jordan 1997, Whitlock and McCauley 1999). Therefore, F_{st} -derived estimates of migration rates typically reflect a mix of current and historical gene flow. In certain cases, this actually might be an advantage. For example, if the human-caused perturbation of interest is recent (on the order of tens of generations into the past), equilibrium gene flow measures may "look back" into the period before the perturbation. Thus, F_{st} -type approaches could give at least a qualitative insight into historical connectivity based on the genetic "signature" arising from past differentiation in allele frequencies among populations.

The use of equilibrium-based measures to quantify levels of gene flow for any time period depends on simplifying assumptions that are unlikely to hold true in many cases (for summaries of critiques see Neigel 1996, Bossart and Prowell 1998, Whitlock and McCauley 1999). For example, all populations are assumed to equally contribute and receive migrants; if the number of migrants (Nm) varies among populations (due to population sizes, distance, barriers, and so on), the estimated gene flow is likely to be negatively biased. Variation in gene flow across time, including extinction and colonization of populations, will also affect F_{st} and Nm estimates and inflate the standard errors of gene flow estimates. While new analytical approaches provide migration rate estimates that are robust to violations of some of the fundamental assumptions of F_{st} -based measures (e.g., Beerli and Felsenstein 2001, Vitalis and Couvet 2001), these methods are so new that they have not been thoroughly tested with field data and so it is not known how they perform for samples collected from natural populations. Likewise, a clever approach for estimating distance moved by the dispersing sex based on analysis of isolation by distance for the philopatric sex (applied to lions, *Panthera leo*, by Spong and Creel 2001) may have potential for application to species with strong sex-biased dispersal (see also Goudet et al. 2002).

In short, we believe that equilibrium gene flow measures can be useful for qualitative comparisons of historical gene flow, and can give some insights into current gene flow if coupled with demographic information

(see "Three case studies evaluating connectivity for mammals" below). In general, however, we advocate the use of equilibrium gene flow measures in categorical as opposed to quantitative applications. For example, an $Nm < 1.0$ might be considered "low" due to loss of alleles via genetic drift (Mills and Allendorf 1996), $Nm > 10.0$ might be considered "high" because local adaptations would begin to be swamped (Mills and Allendorf 1996, Vucetich and Waite 2000), and $1.0 < Nm < 10.0$ considered "medium".

Non-equilibrium genetic measures (assignment tests)

Newly developed "assignment tests" represent a major step forward in genetic analyses of connectivity because these approaches do not assume genetic equilibrium and therefore have potential for quantifying current gene flow (e.g., Paetkau et al. 1995, Rannala and Mountain 1997, Waser and Strobeck 1998, Cornuet et al. 1999, Davies et al. 1999, Luikart and England 1999, Pritchard et al. 2000, Manel et al. 2003). In essence, assignment tests take advantage of the genetic differences at many loci among populations to assign individuals to the population from which they originated. Connectivity is thereby quantified by estimating the number of first-generation immigrants, individuals born in a population other than the one from which they were sampled (Rannala and Mountain 1997).

In general, assignment tests are more likely to fail when the populations are not distinct (F_{st} less than approximately 0.1), although statistical power can be increased with more polymorphic loci and individuals sampled (Olsen et al. 2000, Manel et al. 2002). Another difficulty is that if the true source population is not included in the analyses, it may be harder to detect an immigrant individual because it cannot be properly categorized with its "home" population (Cornuet et al. 1999). Lastly, the assignment test relies on populations maintaining Hardy-Weinberg proportions, although the test may not be overly sensitive to these assumptions (Cornuet et al. 1999). There is a pressing need for simulations (see Cornuet et al. 1999) to evaluate the power and accuracy of assignment tests under a variety of levels of genetic differentiation, number of samples, and number of loci. Ultimately, the robustness of assignment tests under real-world conditions remains unexplored (Sunnucks 2000) and will determine how generally applicable these tests are under the non-equilibrium conditions that will be the rule in conservation applications. The greatest advances may be in assessing assignment tests in settings where connectivity is known from non-genetic-based measures (e.g., Paetkau et al. 1999).

Three case studies evaluating connectivity for mammals

Much of our research has focused on conservation questions centered on connectivity, isolation, and persistence of forest mammals in western North America, using genetic and demographic approaches. Next we provide three concrete examples of the techniques described above.

Columbian mice on edges in Olympic National Park

We employed capture-mark-recapture (CMR) and information theoretic approaches to examine the effects of forest fragmentation and forest edges on the population dynamics of the Columbian mouse (*Peromyscus keeni oreas*). The study is described completely elsewhere (Lair 2001); here we distill only the aspects directly related to measuring connectivity. Trapping grids were established on the west side of the Olympic Peninsula, Washington at sites where 5- to 10-year-old clear-cuts were adjacent to undisturbed old-growth stands. In 1997 two of the sites (Willoughby and Queets) were trapped and in 1998 two additional sites were added (Hoh and Tacoma). At each of the four sites, trapping grids 16 traps long by three traps wide (48 traps total) ran parallel to the forest-clear-cut boundary in each of three "edge classes": (1) 150 m into the forest from the forest/clear-cut edge; (2) along the edge; (3) 150 m into the clear-cut from the edge. The summer trapping schedule followed the "robust design" (Pollock 1982, Pollock et al. 1990), such that multiple "secondary" sampling sessions (six to seven consecutive nights) made up each "primary" sampling period.

We developed multi-state models to obtain maximum-likelihood estimates of state-specific survival rates (S) and transition probabilities (Ψ) between primary periods, and state-specific capture probability (p) within primary periods. The states in our study corresponded to edge classes within a site, so that transition probabilities were estimates of movement rates among edge classes. We specified a set of candidate models that incorporated biologically realistic sources of variation in S , Ψ , and p based on edge classes, sites, gender, and primary periods (temporal variation).

Model selection and parameter estimation were accomplished using the multi-state routine in program MARK (White and Burnham 1999). The best approximating models for 1997 Columbian mouse movement rate (Ψ) identified only variation among sites as important for transitions (movements) among edge classes (Fig. 17.1). Movement rates among edge classes at the Willoughby site were much greater (0.22; SE = 0.066) than that at the Queets site (0.07; SE = 0.022). These rates can be interpreted

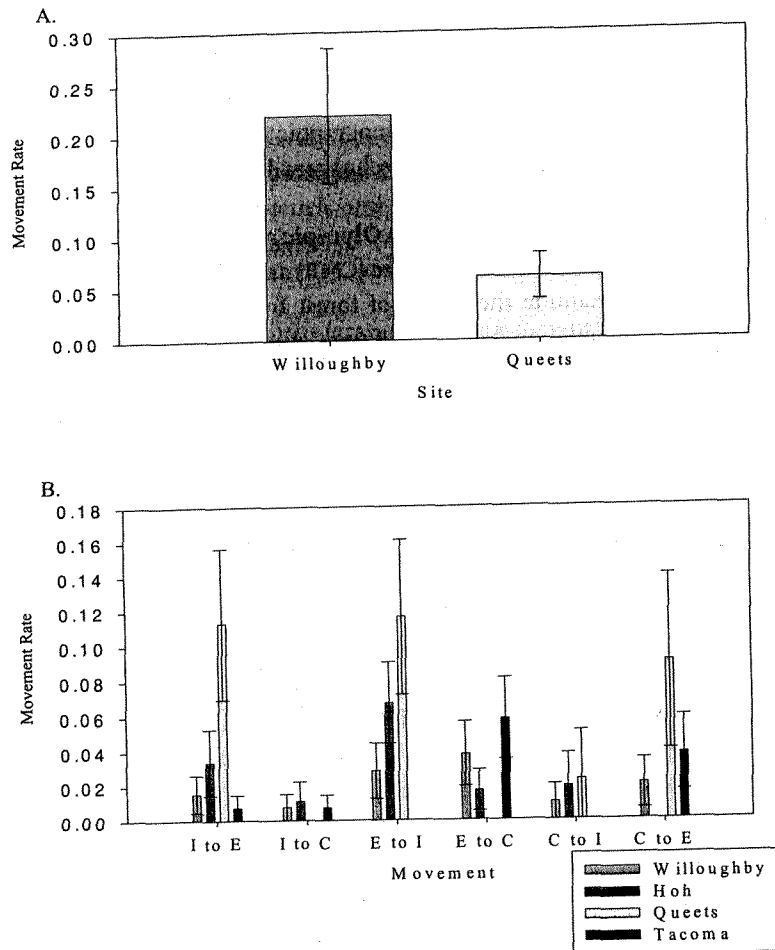


Fig. 17.1. Columbian mouse movement rates between edge classes (forest interior, edge, clear-cut) in 1997 (A) and 1998 (B) under the best approximating multi-state capture-recapture models. In 1997, movement rates were dependent on the site (Queets or Willoughby). In 1998, movement varied among sites and edge classes. Error bars represent one standard error. Letters represent habitat types: I = forest interior, E = forest edge, and C = clear-cut.

as 22% of the mice at the Willoughby site and 7% at the Queets site moved from one edge class to another, on average, every two weeks during summer 1997, with no detectable differences among sexes, time, or specific edge class rates. In 1998, there were again no detectable differences in movement rates among the sexes or over time, but both site and edge class were identified as important sources of variation (Fig. 17.1). Thus, in 1998

Columbian mouse movement rates varied depending upon which habitat the animal was moving to and from. For example, in the Tacoma site movement was greatest from the edge to the clear-cut and the clear-cut to edge, while in the Hoh sites movements were greatest from edge to interior and interior to edge (Fig. 17.1B). In short, quantified movement rates to and from clear-cuts were not radically different than those to and from the other habitats. In addition, our analysis of survival indicated no consistent patterns across sites, primary periods, or years, and movement out of the habitats with higher survival in any year was not greater than movement into these habitats. Together, these results indicate that forest fragmentation is not creating "demographic sinks" for this species on the west side of the Olympic Peninsula (Lair 2001).

Western red-backed voles in Oregon forest fragments

We combined genetic and demographic approaches to evaluate the effects of habitat fragmentation on the connectivity of western red-backed vole (*Clethrionomys californicus*) populations on forest fragments in southwest Oregon. Previous studies suggest this species is closely associated with forests with high litter depth (Rosenberg et al. 1994) and virtually absent from recently clear-cut and burned areas (Tevis 1956, Gashwiler 1970, Mills 1995, 1996), and that voles on forest fragments can show a negative edge effect (Mills 1995, 1996).

To evaluate whether connectivity was affected by fragmentation, we trapped voles in 12 forest fragments, surrounding clear-cuts, and in unharvested control areas in 1997, 1998, and 1999 (a subset of the same sites trapped by Mills 1995). We used capture data and genetic analysis to measure and interpret changes in connectivity (see Tallmon et al. 2002 for details that are summarized here). We were able to consider temporal patterns in genetic variation from populations sampled in 1990–1991, and again in 1998, on two of these fragments and two nearby contiguous control sites. We also used intensive trapping sessions in the summers of 1998 and 1999 to estimate the sizes of these same vole populations.

Our trapping data suggested movement across clear-cuts during summer was extremely limited. In the clear-cuts surrounding the 12 fragments trapped in 1990, 1991, 1997, 1998, and 1999, we detected only 13 voles; only one of these subsequently was trapped in a fragment population. The rate of capture of different voles per trap-night (an index comprised of both number of animals and probability of capture) was much lower on clear-cuts compared to fragments or controls: clear-cuts (13 different voles/4728

Table 17.1. Mitochondrial DNA number of alleles (A) and allelic diversity (\hat{h}) in vole samples from forest fragments (F1, F2) and control sites (C1, C2, C3)

1990 and 1991 samples				1998 samples			
Site	n	A	\hat{h} (S.E.)	Site	n	A	\hat{h} (S.E.)
F1	11	1	0.00 (0.00)	F1	22	3	0.17 (0.07)
F2	9	1	0.00 (0.00)	F2	21	1	0.00 (0.00)
C3	20	3	0.34 (0.09)	C1	23	4	0.59 (0.06)
				C2	22	3	0.58 (0.08)

Table 17.2. The mean number of alleles (\hat{A}) and observed heterozygosities (H_o) at 5 microsatellite loci in samples (n) from vole populations on forest fragments (F1, F2) and control sites (C1, C2, C3)

1990 and 1991 samples			1998 samples		
Site	n	Mean (S.E.)	Site	n	Mean (S.E.)
		(\hat{A}) and (H_o)			(\hat{A}) and (H_o)
F1	16	10.0 (2.6) 0.66 (0.22)	F1	34	11.2 (2.4) 0.73 (0.20)
F2	9	8.0 (1.0) 0.64 (0.15)	F2	35	10.8 (1.5) 0.77 (0.18)
C3	24	11.0 (2.6) 0.78 (0.12)	C1	36	12.4 (1.8) 0.72 (0.18)
			C2	34	11.6 (2.0) 0.78 (0.13)

trap nights = 0.0027); forest fragments (387 voles/24505 trap nights = 0.016); and controls (346 voles/12657 trap nights = 0.027).

Mitochondrial DNA (mtDNA) data from two fragments and two control sites further indicated limited immigration into fragment populations. mtDNA allelic diversity and the number of alleles were lower on the fragments than in the controls in both 1990–1991 and 1998 samples (Table 17.1). This pattern would usually be interpreted as evidence for isolation and possible inbreeding effects in fragment populations. However, in contrast to the trapping and mtDNA data, nuclear DNA heterozygosity and numbers of alleles estimated with five nuclear microsatellite markers did not imply isolation of vole populations on forest fragments (Table 17.2). Instead, we found roughly equivalent levels of genetic

variation across fragments and controls – especially in 1998 when sample sizes were large and roughly equal among sites.

The lower variation detected with mtDNA on forest fragments, but not with microsatellite markers, may be explained by the stronger effects of genetic drift on mtDNA (a single haplotype is passed down only by females, in contrast to the biparental inheritance of nuclear genes). An alternative explanation is that these voles exhibit male-biased dispersal among fragments. That is, there may be a bias toward male dispersal that keeps nuclear variation equal while mtDNA variation is reduced within fragments because females do not bring novel haplotypes. We favor this alternative, as male-biased dispersal is common among closely related vole species and many other mammal taxa (see Wolff 2003). In addition, of the 13 voles that we captured in clear-cuts over the five summers of sampling these sites, nine were males; the binomial probability of detecting nine or more males in a sample of 13 voles with an expected 50:50 sex ratio is 0.13.

Estimates of gene flow based on the microsatellite data and F_{st} -based measures are “medium” (on the order of $Nm = 7.7$ with 95% bootstrapped confidence intervals of 6.2 to 10.4). However, as stated above (equilibrium genetic measures), F_{st} -type measures have the potential to confound recent events with historical population structure. A low F_{st} value (and resultant medium or high gene flow estimates) could come from current high levels of gene flow or it could be a genetic “signal” from a large, panmictic population prior to fragmentation (a historical effect). In our case, we teased apart these possibilities by examining demographic data from the fragments. Based on our intensive CMR data, vole populations fluctuated below 50 individuals on the two fragments throughout the summers of 1998 and 1999. We know the genetic effective size of a population is usually between 30% and 50% of the total population size (Frankham 1995, Kalinowski and Waples 2002) and that these fragments have been surrounded by clear-cuts for at least 20 vole generations. Based on population genetics theory (Wright 1931), we would expect the fragments to show at least 12% to 85% reduction in heterozygosity relative to controls if fragments are truly isolated (Tallmon et al. 2002). Instead, fragment populations had heterozygosity levels intermediate to the controls. Consequently, these small fragment populations must be linked by current gene flow (several migrants per generation) to maintain genetic variation equivalent to that in contiguous forest populations. In addition, the reduction in mtDNA variation on fragments relative to controls in both

1990–1991 and 1998 samples suggests current gene flow may be largely male biased.

Determining movement in a fragmented forest landscape for voles has important implications for forest community dynamics. The western red-backed vole is thought to be one of the primary dispersers of hypogeous ectomycorrhizal fungi (as are several other small mammal species; see Luoma et al. 2003). Conifers in this region depend upon mycorrhizal fungi for soil nutrients and water, and the re-establishment success of seedlings in clear-cuts is increased by mycorrhizae formation (e.g., Perry et al. 1989). Because clear-cuts can be depauperate of ectomycorrhizal fungi (Durall et al. 1999, Hagerman et al. 1999), the movement of voles through clear-cuts may be important for ectomycorrhizae dispersal into recently clear-cut areas. Therefore, the detection of movement through clear-cuts using a combination of genetic and demographic data is an important finding for both vole population biology and forest community dynamics.

Canadian lynx (*Lynx canadensis*) in western North America

Canadian lynx are among the most difficult mammals to study in North American coniferous forests because they are elusive, inhabit rugged terrain, and are found at low densities. Although lynx were listed as “Threatened” under the U.S. Endangered Species Act in 2000 (3/24/2000 Federal Register), little is known about intra-population dynamics and even less about inter-population dynamics (Ruggiero et al. 2000). Anecdotal evidence has shown that lynx can travel long distances, with recorded movements of up to 1100 km (Slough and Mowat 1996). However, we do not know if these long distance movements are exploratory trips, dispersal events, or if gene flow occurs.

We used molecular genetic techniques to test two opposing ideas about lynx population sub-structure (see Schwartz et al. 2002, 2003 for details): (1) lynx at the periphery of their geographic range exist in small isolated populations, and (2) movement is ubiquitous among populations regardless of their position on the landscape. We tested these hypotheses using nine DNA microsatellite loci on 599 samples, from 17 populations in Alaska, Western Canada and Montana (Fig. 17.2). All the markers were highly variable, showing between 1 and 20 alleles per population and having an average heterozygosity across populations of 0.66 (SE = 0.074).

The F_{st} estimate was 0.033 (SE = 0.002) from which we estimated approximately six migrants moving among populations on average each generation (a “medium” level of gene flow by our qualitative categories). We believe the F_{st} estimate is produced by current gene flow and is not a

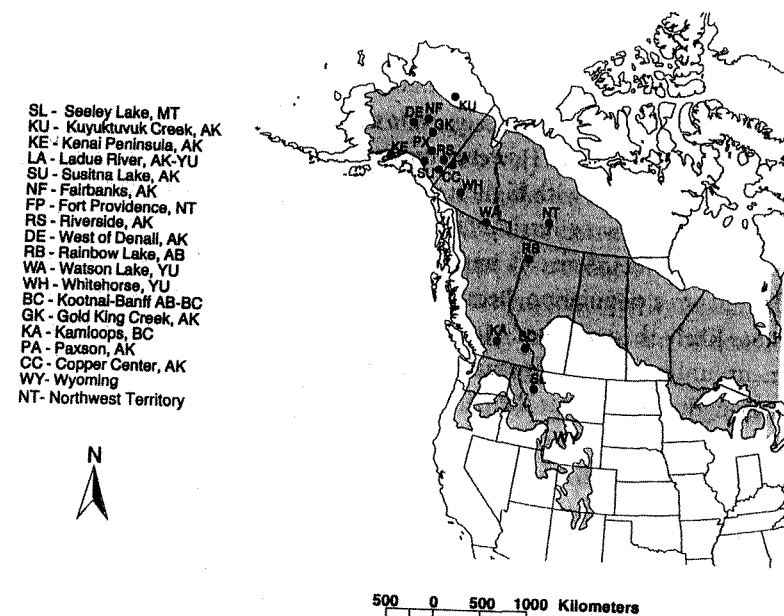


Fig. 17.2. Lynx range map and population identifiers. The shaded area of the map denotes the approximate geographic range of Canadian lynx. Each point and two-letter code is a lynx population (see legend). We only considered a group of lynx a population for sampling purposes if at least 5 samples of different lynx were separated by 100 km from other groups or had a human perceived physical barrier between them.

historical artifact among populations because several peripheral lynx populations (e.g., Kenai Peninsula Lake, Montana) have low abundances that would lead to strong genetic drift, rapidly inflating F_{st} unless gene flow occurred (Tallmon et al. 2002). Decomposing the global F_{st} estimate into pairwise F_{st} estimates (range of pairwise F_{st} values = 0.0–0.07) indicated that gene flow was universal among all populations, with the highest level between Fairbanks (NF) and the Ladue River (LA) and the lowest levels between the Kenai Peninsula (KE) and Seeley Lake Montana (SL) and the Kenai Peninsula and Watson Lake (WA). Overall, based on F_{st} it appears that lynx gene flow is high, even compared to other mobile carnivores.

Lastly, we evaluated the usefulness of assignment tests for studying dispersal using GeneClass, the partially Bayesian assignment test of Cornuet et al. (1999). GeneClass assigned only 40.8% of the lynx to the populations from which they were captured, indicative of relatively high gene flow consistent with our F_{st} -based estimates (see Manel et al. 2002 for comparisons with similar numbers and types of markers in different

applications). We next used GeneClass to assign two samples from the southern extreme of the lynx's geographic range (Wyoming) that were not included in the previous analysis due to small sample size. We expected both of these samples to be assigned to the nearest large lynx population, Seeley Lake, Montana. However, neither lynx assigned to Seeley Lake, but rather assigned with highest probabilities to the Watson Lake, Yukon (WA) and Northwest Territory (NT) populations (6% and 3% assignment probabilities, respectively). Importantly, GeneClass always classifies an individual to a population, because there is always one population that is more likely than another. However, GeneClass's probabilities of assignment, unlike other assignment tests, do not necessarily add up to one, making it explicit that the true population may not have been sampled (Cornuet et al. 1999). For example, the samples from the southern periphery were assigned to the Northwest Territory with only a 3% probability, in contrast to other assignment programs that would likely assign a much higher (but false) probability because the samples fit the Northwest Territory better than any other population. In our case, the assignment test indicates not that these lynx necessarily migrated the thousands of kilometers from the Northwest Territories or the Yukon (although they may have made such movements), but rather that they are from populations more genetically similar to the Northwest Territories and Yukon lynx than to populations closest to Wyoming.

In this case, genetic tools facilitated insight into connectivity that would not have been possible using conventional mark-recapture or telemetry techniques. We now know that lynx not only move long distances, but do it regularly and transfer genes in the process. Furthermore, our data suggest that populations of lynx in Wyoming did not colonize in a stepwise manner (e.g., from Canada, to Seeley Lake, then to Wyoming). Finally, if lynx persistence in the contiguous U.S. depends upon migration from larger populations, then joint international efforts must be initiated to ensure that connectivity between Southern Canada and the U.S. is maintained. Re-introduction efforts alone, without concomitant maintenance of connectivity among southern and northern lynx populations, are unlikely to prevent local extinctions at the southern periphery (Zager et al. 1995).

How much connectivity is desirable, and how to achieve it?

Although we have given a number of reasons why connectivity is important, and some ways of measuring it, it is not always true that "more is

necessarily better." Thus, it is important to consider how much is optimal or desirable, and what is the best way to achieve a desired level of connectivity.

The ability of a population to locally adapt can be overwhelmed when gene flow levels are high, unless selection is very strong (see Allendorf 1983, Slatkin 1985, Lacy 1987, Barton 2001). At the extreme, inappropriately high gene flow can lead to outbreeding depression driven by the breakup of co-adapted gene complexes and the destruction of local adaptation (Leberg 1990, Burton et al. 1999). In addition, connectivity can facilitate ecological problems including subsidizing the movement of exotic species and diseases (Simberloff et al. 1992, Hess 1994).

On the other hand, we have described a number of reasons why connectivity is important and even vital. So how much connectivity is desirable for mammals? The only general "rule of thumb" developed to date is based on purely genetic factors: "one migrant per generation" (OMPG) is sufficient to minimize the loss of heterozygosity within subpopulations while allowing genetic divergence (and local adaptation) among subpopulations (Wright 1931). In an experimental study of the effects of migration on plant fitness, Newman and Tallmon (2001) found that fitness measured in several different traits, and overall, was increased over the 0 migrant control treatment with one migrant per generation, and was approximately equal to that in a 2.5 migrant treatment. At the same time, phenotypic divergence was greater in the 1 migrant treatment than in the 2.5 migrant treatment, providing empirical support for Wright's theory that the trade-off between local adaptation and inbreeding may be optimized by this level of connectivity (see Mills and Allendorf 1996).

If the "rule" is generalized to 1–10 migrants per generation, it appears to be surprisingly robust for genetic considerations (Hedrick 1995, Mills and Allendorf 1996). Of course, ecological and demographic needs can often mandate higher or lower levels of connectivity (see also Vucetich and Waite 2000).

As an alternative to a universal "rule of thumb" such as OMPG, it may be possible to derive an appropriate level of connectivity by estimating historical rates using genetic or ecological data. As mentioned above, emerging genetic tools can provide insight into historical connectivity before human-induced fragmentation. This can be done directly by comparing the genetic structure of extant individuals to that of samples collected prior to fragmentation (e.g., Bouzat et al. 1998), or indirectly by comparing equilibrium estimates of gene flow to assignment test (current)

estimates. Also, it may be possible to use radiotelemetry or CMR studies (Ims and Yoccoz 1997) to estimate connectivity across an unfragmented landscape and compare that to a fragmented landscape. This approach can be limited by the difficulty in finding unfragmented control areas and by the spatial/temporal heterogeneity of "natural" fragmentation (fire/disease/etc.) in control areas. Two examples illuminate the potential utility of this approach: Blundell et al. (2002) quantified sex-biased dispersal and gene flow for river otters (*Lontra canadensis*) in wilderness areas of Alaska as a baseline for understanding background levels of connectivity, and Proctor et al. (2003) used assignment tests and equilibrium approaches in areas with and without major highway development to infer that the Highway 3 corridor in British Columbia had led to a fracture in grizzly bear (*Ursus arctos*) movement.

We believe a combination of genetic and demographic tools, coupled with judicious application of the OMPG rule, can provide insights into the appropriate levels of connectivity for mammals. But how to achieve such connectivity? Throughout this chapter, we have avoided equating "connectivity" with "corridors." We agree that the corridor concept has popularized the importance of connectivity (Beier and Noss 1998), and that corridors may be particularly useful for denoting "large, regional connections that are meant to facilitate animal movements and other essential flows between different sections of the landscape" (Dobson et al. 1999:132). But we also think that the term has been overused. Corridors defined as linear strips can be demographic sinks that increase mortality, can "fix" connectivity in places that may be inappropriate, and could take away funding from the acquisition of larger reserves (Soule and Gilpin 1991, Rosenberg et al. 1997, Dobson et al. 1999).

Without a doubt, some animals will use linear patches as either movement corridors or as additional habitat (see Rosenberg et al. 1997), and even low levels of connectivity in low-quality corridors may be better than none at all (Beier 1993, Beier and Noss 1998). But we believe that, to the extent possible, connectivity for a particular species is best facilitated by managing the intervening matrix. This would involve matching the biophysical nature of the routes between patches with the biology and behavior of the dispersing species (Simberloff et al. 1992, Taylor et al. 1993, Doak and Mills 1994, Mills 1996). For example, Roach et al. (2001) determined likely movement routes using equilibrium and non-equilibrium genetic approaches, demonstrating that black-tailed prairie dogs (*Cynomys ludovicianus*) in Colorado have undergone historical

extinctions, with re-colonizations occurring along low-lying dry creek drainages.

Conclusions

We are strong advocates of merging demographic and genetic approaches to understand connectivity and population structure. Combining approaches can give insights across temporal and conceptual scales that are not possible using only telemetry, mark-recapture, or genetic measures (Peacock 1997, Lindenmayer and Peakall 2000). The new developments in analysis and techniques using mark-recapture and genetic approaches are enormous and have great potential for facilitating insights into movement of mammals across human-modified landscapes. These scientific advances come at exactly the time that forest managers most need to know which populations should be supplemented, which are likely to re-colonize on their own, and which are most likely to have unique evolutionary trajectories by virtue of being isolated.

Nevertheless, we have much to learn about which tools are best used for particular research or management questions. For example, to obtain precise estimates of connectivity using information theoretic approaches and maximum likelihood parameter estimation methods with CMR data sets, many individuals must be captured often, necessitating the sampling of relatively large areas and frequent trapping sessions. To measure temporal variation in movement, the large-scale trapping needs to occur at various times of year. In short, CMR approaches to estimate movement rates require colossal field efforts. To obtain the necessary data to apply these CMR approaches one may need to trap fewer areas more intensively, thereby decreasing replication and potentially limiting the scope of inference, yet obtaining a rich data set for the populations sampled. In some instances (e.g., clear-cuts are too small for large trapping grids, densities of animals are inherently low), these approaches will simply not be possible, pointing again to merging insights from trapping with those from genetic analysis (see western red-backed vole example).

Similar promise and pitfalls arise in the use of genetic tools. In many cases genetic data are the only means to determine whether populations have historically been connected or are currently connected. Genetic data will become increasingly used as the costs and limitations to their application are reduced. However, it is critical that researchers include standard error estimates and carefully consider the assumptions of the molecular

methods and models that must be used to translate genetic data into movement rates (e.g., Steinberg and Jordan 1997, Hedrick 1999). The limitations of equilibrium gene flow estimates lead us to advocate careful qualitative interpretations instead of quantitative point estimates. Genetic information will often have its highest utility in establishing an index of historical movement rates (e.g., whether current movement levels are different than they were during pre-European settlement times), or if movement of organisms is known but breeding is unknown (as in our lynx example). Again, the strongest approach is to use demographic and natural history data to help eliminate confounding interpretations of genetic data or to corroborate conclusions.

We have provided three examples of ways that these techniques can increase our understanding and inform management of mammals in western coniferous forests. By quantifying movement on both sides of forest/clear-cut edges for Columbian mice, we have shown that clear-cuts neither strongly attract nor repel this species from intact forests. Movements of red-backed voles across clear-cuts to forest fragments were relatively common (but still difficult to detect using mark-recapture), with males probably responsible for most movements. This finding has implications for vole population dynamics in a fragmented landscape and potentially for regeneration of forests on the clear-cuts. Finally, despite a fragmented landscape, lynx tend to move across long distances. This may affect both re-introduction strategies and conservation planning across the U.S./Canada border.

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