

Chapter 10

ZOOGEOGRAPHY, SPACING PATTERNS, AND DISPERSAL IN FISHERS:

Insights Gained from Combining Field and Genetic Data

Keith Aubry, Samantha Wisely, Catherine Raley, and Steven Buskirk

Abstract: We demonstrate how research questions generated from radiotelemetry studies of fishers (*Martes pennanti*) can be further elucidated by combining field and genetic data. We genotyped a sample of 20 fishers at 9 polymorphic microsatellite loci and used these data to calculate observed and expected heterozygosity, estimate coefficients of relatedness, and exclude potential parent-offspring combinations. Previous research indicated that the population of fishers occurring in the southern Cascade Range in Oregon is reintroduced. Due to the presence of potentially strong ecological and anthropogenic barriers between that population and fishers occurring in the northern Siskiyou Mountains of Oregon, we hypothesized that they are geographically isolated from each other. Analyses of microsatellite genotypes supported this hypothesis by providing empirical evidence that genetic introgression of fishers from the northern Siskiyou Mountains into the southern Cascade Range has not occurred. Results from our field study indicated that male fishers may exhibit either of 2 distinct behavioral strategies during the breeding season. For 3 successive breeding seasons, 2 adult males in our study area remained resident on their non-breeding home ranges, whereas 1 or 2 other males (one died after year 1) abandoned their non-breeding home ranges and encroached on the home ranges of resident males. To determine which strategy resulted in greater reproductive success, we used field and genetic data to exclude potential parent-offspring relationships between these 4 males and 7 juveniles. In contrast to resident males, encroaching males could not have fathered any of the juveniles. These results suggest that maintaining intrasexual territoriality during the breeding season may provide a reproductive advantage to male fishers. Our research also provides the first empirical evidence of male-biased juvenile dispersal and female philopatry in fishers. In accordance with predictions from genetic theory, our analyses showed that adult females had significantly higher relatedness values than adult males, and that there were many more potential first-order relationships among adult females than among adult males. As these examples demonstrate, including genetic information in data analysis can substantially improve the heuristic value of field studies and enable researchers to study additional aspects of population biology.

1. INTRODUCTION

Researchers generally infer social structure and spacing patterns of mammals from behavioral observations, mark-recapture data, or radiotelemetry locations. Obtaining such data in the field is challenging, and resulting datasets often suffer from small sample sizes or lack of data for 1 or more study animals. Logistical constraints on the geographic extent of most radiotelemetry studies may prevent long-distance movements or dispersal events from being detected, and such movements can also be confused with transmitter failure. Furthermore, unsuccessful copulations, cuckoldry, or multipaternity litters can be impossible to detect with traditional research approaches, and familial relationships can be inferred incorrectly when adults who are not the biological parents are behaviorally or spatially associated with young (Awise 1994).

Recent developments in genetic techniques (Parker et al. 1998) and the widespread application of genetic data to wildlife conservation (Haig 1998) have led many field biologists, including those studying fishers (*Martes pennanti*) and American martens (*M. americana*), to routinely collect tissue samples from their study animals for potential use in genetic studies. Several researchers have measured genetic variation in fisher and marten populations (Mitton and Raphael 1990; Carr and Hicks 1997; McGowan et al. 1999; Williams et al. 1999, 2000; Kyle et al. 2000, 2001; Drew et al. 2003; Kyle and Strobeck 2003), but the use of genetic information to augment field studies of wild populations of fishers or martens has not been reported. Here, we demonstrate how genetic information can be used to test research hypotheses generated from field data and published literature, and provide insights into the biology of fishers both within and among populations that could not be obtained by analyses of field data alone.

1.1 The Study Population

From 1995 to 2001, we (KA and CR) conducted a radiotelemetry study of fishers on the west slope of the Cascade Range in southern Oregon (Fig. 10.1; Aubry and Raley 2002). Based on trapping results in our study area and extensive survey efforts by resource management agencies in Oregon using remote cameras and trackplate boxes (Aubry and Lewis 2003, K. Aubry, unpublished data), we concluded that the geographic distribution of our study population was restricted primarily to the shaded area shown in Fig. 10.1. Fisher populations in the Pacific states are unharvested; commercial trapping of fishers has been prohibited in Oregon and California since 1937 and 1946, respectively.

Figure 10.1. Distribution of fishers in southwestern Oregon and northwestern California. Open circles indicate capture sites of the 18 fishers from our study population in the southern Cascade Range in Oregon; the shaded polygon is the 100% minimum convex polygon (MCP) for all radio-marked animals in our study. Open triangles are the localities where 2 adult male fishers were trapped incidentally in the northern Siskiyou Mountains in Oregon. Solid circles are localities where fishers were detected during track-plate and remote-camera surveys in northwestern California (Zielinski et al. 1995) and in southwestern Oregon (Aubry and Lewis 2003, K. Aubry, unpublished data). Interstate Highway 5 is shown as a heavy banded line and county boundaries are shown as thin solid lines.



Several attempts have been made to reintroduce fishers to Oregon; between 1961 and 1981, 41 fishers were translocated to various locations in or adjacent to our study area (Kebbe 1961, Aubry and Lewis 2003). There is no evidence that fishers have been translocated into California. Extant populations of fishers in northwestern California (Fig. 10.1) are believed to be descended entirely from indigenous animals, which are significantly smaller in size (based on condylobasal length) than fishers from western and central Canada (Hagmeier 1959, Zielinski et al. 1995, Aubry and Lewis 2003). Based on historical records, and differences in body weights and mitochondrial DNA haplotypes between fishers in southern Oregon and northern California, Aubry and Lewis (2003) concluded that the extant population of fishers in the southern Cascade Range in Oregon was reintroduced to that area by a series of translocations from British Columbia and Minnesota in the late 1970s and early 1980s.

1.2 Research Hypotheses

1.2.1 Zoogeography

Habitat conditions in the area between our study population and fishers in the northern Siskiyou Mountains in Oregon (Fig. 10.1) are generally unsuitable for fishers. This area contains an interstate highway corridor (I-5), urban and agricultural development in and around the city of Medford, and extensive areas of open grassland and oak savannah in the interior Rogue River valley (Franklin and Dyrness 1973). We hypothesized that these ecological and anthropogenic barriers have resulted in the geographic isolation of our study population from fishers southwest of the I-5 corridor (Fig. 10.1). If so, then the 2 fishers we sampled from the northern Siskiyou Mountains of Oregon do not belong to the southern Cascade Range gene pool and will differ genetically from fishers in our study population.

1.2.2 Spacing Patterns

Fishers are polygynous and intrasexually territorial; home-range overlap is minimal within sexes, but extensive between sexes (Powell 1993). Male home ranges are larger than those of females; the large home ranges of males provide them with primary access to receptive females during the breeding season, whereas the smaller home ranges of females provide them with primary access to sufficient resources to survive and successfully raise kits (Leonard 1986; Powell 1993, 1994). Leonard (1986) hypothesized that male fishers could maximize their reproductive success by adopting either of 2 strategies during the breeding season: continuing to defend their non-breeding home

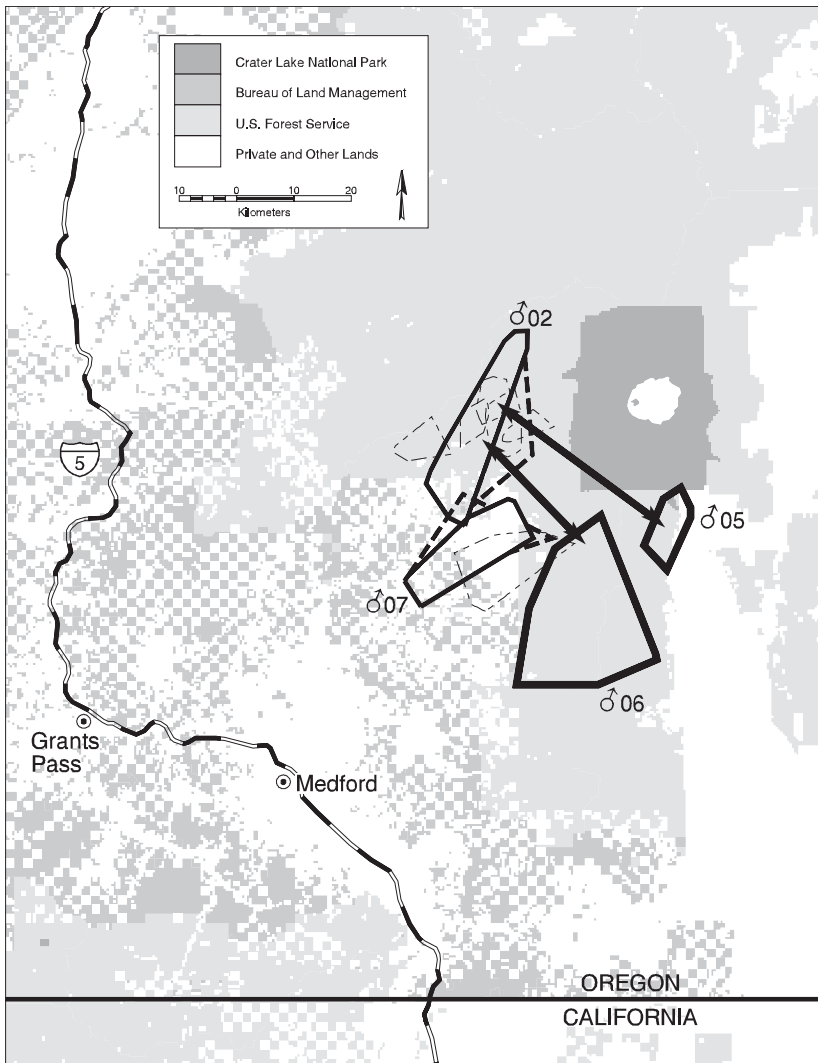
range against other males and mating with as many resident females within their home range as possible (here referred to as “resident” males), or abandoning their territories and trying to mate with as many females as possible (here referred to as “encroaching” males). Based on field observations of extensive movements by adult males during the breeding season, Leonard (1986) predicted that the second strategy was more likely the typical breeding strategy for male fishers. Movements by adult males outside their home ranges during the breeding season have also been reported by other researchers (Buck 1982, Arthur et al. 1989), and are generally assumed to result in increased reproductive success.

Field observations revealed that adult males in our study population exhibited both of these breeding strategies (Fig. 10.2). We captured one adult male (05) within the home range of another male (02) during 3 successive breeding seasons (1996–1998); during this time, male 05 occupied a non-breeding home range about 30 km SE of the home range of male 02. Another male (06) also made a breeding-season movement into 02’s home range in 1996, but died before the next breeding season. Both resident males (02 and 07) extended the boundaries of their home ranges slightly during the breeding season, but maintained stable and apparently exclusive home ranges throughout the year; neither made breeding-season movements similar to those exhibited by the encroaching males (05 and 06). Both resident males had home ranges that overlapped those of females, but we do not know if females were present within the non-breeding home ranges of the encroaching males. If Leonard’s (1986) hypothesis is correct, then the reproductive success of the 2 encroaching males will be greater than that of the 2 resident males.

1.2.3 Dispersal

Polygyny and intrasexual territoriality are associated with an imbalance in parental investment between the sexes; male fishers do not contribute to raising young, whereas females make a substantial investment by gestating a litter of 2–5 kits, nursing them to weaning, and feeding them until they are independent (Powell 1993, 1994). Competition for mates is therefore much stronger among male fishers than among females. Accordingly, a territorial male would be expected to allow juvenile females to establish home ranges within or near his home range, but would not be expected to allow juvenile males to do so. Juvenile males must therefore disperse relatively far from their natal areas to find unoccupied home ranges, whereas females can remain close to their natal areas, where the risks associated with dispersal are low and where resource availability is known to be sufficient for survival and reproduction (Greenwood 1980, Dobson 1982). Thus, as in other polygynous and intrasexually

Figure 10.2. Breeding-season movements for 4 adult male fishers in the southern Cascade Range in Oregon. Thick solid lines indicate the home ranges of males 05 and 06 during the non-breeding season (NBRS = May–Jan), and the direction and distance of breeding-season (BRS = Feb–Apr) movements. Medium solid lines indicate NBRS home ranges for males 02 and 07; dashed lines indicate movements during BRS that extended beyond the NBRS home ranges. Thin dashed lines indicate home ranges of adult female fishers within the study area. Home range boundaries for adult males are 100% MCPs encompassing the following telemetry locations: male 02: $n_{\text{NBRS}} = 104$ (1995–1999), $n_{\text{BRS}} = 51$ (1996–2000); male 05: $n_{\text{NBRS}} = 24$ (1996–1997); male 06: $n_{\text{NBRS}} = 18$ (1996–1997); male 07: $n_{\text{NBRS}} = 150$ (1996–1999), $n_{\text{BRS}} = 48$ (1997–1999).



territorial species, we hypothesized that juvenile dispersal in fishers is male-biased, resulting in greater philopatry among females.

The minimum dispersal distances (*sensu* Arthur et al. 1993) we documented for 1 juvenile male and 1 juvenile female in our study population were consistent with these predictions. The female dispersed a relatively short distance (16.9 km) from her capture site and remained within our core study area, whereas the male dispersed a much greater distance (55.3 km), and settled well beyond the boundaries of our core study area (Fig. 10.3). Genetic theory predicts that for species with a polygynous mating system and female philopatry, adult females in a given area will be more closely related to one another than are adult males (Chesser 1991). This is because female offspring are more likely to disperse short distances and establish home ranges near their close relatives, whereas male offspring are more likely to disperse long distances and establish home ranges in different geographic areas than their close relatives. If our study population was socially structured due to male-biased juvenile dispersal and female philopatry, then adult females will have higher mean relatedness than adult males, and there will be more first-order (i.e., parent-offspring) relationships among adult females than among adult males.

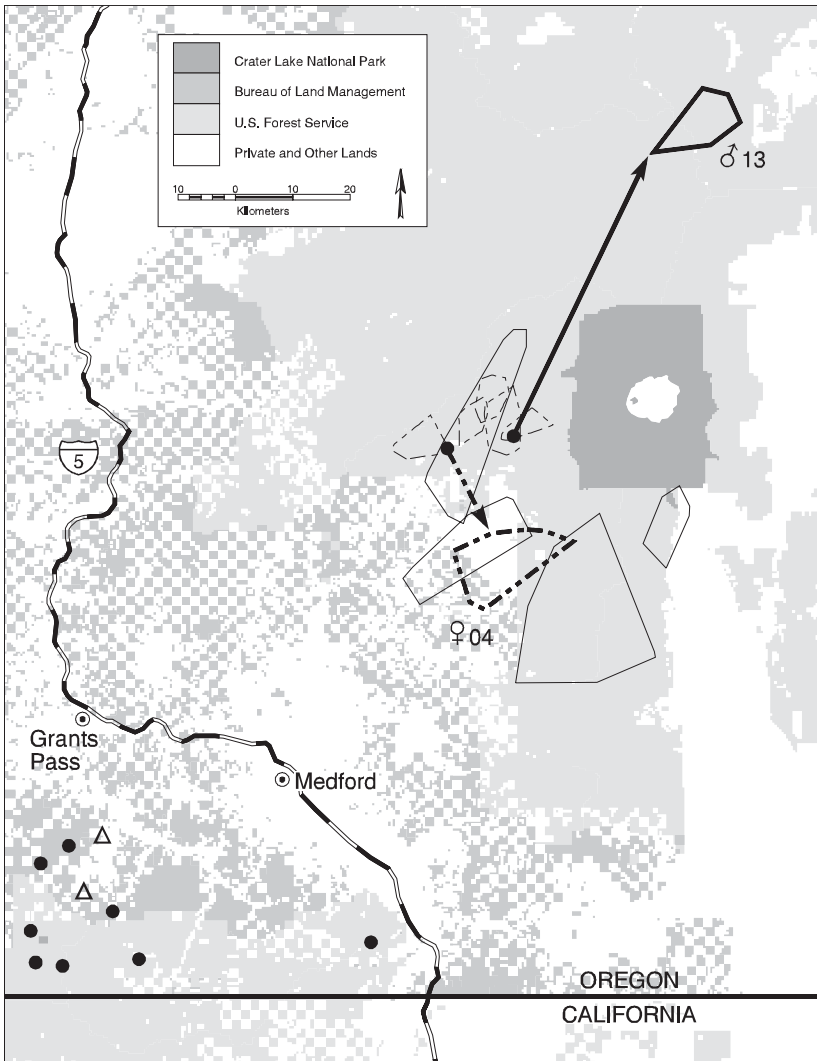
2. METHODS

2.1 Molecular Markers

We obtained genotypic data on our study animals by measuring variation in microsatellite DNA extracted from ear or muscle tissue that we collected from 5 adult and 2 juvenile (<1 yr old) males, and 6 adult and 3 juvenile females in the southern Cascade Range in Oregon. We also collected tissue samples from 1 male and 1 female kit of known maternity that we found dead in a natal den. In addition, we obtained tissue samples from 2 adult male fishers that were trapped incidentally about 70 km SW of our study area in the Siskiyou Mountains of southwestern Oregon (Fig. 10.1).

Microsatellite DNA loci are repeated sequences of 2–5 nucleotides that occur in non-coding regions of nuclear DNA and have high mutation rates compared to mitochondrial DNA or genes that code for allozymes (McDonald and Potts 1997). With information on the unique genetic sequences complementary to the regions that flank a microsatellite locus (primers), researchers can use the polymerase chain reaction (PCR) to produce billions of copies of the target locus. Because fragments of different length (alleles) travel at different rates in an electrophoretic gel, unique alleles can be identified within and among individuals at each locus, providing a measure of genetic variation.

Figure 10.3. Dispersal of 2 juvenile fishers in the southern Cascade Range in Oregon. Thick solid lines (male) and thick dashed lines (female) show the direction and distance of dispersal, and post-dispersal home ranges. Thin solid lines (males) and thin dashed lines (females) indicate home ranges for adult fishers within the study area. Boundaries of post-dispersal home ranges are 100% MCPs encompassing the following telemetry locations: male 13, $n = 16$ (Jun–Dec 1999); female 04, $n = 117$ (Apr 1996–Jun 2000). Solid circles and open triangles are as described in Fig. 10.1.



Microsatellite markers are useful for studying genetic differentiation over relatively short time frames both within and among populations (Awise 1994); thus, they are particularly appropriate for investigating the genetic affinities of radio-marked study animals.

2.2 Microsatellite Genotyping

We (SW and SB) used microsatellite DNA to describe the molecular genetic characteristics of fishers from southwestern Oregon. No microsatellite primers have been developed specifically for fishers, but primers developed for other carnivore species have been shown to amplify across species and genera (O'Connell et al. 1996). Consequently, we screened our sample of fishers for polymorphic loci using 19 primers developed for American marten, American mink (*Mustela vison*), ermine (*M. erminea*), American badger (*Taxidea taxus*), and black bear (*Ursus americanus*; Table 10.1).

We extracted DNA from 20 µg of ear plug or muscle tissue with 700 µl of lysis buffer that contained 20 µl of 1M DTT, 20 µl of 20 µg/µl proteinase k, and 10 µl of 10 µg/µl RNase. We agitated each sample in 55°C water for 40 hr; midway through the incubation, we added 10 µl of DTT, 10 µl of proteinase k, and 5 µl of RNase. We extracted DNA from the solution using 5 M ammonium acetate. To precipitate DNA from solution, we used a 70% ethanol wash. We resuspended DNA in a 1 X Tris EDTA solution and stored all samples at -20°C. We ran each reaction with a negative control to identify spurious results due to contamination. We used ear and muscle samples from the same individual as a positive control to verify that they produced similar results across loci. We resolved individual profiles electrophoretically with polyacrylamide gels using a LI-COR Model 4200 IR² Series DNA Sequencer (LI-COR Inc., Lincoln, NE). Resulting digital images characterized the size (number of nucleotide base-pairs) of alleles, and whether individuals were homozygous or heterozygous at each locus.

2.3 Genetic Analyses

2.3.1 Zoogeography

We used an assignment test (Paetkau et al. 1995) to determine whether the 2 fishers from the northern Siskiyou Mountains belonged to the southern Cascade Range gene pool. This test calculates the probability of an individual's genotype occurring in the population from which it was sampled and the probability of the genotype occurring in the other sampled population. We calculated probabilities with the software program GeneClass 1.0 (Cornuet et al.

1999) using a maximum-likelihood approach based on a Bayesian estimation of genotype frequencies to assign individuals to a population. We believe that our sample of 18 fishers from the southern Cascade Range represented a large proportion of the animals present in that population during our field study (Fig. 10.1); however, our sample of 2 fishers from the northern Siskiyou Mountains was clearly not a representative sample from that population. Accordingly, we only drew inferences from this analysis regarding the likelihood that the 2 Siskiyou fishers belonged to the Cascade Range gene pool and, consequently, whether or not they were to be included in subsequent genetic analyses.

We then tested for departures from Hardy-Weinberg (H-W) equilibrium in our resulting dataset. Departures from H-W equilibrium indicate an excess or deficit of heterozygosity in a population, and provide information on the potential influence of migration, genetic drift, or non-random mating on our analyses. In addition, many statistical analyses used in genetic studies are based on the assumption that populations are in H-W equilibrium. We tested for such departures by comparing observed (H_o) and expected heterozygosity (H_e) with a H-W exact test of P using the software program Arlequin 2.0 (Excoffier et al. 1996–2002). We adjusted for experiment-wise Type 1 error using a sequential Bonferroni adjustment (initial $\alpha = 0.05$, Rice 1989).

2.3.2 Spacing Patterns

To test the hypothesis that the 2 encroaching males had greater reproductive success than the 2 resident males, we used field and genotypic data to determine which of these adult males could be excluded as a potential father of the 7 juveniles we sampled during our field study. Due to delayed implantation of blastocysts in fishers, 11–12 months elapse between mating and parturition (Mead 1994); thus, we first excluded males as potential fathers if they had been dead ≥ 1 year prior to the birth of each offspring. We then excluded males as potential fathers if they did not share at least 1 allele at each locus with the offspring in question.

2.3.3 Dispersal

To test the hypothesis of female philopatry in fishers, we calculated genetic relatedness (R) among the entire sample of adult animals and within each sex. A positive R value indicates that a given group of animals are more closely related to one another than would be expected by random mating; a negative R value indicates the opposite. We estimated R and generated 95% confidence intervals around each estimate using a jackknife procedure in the software program Relatedness 5.0 (Queller and Goodnight 1989). To further investigate

this hypothesis, we used genotypes to exclude potential first-order relationships among adult animals.

3. RESULTS

3.1 Zoogeography

Nine of the 19 microsatellite loci we screened produced clear polymorphisms, with an average of 3.0 ± 0.3 (\pm SE) alleles per polymorphic locus (Table 10.1). At 2 loci (Mvi 39 and Mvis 002), both fishers from the northern Siskiyou Mountains were homozygous for alleles that were not detected among fishers from the southern Cascade Range; at a third locus (Mer 041), they were homozygous for an allele that was rare among Cascade fishers (Table 10.2). Because of these strong genotypic differences, the assignment test resulted in probabilities <0.0001 that either fisher from the Siskiyou Mountains was a member of the southern Cascade Range gene pool. Consequently, all subsequent genetic analyses were conducted only on the sample of 18 fishers from

Table 10.1. Microsatellite loci screened for polymorphisms using DNA from fishers in southwestern Oregon. Allele lengths are expressed in numbers of base pairs.

Locus	Species for which primers were developed	No. of alleles	Allele length	Source
G1A	<i>Ursus americanus</i>	1	173	Paetkau et al. (1995)
Ma 1	<i>Martes americana</i>	5	218–226	Davis and Strobeck (1998)
Ma 14		1	219	
Ma 19		3	221–225	
Mer 030	<i>Mustela erminea</i>	1	278	Fleming et al. (1999)
Mer 041		4	175–181	
Mer 082		1	130	
Mer 095		1	178	
Mvi 39	<i>Mustela vison</i>	3	142–152	O'Connell et al. (1996)
Mvi 87		2	103–105	
Mvi 111		1	112	
Mvi 114		2	104–106	
Mvi 219		1	265	
Mvis 002	<i>Mustela vison</i>	3	220–228	Fleming et al. (1999)
Mvis 020		2	216–222	
Mvis 022		1	302	
Mvis 027		1	207	
Mvis 072		3	291–297	
Tt 4	<i>Taxidea taxus</i>	1	182	Davis and Strobeck (1998)

Table 10.2. Occurrence of microsatellite genotypes at selected loci in fishers from the southern Cascade Range and northern Siskiyou Mountains of Oregon.

Geographic location	Microsatellite loci		
	Mer 041 ^a	Mvi 39 ^a	Mvis 002 ^b
Southern Cascade Range	175–177	142–144	220–220
	177–177	144–144	220–228
	177–179		228–228
	177–181		
Northern Siskiyou Mountains	181–181	152–152	224–224

^a $n = 17$ for the southern Cascade Range, $n = 2$ for the northern Siskiyou Mountains.

^b $n = 18$ for the southern Cascade Range, $n = 2$ for the northern Siskiyou Mountains.

our study population in the southern Cascade Range. We found 1 locus (Mvis 020) to have a heterozygote deficiency; after accounting for experiment-wise error, however, all loci were in Hardy-Weinberg equilibrium (Table 10.3).

3.2 Spacing Patterns

Parent-offspring exclusions for the 2 encroaching males, the 2 resident males, and the 7 juveniles we sampled during our field study included 5 by date and 19 by genotype (Table 10.4). Based on this analysis, neither of the encroaching males could have fathered any of these juveniles, whereas 1 of the resident males (02) was a potential father for 4 of the 7 juveniles.

Table 10.3. Observed heterozygosity (H_o), expected heterozygosity (H_e), and the exact probability for the test of Hardy-Weinberg equilibrium (HWE P) for 9 polymorphic loci among 18 fishers from the southern Cascade Range in Oregon.

Locus	n^a	H_o	H_e	HWE P^b
Ma 1	16	0.59	0.74	0.39
Ma 19	18	0.67	0.56	0.48
Mer 041	17	0.59	0.52	1.00
Mvi 39	17	0.23	0.27	1.00
Mvi 87	18	0.39	0.51	0.37
Mvi 114	15	0.41	0.40	1.00
Mvis 002	18	0.28	0.29	1.00
Mvis 020	18	0.11	0.34	0.04
Mvis 072	18	0.55	0.54	0.34

^aSample sizes vary among loci because some DNA samples failed to amplify.

^bWe adjusted for experiment-wise Type 1 error using a sequential Bonferroni adjustment (initial $\alpha = 0.05$).

Table 10.4. Inferred paternity of juvenile fishers among 2 resident (02, 07) and 2 encroaching (05, 06) males from our study population in the southern Cascade Range in Oregon. For each juvenile, we excluded adult males as potential fathers by date if they died ≥ 1 year prior to that juvenile's birth date, and by genotype if they did not share at least 1 allele at each locus with that juvenile.

Offspring	Potential fathers excluded by date	Potential fathers excluded by genotype	Potential fathers
04	none	02, 05, 06, 07	none
10	none	02, 05, 06, 07	none
12	06	02, 05, 07	none
13	06	05, 07	02
14	06	05, 07	02
16	06	05, 07	02
17	06	05, 07	02

3.3 Dispersal

Mean relatedness (R) among all adult fishers in our sample was -0.05 ± 0.11 ; mean R among males and females was -0.29 ± 0.15 and 0.19 ± 0.30 , respectively. For R values, variance was represented by 95% confidence intervals; the lack of overlap between intervals for males and females indicated that adult females were significantly more related to each other than were adult males (Zar 1984). Separate genotypic comparisons among adult males and adult females showed that there were no possible first-order relationships among any of the 5 adult male fishers in our sample; in contrast, each of 6 females had at least 2 potential first-order relationships with another adult female (Table 10.5).

4. DISCUSSION

4.1 Zoogeography

The population of fishers we studied in the southern Oregon Cascade Range was reintroduced to that area approximately 25 years ago (Aubry and Lewis 2003). Since that time, there would have been numerous opportunities for juvenile dispersals or long-distance movements by adults from the Siskiyou Mountains into our study area (Fig. 10.1). Dispersals by juvenile fishers >50 km have been reported by several researchers (Leonard 1980, York 1996, this study), demonstrating that the southern Oregon Cascades are within the dispersal range of fishers in the northern Siskiyou Mountains (Figs. 10.1, 10.3). However, the

Table 10.5. Potential first-order (parent-offspring) relationships among conspecifics for 11 adult fishers from the southern Cascade Range in Oregon. We excluded potential first-order relationships if they did not share at least 1 allele at each locus.

Adult fishers	Potential first-order relationships
Females	
01	03, 08, 18
03	01, 08, 11, 18
08	01, 03, 11, 18
09	11, 18
11	03, 08, 09, 18
18	01, 03, 08, 09, 11
Males	
02	none
05	none
06	none
07	none
15	none

large genotypic differences we found between fishers in our study population and those in the northern Siskiyou Mountains support our hypothesis that ecological or anthropogenic barriers in the intervening area have resulted in the geographic isolation of reintroduced fishers in the southern Cascade Range in Oregon. Thus, it appears that expanses of unsuitable habitat as narrow as 50 km might impede genetic exchange between fisher populations.

Our findings are consistent with recent genetic studies across Canada and in the northeastern U.S. which suggested that fishers may have relatively poor dispersal capabilities (Kyle et al. 2000, 2001; Kyle and Strobeck 2003). These studies revealed that fishers exhibited much more genetic structure than martens; i.e., there is less gene flow among fisher populations than among marten populations. These findings were unexpected because fishers are assumed to have better dispersal capabilities than martens due to their larger body size, which should result in less genetic structure among fisher populations. Kyle et al. (2001) speculated that this difference may be due to fisher populations being exposed to stronger anthropogenic influences (e.g., human development, transportation corridors, and habitat fragmentation) than marten populations. This hypothesis cannot be evaluated with field data, however, because information on juvenile dispersal is extremely limited for both fishers (Arthur et al. 1993, York 1996, this study) and American martens (Phillips 1994, Bull and Heater 2001, Fecske and Jenks 2002). This dearth of information underscores

Caughley's (1977) assertion that dispersal is the most challenging of all population processes to study in the field. Based on results of this study, we suggest that dispersal characteristics can be elucidated most effectively through a combination of field and genetic studies.

Recent genetic analyses of fishers from the region depicted in Fig. 10.1 indicated that fishers in the Siskiyou Mountains of Oregon represent the northern limit of the California gene pool. Ancillary to a phylogeographic study of fisher populations in the Pacific states (Wisely et al. 2004), an assignment test was used to evaluate the genetic affinities of 21 fishers from the southern Cascade Range in Oregon (including 16/18 analyzed in this study), the 2 fishers we genotyped from the northern Siskiyou Mountains in Oregon, and 23 additional animals from northwestern California. Both fishers from the Siskiyou Mountains in Oregon were assigned to the population in northwestern California (S. Wisely, unpublished data). These results, combined with a lack of strong ecological or anthropogenic barriers between these areas (Franklin and Dyrness 1973), indicate that fishers occurring southwest of I-5 in Oregon (Fig. 10.1) represent the only extant populations of indigenous fishers in Oregon.

4.2 Spacing Patterns

Contrary to Leonard's (1986) hypothesis that the typical breeding strategy for male fishers is to abandon their non-breeding home ranges and search for receptive females, our field observations indicated that adult males may exhibit either "resident" or "encroaching" behavioral strategies during the breeding season. Furthermore, our genetic results suggest that Sandell's (1986) findings for stoats (*Mustela erminea*), in which dominant, roaming males secured all of the mating opportunities, does not apply to fishers. Although several males encroached on the home range of a resident male whose home range encompassed those of several females (Fig. 10.2), these encroachments appear not to have resulted in successful matings (Table 10.4). Ours is the first study to explore the relationship between spacing patterns of male fishers or martens during the breeding season and subsequent reproductive success. However, results reported for martens in Maine appear to be consistent with our observations (Katnik et al. 1994). All of the 14 adult male martens that were monitored with radiotelemetry remained resident on their non-breeding home ranges during the breeding season. At least 11 of these males occupied home ranges that overlapped those of 1 or more females and 7 had ranges that overlapped with 2 or more, suggesting that males may have remained in established territories during the breeding season to maximize their reproductive potential (Katnik et al. 1994).

Our observations are consistent with Sandell's (1989) theory that territoriality in male solitary carnivores (including fishers) during the breeding season is flexible and influenced primarily by the availability of receptive females. Sandell (1989) predicted that the distribution of females will determine whether or not males maintain exclusive home ranges throughout the year, or adopt a roaming strategy during the breeding season. He reasoned that when females are densely and evenly distributed, a male will secure more matings by staying and mating with the females in his home range; in all other situations, a male will secure more matings by searching for receptive females beyond the boundaries of his home range.

The 2 males in our study population whose non-breeding home ranges overlapped those of 1 or more females maintained their home ranges throughout the year. We speculate that the 2 males who adopted an encroaching strategy during the breeding season did so because they were unable to establish a home range that encompassed 1 or more resident females. Although other researchers have reported similar roaming behavior by adult male fishers during the breeding season (Buck 1982, Leonard 1986, Arthur et al. 1989), they did not determine whether roaming behavior was typical of adult males in the populations they studied, nor if it resulted in successful matings. Additional research involving both field and genetic studies will be needed to further elucidate the causal mechanisms of these behavioral strategies.

4.3 Dispersal

Published information providing empirical support for the theory of male-biased juvenile dispersal and female philopatry in fishers is extremely limited. Heterozygote deficiencies found by Williams et al. (2000) in all 8 of the fisher populations they sampled from the north-central and northeastern portions of its range indicated the presence of fine-scale genetic structuring within populations. They speculated that such structuring may reflect gene correlations that have accrued over time due to male-biased juvenile dispersal and female philopatry.

Two studies have investigated juvenile dispersal in wild fishers, yet neither supported these predictions. In a heavily trapped population in south-central Maine, Arthur et al. (1993) measured straight-line distances from the sites where 13 fishers were captured as juveniles to the nearest locations in their adult home ranges, and found no significant difference between males ($n = 8$, mean = 10.8, range = 4.1–19.5 km) and females ($n = 5$, mean = 11.3, range = 5.0–18.9 km). Similarly, York (1996) found no significant difference in male and female dispersal distances among fishers in a population in central Massa-

chusetts with lower trapping mortality and higher population density (males: $n = 10$, mean = 25, range = 10–60 km; females: $n = 19$, mean = 37, range = 12–107 km). However, in our study of an untrapped fisher population, the 2 juvenile dispersals we documented in the field, the significantly higher relatedness of adult females compared to adult males, and the strong disparity in potential first-order relationships among adult females compared to adult males provide empirical evidence of male-biased juvenile dispersal and female philopatry in fishers. As several authors have argued (Arthur et al. 1993, Powell 1994), trapping mortality is likely to disrupt many aspects of fisher population ecology, including spacing patterns and dispersal processes. We suspect that similarities in male and female juvenile dispersal distances in both Maine and Massachusetts were related to trapping mortality.

5. CONCLUSIONS

Combining information on the distribution, spatial organization, and movements of fishers obtained in the field with genotypic data enabled us to gain important new insights about the zoogeography and population ecology of fishers in the Pacific Northwest. These insights have potentially important implications for the conservation of fisher populations in the Pacific states, and for refining our current understanding of adult spacing patterns and juvenile dispersal in fishers. We have provided evidence that genetic introgression of fishers from the northern Siskiyou Mountains to the southern Cascade Range in Oregon has not occurred, suggesting that these populations are geographically isolated. These results bear directly on questions regarding connectivity and gene flow among extant fisher populations in the Pacific states. We have also provided the first empirical evidence that behavioral strategies of male fishers during the breeding season are flexible and appear to be influenced primarily by the density and distribution of receptive females, and that juvenile dispersal in fishers is male-biased, resulting in greater philopatry among females.

Genetic analyses can substantially improve the interpretive value of radiotelemetry data and, ultimately, the usefulness and applicability of wildlife field studies. To maximize the heuristic value of radiotelemetry studies, which involve significant investments of time and money, we urge researchers to consider incorporating genetic data into their field studies. As shown here, such data can be obtained through collaborative research efforts, which have the added benefit of bringing several disciplines together during the analytical and interpretive phases of the research process; alternatively, a number of commercial laboratories now provide genotyping services at relatively low cost.

6. ACKNOWLEDGMENTS

We thank Daniel Harrison, Angela Fuller, and several anonymous reviewers for many valuable suggestions that greatly improved the quality of this manuscript. Greg Russell and Natalie Schenker assisted with genotyping, David McDonald provided statistical consultation, and Kent van Wagtenonk prepared the figures. Funding for this research was provided by the Pacific Northwest Research Station, U.S. Forest Service.

7. LITERATURE CITED

- Arthur, S. M., W. B. Krohn, and J. R. Gilbert. 1989. Home range characteristics of adult fishers. *Journal of Wildlife Management* 53:674–679.
- _____, T. F. Paragi, and W. B. Krohn. 1993. Dispersal of juvenile fishers in Maine. *Journal of Wildlife Management* 57:868–874.
- Aubry, K. B., and J. C. Lewis. 2003. Extirpation and reintroduction of fishers (*Martes pennanti*) in Oregon: implications for their conservation in the Pacific states. *Biological Conservation* 114:79–90.
- _____, and C. M. Raley. 2002. Ecological characteristics of fishers in the southern Oregon Cascade Range. Final progress report on file at the Pacific Northwest Research Station, U.S. Forest Service, Olympia, Washington, USA.
- Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, USA.
- Buck, S. 1982. Habitat utilization by fisher (*Martes pennanti*) near Big Bar, California. Thesis, Humboldt State University, Arcata, California, USA.
- Bull, E. L., and T. W. Heater. 2001. Home range and dispersal of the American marten in northeastern Oregon. *Northwestern Naturalist* 82:7–11.
- Carr, S. M., and S. A. Hicks. 1997. Are there two species of marten in North America? Genetic and evolutionary relationships within *Martes*. Pages 15–28 in G. Proulx, H. N. Bryant, and P. M. Woodard, editors. *Martes: taxonomy, ecology, techniques, and management*. Provincial Museum of Canada, Edmonton, Alberta.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, USA.
- Chesser, R. K. 1991. Gene diversity and female philopatry. *Genetics* 127:437–447.
- Cornuet, J. M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* 153:1989–2000.
- Davis, C. S., and C. Strobeck. 1998. Isolation, variability, and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. *Molecular Ecology* 7:1771–1788.
- Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behavior* 30:1183–1192.
- Drew, R. E., J. G. Hallett, K. B. Aubry, K. W. Cullings, S. M. Koepf, and W. J. Zielinski. 2003. Conservation genetics of the fisher (*Martes pennanti*) based on mitochondrial DNA sequencing. *Molecular Ecology* 12:51–62.
- Excoffier, L., S. Schneider, and D. Roessli. 1996–2002. Arlequin ver. 2.0: a software for population genetic analysis. University of Geneva, Switzerland.

- Fecske, D. M., and J. A. Jenks. 2002. Dispersal by a male American marten, *Martes americana*. *Canadian Field-Naturalist* 116:309–311.
- Fleming, M. A., E. A. Ostrander, and J. A. Cook. 1999. Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). *Molecular Ecology* 8:1351–1362.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Forest Service General Technical Report PNW-8.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Hagmeier, E. M. 1959. A re-evaluation of the subspecies of fisher. *Canadian Field-Naturalist* 73:185–197.
- Haig, S. M. 1998. Molecular contributions to conservation. *Ecology* 79:413–425.
- Katnik, D. D., D. J. Harrison, and T. P. Hodgman. 1994. Spatial relations in a harvested population of marten in Maine. *Journal of Wildlife Management* 58:600–607.
- Kebbe, C. E. 1961. Return of the fisher. *Oregon State Game Commission Bulletin* 16:3–7.
- Kyle, C. J., C. S. Davis, and C. Strobeck. 2000. Microsatellite analysis of North American pine marten (*Martes americana*) populations from the Yukon and Northwest Territories. *Canadian Journal of Zoology* 78:1150–1157.
- _____. J. F. Robitaille, and C. Strobeck. 2001. Genetic variation and structure of fisher (*Martes pennanti*) populations across North America. *Molecular Ecology* 10:2341–2347.
- _____. and C. Strobeck. 2003. Genetic homogeneity of Canadian mainland marten populations underscores the distinctiveness of Newfoundland pine martens (*Martes americana atrata*). *Canadian Journal of Zoology* 81:57–66.
- Leonard, R. D. 1980. The winter activity and movements, winter diet and breeding biology of the fisher (*Martes pennanti*) in southeastern Manitoba. Thesis, University of Manitoba, Winnipeg, Canada.
- _____. 1986. Aspects of reproduction of the fisher, *Martes pennanti*, in Manitoba. *Canadian Field-Naturalist* 100:32–44.
- McDonald, D. B., and W. K. Potts. 1997. Microsatellite DNA as a genetic marker at several scales. Pages 29–49 in D. Mindell, editor. *Avian molecular evolution and systematics*. Academic Press, New York, USA.
- McGowan, C., L. A. Howes, and W. S. Davidson. 1999. Genetic analysis of an endangered pine marten (*Martes americana*) population from Newfoundland using randomly amplified polymorphic DNA markers. *Canadian Journal of Zoology* 77:661–666.
- Mead, R. A. 1994. Reproduction in *Martes*. Pages 404–422 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Cornell University Press, Ithaca, New York, USA.
- Mitton, J. B., and M. G. Raphael. 1990. Genetic variation in the marten, *Martes americana*. *Journal of Mammalogy* 71:195–197.
- O’Connell, M., J. M. Wright, and A. Farid. 1996. Development of PCR primers for nine polymorphic American mink (*Mustela vison*) microsatellite loci. *Molecular Ecology* 5:311–312.
- Paetkau D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: choosing and using a molecular marker. *Ecology* 79:361–382.
- Phillips, D. M. 1994. Social and spatial characteristics, and dispersal of marten in a forest preserve and industrial forest. Thesis, University of Maine, Orono, USA.

- Powell, R. A. 1993. The fisher: life history, ecology, and behavior. Second edition. University of Minnesota Press, Minneapolis, USA.
- _____. 1994. Structure and spacing of *Martes* populations. Pages 101–121 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Cornell University Press, Ithaca, New York, USA.
- Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. *Evolution* 43:258–275.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Sandell, M. 1986. Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. *Oikos* 47:63–70.
- _____. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Volume 1. Cornell University Press, Ithaca, New York, USA.
- Williams, R. N., L. K. Page, T. L. Serfass, and O. E. Rhodes, Jr. 1999. Genetic polymorphisms in fishers (*Martes pennanti*). *American Midland Naturalist* 141:406–410.
- _____, O. E. Rhodes, Jr., and T. L. Serfass. 2000. Assessment of genetic variance among source and reintroduced fisher populations. *Journal of Mammalogy* 81:895–907.
- Wisely, S. M., S. W. Buskirk, G. A. Russell, K. B. Aubry, and W. J. Zielinski. 2004. Phylogeography and genetic diversity of the fisher (*Martes pennanti*) in a peninsular and peripheral metapopulation. *Journal of Mammalogy* 85:in press.
- York, E. C. 1996. Fisher population dynamics in north-central Massachusetts. Thesis, University of Massachusetts, Amherst, USA.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.
- Zielinski, W. J., T. E. Kucera, and R. H. Barrett. 1995. Current distribution of fishers, *Martes pennanti*, in California. *California Fish and Game* 81:104–112.