Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations

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Abstract

River otters (Lontra canadensis) were extirpated from much of their historic distribution because of exposure to pollution and urbanization, resulting in expensive reintroduction programmes that continue today for this and other species of otters worldwide. Bioaccumulation of toxins negatively affects fecundity among mustelids, but high vagility and different dispersal distances between genders may permit otter populations to recover from extirpation caused by localized environmental pollution. Without understanding the influence of factors such as social structure and sex-biased dispersal on genetic variation and gene flow among populations, effects of local extirpation and the potential for natural recolonization (i.e. the need for translocations) cannot be assessed. We studied gene flow among seven study areas for river otters (n = 110 otters) inhabiting marine environments in Prince William Sound, Alaska, USA. Using nine DNA microsatellite markers and assignment tests, we calculated immigration rates and dispersal distances and tested for isolation by distance. In addition, we radiotracked 55 individuals in three areas to determine characteristics of dispersal. Gender differences in sociality and spatial relationships resulted in different dispersal distances. Male river otters had greater gene flow among close populations (within 16–30 km) mostly via breeding dispersal, but both genders exhibited an equal, low probability of natal dispersal; and some females dispersed 60–90 km. These data, obtained in a coastal environment without anthropogenic barriers to dispersal (e.g. habitat fragmentation or urbanization), may serve as baseline data for predicting dispersal under optimal conditions. Our data may indicate that natural recolonization of coastal river otters following local extirpation could be a slow process because of low dispersal among females, and recolonization may be substantially delayed unless viable populations occurred nearby. Because of significant isolation by distance for male otters and low gene flow for females, translocations should be undertaken with caution to help preserve genetic diversity in this species.

Keywords: assignment tests, breeding dispersal, dispersal distances, isolation by distance, microsatellite DNA, social structure

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Introduction

River otters (Lontra canadensis) are piscivorous predators that forage near the apex of the trophic pyramid and readily accumulate high levels of pollutants (Duffy et al. 1994, 1996; Francis & Bennett 1994; Halbrook et al. 1996; Elliott et al. 1999; Taylor et al. 2000; Ben-David et al. 2001a,b). Indeed, river otters in North America were reduced throughout much of their historic range in the eastern and midwestern United States by the early 1900s because of pollution, urbanization and overharvest (Serfass et al. 1993;
Larivière & Walton 1998). Consequently, numerous projects have been initiated to reintroduce river otters to areas from which they were extirpated (Erickson & McCullough 1987; Polechla 1990; Ralls 1990; Serfass et al. 1993; Hartup et al. 1999). Translocation projects are currently underway in the US, and other projects are being considered (T. L. Serfass, North American Continental Representative for the IUCN Otter Specialist Group, personal communication).

Because of their susceptibility to pollution, these mustelids have recently been recognized as an indicator of environmental health in aquatic ecosystems (Melquist & Dronkert 1987; Duffy et al. 1996; Larivière & Walton 1998), but comparatively little is known about their ecology. Blundell et al. (2002) noted that sociality among river otters inhabiting marine environments was related to cooperative foraging for pelagic fishes, and that male otters were more social than females. Without a more complete understanding of population genetics and how factors such as social structure, mating system or sex-biased dispersal influence genetic variation and gene flow among populations (Shields 1987; Avise 1994; Perrin & Mazalov 2000), effects of local extirpation and the potential for natural recolonization (i.e. the need for reintroduction projects) cannot be assessed.

We hypothesized that coastal river otters occurred in genetically distinct populations with gene flow among populations, and that social structure and sex-biased dispersal mediated genetic differentiation between populations. Among most species of mammals, females show philopatry, whereas males are more likely to disperse from their natal area (Greenwood 1980; Shields 1987). Accordingly, with microsatellite DNA, we tested the hypothesis that, among adults, female otters within a population would be more related to each other than to males in that population. Because male river otters are more social (Blundell et al. 2002) and, in some mammals, male groups are composed of siblings (Packer et al. 1991), we also hypothesized that male otters within a population would be more related to other males (if sibling groups dispersed together) than to females. For both genders, we hypothesized that relatedness of adult otters would be higher within than among populations.

In addition, we tested the hypothesis of isolation by distance, predicting that genetic differentiation among populations would increase with increasing geographical distance and that the effect would be more pronounced for females if dispersal was male-biased. To further assess whether sex-biased dispersal was influencing genetic differentiation among populations, we used assignment tests (Cornuet et al. 1999) to estimate immigration rates and dispersal distances for each sex in conjunction with telemetry data.

Methods

Study areas

Study areas were located throughout western Prince William Sound, spanning an area of ~4800 km² (Fig. 1). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan and Paddy bays along Dangerous Passage (hereafter collectively referred to as Jackpot Bay), and in Herring Bay and surrounding areas on northern Knight Island (hereafter referred to as Herring Bay). In 1998, otters were captured at Herring Bay, Eleanor Island, Esther Passage, Unakwik Inlet, Wells Bay and Naked Island (Fig. 1). Detailed descriptions of the study sites are provided in Ben-David et al. (1998) and Bowyer et al. (1999).

Live capture of otters

We captured 111 individual river otters (Table 1), from May to July in 1996 and 1997, and from mid-April to May in 1998, using no. 11 Sleepy Creek® double-jaw leg-hold traps or with Hancock traps (Blundell et al. 1999). Otters were anaesthesized with Telazol® (9 mg/kg) administered by Telinject® darts with a blowgun, or by hand injection for otters captured in Hancock traps. Blood samples (7 mL) were drawn from the jugular vein of each otter and allowed to clot. Serum was extracted from the samples for analyses associated with companion studies (Holland-Bartels 1999) and the remaining clots were frozen for DNA analysis. Further details on capture and handling are provided in Blundell et al. (1999, 2000).

Radiotelemetry

Fifty-five otters were surgically implanted with radiotransmitters (Blundell et al. 2000). Otters receiving transmitters were captured in the vicinities of Jackpot Bay in 1996 and 1997, Herring Bay in 1997 and 1998, and at Eleanor Island in 1998 (Fig. 1). Otters were radiotracked, mostly from a plane, from 1996 to 1999 at Jackpot Bay, 1997 to 1999 at Herring Bay and 1998 to 1999 at Eleanor Island (n = 2230 total locations). Tracking occurred year-round, but locations were obtained with greater intensity during the mating season.
season (every 4 days) and in summer (every 5–7 days) when the weather was more conducive to regular flights. Further details on radiotracking are provided in Blundell et al. (2001, 2002).

**DNA laboratory procedures**

DNA was extracted from frozen blood samples from 110 individual otters with a modification of a protocol described by Groves & Shields (1997). Nine microsatellite loci were screened for this study. These included seven tetranucleotide markers (701, 715, 733, 782, 801, 818 and 829) developed for Eurasian otters (*Lutra lutra*; Dallas & Piertney 1998; J. F. Dallas personal communication) and two dinucleotide markers (Mvis075 and Mer022) developed for mink (*Mustela vison*) and ermine (*Mustela erminea*; Fleming et al. 1999). Using these nine markers, we were able to identify unique multilocus genotypes for all individuals examined. Amplifications of microsatellites followed protocols described in Blundell (2001). Data were sized and

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**Table 1** Genetic diversity for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998

<table>
<thead>
<tr>
<th>Study area</th>
<th>Males (n)</th>
<th>Females (n)</th>
<th>Mean (SE) Heterozygosity</th>
<th>HWE (SE) expected*</th>
<th>Mean (SE)† alleles/locus</th>
<th>F_Ps</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eleanor Island</td>
<td>7</td>
<td>2</td>
<td>0.383 (0.056)</td>
<td>0.542 (0.055)</td>
<td>3.2 (0.3)</td>
<td>0.306</td>
</tr>
<tr>
<td>Esther Passage</td>
<td>8</td>
<td>2</td>
<td>0.396 (0.073)</td>
<td>0.522 (0.038)</td>
<td>3.1 (0.4)</td>
<td>0.251</td>
</tr>
<tr>
<td>Herring Bay</td>
<td>25</td>
<td>14</td>
<td>0.510 (0.054)</td>
<td>0.553 (0.057)</td>
<td>4.4 (0.5)</td>
<td>0.079</td>
</tr>
<tr>
<td>Jackpot Bay</td>
<td>20</td>
<td>11</td>
<td>0.484 (0.073)</td>
<td>0.512 (0.071)</td>
<td>4.4 (0.7)</td>
<td>0.055</td>
</tr>
<tr>
<td>Naked Island</td>
<td>6</td>
<td>2</td>
<td>0.444 (0.089)</td>
<td>0.504 (0.054)</td>
<td>3.2 (0.4)</td>
<td>0.125</td>
</tr>
<tr>
<td>Unakwik Inlet</td>
<td>4</td>
<td>1</td>
<td>0.444 (0.087)</td>
<td>0.553 (0.056)</td>
<td>3.0 (0.4)</td>
<td>0.216</td>
</tr>
<tr>
<td>Wells-Bay</td>
<td>5</td>
<td>3</td>
<td>0.403 (0.074)</td>
<td>0.521 (0.056)</td>
<td>3.1 (0.3)</td>
<td>0.240</td>
</tr>
</tbody>
</table>

*Hardy–Weinberg equilibrium; unbiased estimate (Nei 1978). †Minimum and maximum number of alleles per locus were 2 and 10, respectively.
analysed with ABI GENESCAN Version 3.1 and GENOTYPER Version 2.1 software (Applied Biosystems, Foster City, CA, USA).

Data analysis
The mutation process of microsatellite DNA is not fully resolved and differs from that of other molecular markers for which earlier methods of genetic differentiation were developed (Slatkin 1995; Goldstein & Pollock 1997; Paetkau et al. 1997). Because the efficacy of statistical methods depends upon how closely a marker adheres to assumptions of the statistical model, we used several measures of genetic differentiation and genetic distances to test our hypotheses. In the absence of a complete understanding of mutational processes of microsatellites, if results from several methods of analysis (each of which are based upon different hypotheses of mutation or different algorithms) are in agreement, greater confidence in the correct interpretation of data is possible.

Genetic differentiation between study areas. We tested for linkage disequilibrium and departure from Hardy–Weinberg equilibrium (HWE), and calculated Weir & Cockerham (1984) F-statistics with Genepop software (Raymond & Rousset 1995). Data assessing genetic parameters for populations (e.g. average heterozygosity) were obtained with BIOSYS-1 (Swofford & Selander 1980). RSTAY (Goudet 2000) was used to conduct tests of population differentiation not assuming HWE. For those analyses, genotypic and allelic frequencies were randomized among samples and G-statistics (log-likelihood) were calculated (Goudet 2000), adjusting significance levels with sequential Bonferroni corrections (Rice 1989). RSTCALL (Goodman 1997) was used to calculate standardized \( R_{ST} \) values with MNSPNET (Excoffier 1993).

As a measure of how sociality might affect potential inbreeding within a population, we compared the association between average sociality of otters in a population and \( F_{IS} \) value for that population for sites with radiotagged animals. Average sociality was calculated by determining how closely a marker adheres to assumptions of the statistical model, we used several measures of genetic differentiation and genetic distances to test our hypotheses. In the absence of a complete understanding of mutational processes of microsatellites, if results from several methods of analysis (each of which are based upon different hypotheses of mutation or different algorithms) are in agreement, greater confidence in the correct interpretation of data is possible.

Migrants per generation. We estimated effective number of migrants (i.e. average number of individuals exchanged) per generation based upon private alleles (Barton & Slatkin 1986) to measure overall immigration into populations. We conducted that analysis for all populations with both genders considered together, and performed a separate analysis for each gender to further assess sex-biased dispersal. When more individuals are sampled per population, a greater number of private alleles is identified, which increases the accuracy of estimates of number of migrants (Slatkin 1985). Therefore, we also assessed private alleles between the two populations for which we had the largest sample sizes (Table 1).

Relatedness by gender and study area. Analyses were conducted to test whether mean relatedness of females to females, females to males, and males to males within and between areas was significantly different from that expected if relatedness is distributed at random. Juveniles were not included in the analyses to eliminate relatedness of parent–offspring dyads prior to dispersal of offspring, which could potentially mask the effects of sex-biased dispersal. A total of 1000 randomizations comparing mean coefficient of relatedness (\( R \); Kinship, Goodnight et al. 1994) between dyads were conducted to simultaneously evaluate relatedness within and between areas, keeping group and sex composition constant (i.e. only \( R \)-values between dyads were randomized). The randomization code for that analysis was written in quickbasic by E. Geffen.

Each set of gender analyses was conducted twice. The first analyses compared between and within the two areas for which we had telemetry data and the most genetic data (Herring Bay \( n = 39 \) and Jackpot Bay \( n = 31 \); Table 1). A second set of analyses was conducted on all samples collected in 1998, when samples from the other five areas were obtained and included samples obtained from Herring Bay that year (seven males, one female). A separate analysis was performed because our sampling design and sample sizes differed among years. At each site in 1998, trapping occurred for only five calendar days, 5–10 individuals were captured per study area; thus otters captured that year may represent individuals most vulnerable to capture,
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compared with otters captured over a period of several months in previous years.

Assignment tests and dispersal distances. We used the Bayesian method for assignment tests (GIRLCLASS; Cornuet et al. 1999) to detect immigrants into each area. Assignment tests result in the assignment of individuals to a population based on highest probability, even though reference populations may not include the true area of origin for an individual. To reduce the potential for assigning otters to unlikely populations, we eliminated individuals from subsequent analyses that had an assignment probability that was less than by chance (i.e. 100/7 study areas = 14.3 assignment probability). We used simulations to assign all otters to a study area; simulating multilocus genotypes for 10 000 individuals by randomly sampling alleles according to their frequencies in the samples (Cornuet et al. 1999). After eliminating otters with assignment probabilities of ≤ 0.143, we conducted chi-squared analysis to compare the proportion of males and females that were misassigned or correctly assigned to the area in which they were captured (i.e. source study area). We also performed a Kruskal–Wallis test to determine whether assignment probability differed between study areas and a Mann–Whitney U-test to compare assignment probability between genders.

We evaluated dispersal distances with assignment tests by assessing misassigned individuals (i.e. individuals not assigned to the area in which they were captured). For those individuals, we estimated dispersal distances as otter (swimming) distance between the study area in which they were captured and the site to which they were assigned.

Radiotelemetry and dispersal. We used telemetry data to estimate probability, characteristics and distance of dispersal for each gender. In this study, we refer to two types of dispersal: natal and breeding. By natal dispersal we imply long-range movement (> 20 km) from the natal range without return. Breeding dispersal (Greenwood 1980; Shields 1987) is characterized by movements during the mating season of several kilometres beyond the normal range for an otter, eventually returning to the normal range. To assess breeding dispersal, we conducted multiresponse permutation procedure analyses with blossom software (Slauson et al. 1994), comparing telemetry locations for adult male otters during the mating season with those for the remainder of the year. An exact test was conducted for each year of data, comparing the spatial distribution of Universal Transverse Mercator (UTM) coordinates for each individual from 15 April to 31 May to the use of space by that male during the rest of the year. Those dates correspond to 2 weeks before the first oestrus was detected in female otters in our study areas until 5 days after the last oestrus was noted (Blundell et al. 2002). Herein, we report only those patterns of space use that would result in the potential for gene flow during mating season beyond the bay or general area in which an otter was located during the rest of the year.

Isolation by distance. We applied Mantel’s test (PERMUTE! Version 3.4, Alpha & Casgrain 2000) to assess correlation between genetic and geographical distances for all otters in all study areas, and in separate analyses for each sex. Genetic distances assessed were $F_{ST}$, standardized $R_{ST}$, Nei’s unbiased genetic distance (Nei 1978), genotype likelihood ratio distance ($D_{LR}$; Paetkau et al. 1997), and a measure of fuzzy set similarity ($D_{fs}$; Dubois & Prade 1980), the latter of which was calculated as $1 - D_{fs}$ using MICROAT software (Minch et al. 1997). $D_{fs}$ calculates the proportion of shared alleles divided by the proportion of unique alleles among each pair of study areas (Dubois & Prade 1980).

We calculated geographical distances by measuring the linear distance between the midpoints (i.e. centre) of each study area. Although this represents an unbiased estimate of geographical distance and is therefore useful in comparisons of genetic vs. geographical distance, it is not representative of how an otter likely would travel between study areas, because otters generally swim, limiting over-land crossings to short distances (Blundell et al. 2000, 2001). Accordingly, we also compared genetic distances with ‘otter distances’ in a manner similar to that used by Dallas et al. (1999) for Lutra lutra. Otter distance measured a linear course parallel with the shore, incorporating the shortest over-water crossing between landmasses (e.g. across the mouth of a bay, the shortest distance between islands) in the most direct route possible between midpoints of study areas. Measures of geographical distances were obtained with ARCINFO (ESRI, Redlands, CA, USA).

Results

Genetic differentiation between study areas

Genotypes at one locus were independent of genotypes at another locus for each locus pair across all study areas ($P \geq 0.12$, linkage disequilibrium); thus all loci are diagnostic for the purposes of differentiation between sites. Mean heterozygosity among study sites was 43.8% ($\pm 0.02$ SE) and within sites was > 38% (Table 1). Mean number of alleles/locus was similar between areas. Study areas with greater sample sizes had higher heterozygosity and lower $F_{IS}$ values (Table 1).

Most loci were in HWE in each study area with the exception of two loci at Esther Passage, and one locus each at Naked Island and Unakwik Inlet (Table 2). A global test of HWE ($\chi^2$) random union of gametes, when the alternative hypothesis was heterozygote deficit, revealed that all study areas across all loci were not in HWE ($P < 0.0001$) and a multilocus test by individual site revealed that all areas had a heterozygote deficit ($P \leq 0.051$).
Standardized $R_{ST}$ values detected greater differentiation between areas compared with $F_{ST}$ values (Table 3). Most loci, however, afforded moderate genetic differentiation with $F$-statistics (i.e. $F_{ST} 0.05$–$0.15$; Hartl & Clark 1997), with females exhibiting higher differentiation than males (Table 4). Similarly, $F_{IS}$ and $F_{IT}$ values were higher for females than for males (Table 4). Genotypic and allelic distribution differed across all loci and all areas ($\chi^2 = \infty$, d.f. = 18, $P < 0.0001$). Because study areas were not in HWE, we tested for pairwise differentiation between sites not assuming HWE. A comparison of genotypic frequencies by randomization revealed that Herring and Jackpot bays were genetically differentiated ($P < 0.05$ after sequential Bonferroni corrections) from all other areas with

### Table 2
A test of Hardy–Weinberg equilibrium (exact probabilities) by locus and study area for river otters captured in Prince William Sound, Alaska, from 1996 to 1998

<table>
<thead>
<tr>
<th>Locus</th>
<th>Study Area</th>
<th>Eleanor Island</th>
<th>Esther Passage</th>
<th>Herring Bay</th>
<th>Jackpot Bay</th>
<th>Naked Island</th>
<th>Unakwik Inlet</th>
<th>Wells Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>701</td>
<td>0.064</td>
<td>0.037</td>
<td>0.141</td>
<td>0.138</td>
<td>0.098</td>
<td>0.171</td>
<td>0.074</td>
<td>0.194</td>
</tr>
<tr>
<td>715</td>
<td>0.034</td>
<td>0.056</td>
<td>0.023</td>
<td>0.168</td>
<td>0.071</td>
<td>0.197</td>
<td>0.226</td>
<td>0.049</td>
</tr>
<tr>
<td>733</td>
<td>0.259</td>
<td>0.261</td>
<td>0.238</td>
<td>0.145</td>
<td>0.114</td>
<td>0.366</td>
<td>0.368</td>
<td>0.325</td>
</tr>
<tr>
<td>782</td>
<td>0.031</td>
<td>0.026</td>
<td>0.050</td>
<td>0.166</td>
<td>0.041</td>
<td>0.162</td>
<td>0.214</td>
<td>0.058</td>
</tr>
<tr>
<td>801</td>
<td>0.031</td>
<td>0.026</td>
<td>0.050</td>
<td>0.166</td>
<td>0.041</td>
<td>0.162</td>
<td>0.214</td>
<td>0.058</td>
</tr>
<tr>
<td>818</td>
<td>0.069</td>
<td>0.049</td>
<td>0.098</td>
<td>0.109</td>
<td>0.325</td>
<td>0.171</td>
<td>0.076</td>
<td>0.391</td>
</tr>
<tr>
<td>829</td>
<td>0.060</td>
<td>0.032</td>
<td>0.170</td>
<td>0.007</td>
<td>0.008</td>
<td>0.067</td>
<td>0.007</td>
<td>0.176</td>
</tr>
<tr>
<td>m22</td>
<td>0.035</td>
<td>0.059</td>
<td>0.010</td>
<td>0.175</td>
<td>0.363</td>
<td>0.212</td>
<td>0.153</td>
<td>0.357</td>
</tr>
<tr>
<td>m75</td>
<td>0.020</td>
<td>-0.040</td>
<td>0.395</td>
<td>0.298</td>
<td>0.376</td>
<td>0.304</td>
<td>0.105</td>
<td>0.622</td>
</tr>
<tr>
<td>All loci</td>
<td>0.074</td>
<td>0.064</td>
<td>0.131</td>
<td>0.127</td>
<td>0.171</td>
<td>0.191</td>
<td>0.148</td>
<td>0.279</td>
</tr>
</tbody>
</table>

*Both genders analysed together.

**Table 3** Genetic distances ($F_{ST}$ lower diagonal, standardized $R_{ST}$ upper diagonal) between study areas in Prince William Sound, Alaska, USA, for river otters captured from 1996 to 1998

<table>
<thead>
<tr>
<th>Study area</th>
<th>Eleanor Island</th>
<th>Esther Passage</th>
<th>Herring Bay</th>
<th>Jackpot Bay</th>
<th>Naked Island</th>
<th>Unakwik Inlet</th>
<th>Wells Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eleanor Island</td>
<td>1.001</td>
<td>0.0784</td>
<td>0.0153</td>
<td>-0.0310</td>
<td>0.0389</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Esther Passage</td>
<td>0.1212</td>
<td>0.1049</td>
<td>0.0110</td>
<td>-0.0300</td>
<td>0.0063</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herring Bay</td>
<td>0.1983</td>
<td>0.0339</td>
<td>0.0877</td>
<td>0.0101</td>
<td>0.0865</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackpot Bay</td>
<td>0.1434</td>
<td>0.0910</td>
<td>0.0907</td>
<td>0.1128</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Naked Island</td>
<td>0.1423</td>
<td>-0.0139</td>
<td>0.1359</td>
<td>-0.0385</td>
<td>-0.235</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unakwik Inlet</td>
<td>-0.0246</td>
<td>-0.0019</td>
<td>0.1467</td>
<td>0.0311</td>
<td>-0.0175</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wells Bay</td>
<td>0.0347</td>
<td>0.1667</td>
<td>0.1289</td>
<td>-0.0302</td>
<td>-0.0190</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$F_{ST}$ $F_{IS}$ $F_{IT}$ $Locus$ Both* Males Females Both* Males Females Both* Males Females

701 $0.064$ $0.037$ $0.141$ $0.138$ $0.098$ $0.194$ $0.162$ $0.225$
715 $0.034$ $0.056$ $0.023$ $0.168$ $0.071$ $0.197$ $0.226$ $0.049$
733 $0.259$ $0.261$ $0.238$ $0.145$ $0.114$ $0.366$ $0.368$ $0.325$
782 $0.031$ $0.026$ $0.050$ $0.166$ $0.041$ $0.162$ $0.214$ $0.058$
801 $0.031$ $0.026$ $0.050$ $0.166$ $0.041$ $0.162$ $0.214$ $0.058$
818 $0.069$ $0.049$ $0.098$ $0.109$ $0.325$ $0.171$ $0.076$ $0.391$
829 $0.060$ $0.032$ $0.170$ $0.007$ $0.008$ $0.067$ $0.007$ $0.176$
m22 $0.035$ $0.059$ $0.010$ $0.175$ $0.363$ $0.212$ $0.153$ $0.357$
m75 $0.020$ $-0.040$ $0.395$ $0.298$ $0.376$ $0.304$ $0.105$ $0.622$
All loci $0.074$ $0.064$ $0.131$ $0.127$ $0.171$ $0.191$ $0.148$ $0.279$

$*Both genders analysed together.
the exception of Unakwik Inlet. All other sites were not significantly different from each other ($P > 0.05$). With allelic frequencies, Herring Bay was significantly different from all other sites, but Jackpot Bay still could not be distinguished from Unakwik Inlet. As with genotypic frequencies, all other study areas were genetically similar in allelic frequencies.

Multidimensional scaling based on standardized Euclidean distances for allelic frequencies resulted in differentiation between study areas (Fig. 2). Jackpot Bay and Herring Bay are separated from the rest by the dimension 1 axis alone (Fig. 2), and Esther Passage and Eleanor Island are separated from Wells Bay and Naked Island by the dimension 2 axis.

The minimum spanning trees for standardized $R_{ST}$ (Fig. 3a) and $F_{ST}$ (Fig. 3b) generated similar spatial patterns between sites. Unakwik Inlet appears as the centre point in both networks with Esther Passage as a closely related population; Naked Island–Wells Bay and Jackpot Bay–Herring Bay emerge as two distant clusters. The topology of Eleanor Island is undefined, but is more proximate to Unakwik Inlet than to other study areas.

Social groups within study areas also showed lower $F$-statistics (overall $F_{IS} = 0.070$, range among loci $0.2166–0.23$; $F_{ST} = 0.038$, range $–0.0008–0.06$; $F_{IT} = 0.105$, range $–0.13–0.23$) compared with those values at the level of the study site. A test of HWE among social groups could not be calculated for some groups, probably because of small sample size (mean group size = 2.9 otters $± 0.05$ SE). Commensurate with a reduction in $F_{IS}$ scores of social groups compared with populations, averaging over all loci, 22.8 groups ($± 1.3$ SE) were in HWE, 1.9 $± 0.39$ groups showed a heterozygote deficit, and $10.3 ± 1.4$ groups had insufficient data to assess HWE at $≥ 1$ locus. There also was a positive association between average sociality of otters in an area and $F_{IS}$ values for that site (Jackpot Bay average sociality = 21.8%, $F_{IS} = 0.053$; Herring Bay sociality = 24.2%, $F_{IS} = 0.079$; Eleanor Island sociality = 47.4%, $F_{IS} = 0.306$).
females, 0.9 migrants (private alleles females.
are larger, it is evident that male otters migrate more than population = 12.5). Therefore, even when sample sizes
in their resident area than to males in that area. In addition,
chance. In accordance with male-biased dispersal, females
otters within sites were more related than expected by
bays; Table 1), differences were significant, indicating that
those areas with large sample sizes (Herring and Jackpot
areas compared with otters among all sites (Table 5). For
otters were more related to otters within resident study
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bays; Table 1), differences were significant, indicating that
otters within sites were more related than expected by
chance. In accordance with male-biased dispersal, females
in Herring and Jackpot bays were more related to females
in their resident area than to males in that area. In addition,
female–female relatedness was greater than male–male
relatedness for those areas (Table 5), indicating that male
dispersal may not occur in sibling groups. Although there
was a trend for higher relatedness within than between
study areas in 1998, the test was not significant for any
gender combination (Table 5).

**Migrants per generation**

The corrected estimate of the effective number of migrants per generation based on private alleles (Barton & Slatkin 1986) for all otters (both genders) was 6.68 migrants (frequency of private alleles \( \bar{x} = 0.035 \), mean size of population = 16.7). For male otters, effective number of migrants was estimated at 7.28 individuals per generation (private alleles \( \bar{x} = 0.041 \), mean population = 10.7), and for females, 1.46 migrants (private alleles \( \bar{x} = 0.123 \), mean population = 5.7).

We caution that those estimates may be high because of sampling error as a result of small sample sizes, however, the primary purpose of the analysis was to compare overall movements and differences between genders as a means of detecting sex-biased dispersal. The estimate for both sexes in Herring and Jackpot bays was 4.49 migrants (private alleles \( \bar{x} = 0.027 \), mean population = 35). For male otters in Herring and Jackpot bays, 3.88 migrants were identified (private alleles \( \bar{x} = 0.038 \), mean population = 22.5), and for females, 0.9 migrants (private alleles \( \bar{x} = 0.11 \), mean population = 12.5). Therefore, even when sample sizes are larger, it is evident that male otters migrate more than females.

**Relatedness by gender and study area**

Consistent with our hypotheses, regardless of gender, otters were more related to otters within resident study areas compared with otters among all sites (Table 5). For those areas with large sample sizes (Herring and Jackpot bays; Table 1), differences were significant, indicating that otters within sites were more related than expected by chance. In accordance with male-biased dispersal, females in Herring and Jackpot bays were more related to females in their resident area than to males in that area. In addition, female–female relatedness was greater than male–male relatedness for those areas (Table 5), indicating that male dispersal may not occur in sibling groups. Although there was a trend for higher relatedness within than between study areas in 1998, the test was not significant for any gender combination (Table 5).

**Assignment tests and dispersal distances**

Simulations conducted by Cornuet et al. (1999) determined that assignment tests performed well when \( F_{ST} \) values were > 0.05, and Bayesian assignment was most accurate. Given a mean \( F_{ST} \) of 0.06 among loci in this study (Table 4), our Bayesian assignments are high (81.9% correctly assigned), following elimination of otters with low assignment probabilities. We did not consider population assignments for 10 males (13.3%) and four females (11.4%) because probability of assignment was below the value equivalent to assignment by chance to any of the seven study areas sampled. Of the remaining 94 animals, 78.1% of males and 83.3% of females were correctly assigned to the study area in which they were captured (i.e. the source site). There was no difference among areas (\( \chi^2 = 4.11, d.f. = 6, P = 0.66 \), Kruskal–Wallis) in assignment probability values (\( \bar{x} = 0.60 \pm 0.03 \) SE; range 0.17–0.999). For those otters assigned correctly, assignment probabilities did not differ between genders (males \( \bar{x} = 0.60 \pm 0.04 \) SE; females \( \bar{x} = 0.56 \pm 0.07 \), \( U = 940.5, P = 0.87 \), Mann–Whitney).

Although the trend was for a higher proportion of male otters misassigned (21.9%) than females (16.7%), the proportion of misassigned and correctly assigned individuals (males = 78.1%, females = 83.3%) was not significantly different between genders (\( \chi^2 = 0.34, d.f. = 1, P = 0.6 \)). Most misassigned males were assigned to nearby study areas (16–30 km distance; Fig. 4), whereas most misassigned females were identified as originating from more distant sites (> 60 km; Fig. 4). Average (± SE) dispersal distance (as determined by ‘ofter’ distance between source and assigned population along the most likely route taken) for male otters was 34.7 (± 4.3) km, with a maximum dispersal distance of 79 km; average and maximum dispersal distances for females were 57.9 (± 11.8) km and 96.6 km, respectively.

**Radiotelemetry and dispersal**

Telemetry data for river otters also indicated that males and females had an approximately equal probability of natal dispersal. One of 15 females (6.7%) and three of 40

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Table 5 A comparison of the mean (± SD) coefficient of relatedness (\( R \)-values from Kinship; Goodnight et al. 1994) within and between study areas by gender for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998

<table>
<thead>
<tr>
<th>Study area</th>
<th>Year</th>
<th>Gender</th>
<th>Mean within (( \bar{x} ))</th>
<th>Mean between (( \bar{x} ))</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>HB vs. JP</td>
<td>1996–1998</td>
<td>F–F</td>
<td>0.143 ± 0.24 (146)</td>
<td>−0.043 ± 0.24 (154)</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>HB vs. JP</td>
<td>1996–1998</td>
<td>F–M</td>
<td>0.079 ± 0.24 (495)</td>
<td>0.030 ± 0.26 (480)</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>HB vs. JP</td>
<td>1996–1998</td>
<td>M–M</td>
<td>0.086 ± 0.23 (374)</td>
<td>0.023 ± 0.26 (367)</td>
<td>0.002</td>
</tr>
<tr>
<td>All 7 areas</td>
<td>1996</td>
<td>F–F</td>
<td>0.184 ± 0.23 (6)</td>
<td>0.051 ± 0.30 (49)</td>
<td>0.15</td>
</tr>
<tr>
<td>All 7 areas</td>
<td>1996</td>
<td>F–M</td>
<td>0.090 ± 0.27 (54)</td>
<td>0.046 ± 0.26 (276)</td>
<td>0.12</td>
</tr>
<tr>
<td>All 7 areas</td>
<td>1996</td>
<td>M–M</td>
<td>0.087 ± 0.26 (67)</td>
<td>0.100 ± 0.25 (368)</td>
<td>0.63</td>
</tr>
</tbody>
</table>

* HB = Herring Bay; JP = Jackpot Bay. \( P \)-values were calculated using a randomization test.
males (7.5%) that were radio tracked showed movement patterns consistent with natal dispersal. Generally, those otters remained in their area of capture for 3–5 months before initiating exploratory movements beyond their previously established range, after which radio contact with some individuals was lost. One young male spent most of 1 year in transit, travelling 47 km southward before eventually settling in an area 32 km south of its original point of capture. Another young male dispersed from Eleanor Island immediately after capture and travelled 71 km southward in $\approx 14$ days, remaining at that location for approximately 4 months before radio contact was lost.

Nine adult males (22.5% of all telemetered male otters) showed patterns of movement during mating season that differed with space use during the rest of the year, and likely were consistent with breeding dispersal (Fig. 5). Four otters (44.4% of males exhibiting breeding dispersal) shifted locations completely, crossing substantial bodies of open water ($\approx 6$ km; Fig. 5) to spend mating season in a different area, after which they returned to their original home ranges. Multiresponse permutation procedure (MRPP) analyses noted a significant difference in spatial distribution for mating season compared with the rest of the year for three of those four otters ($P \leq 0.047$, MRPP). The fourth otter ($P = 0.07$, MRPP) took a brief excursion in February, making an open-water crossing of 6 km, but returned to his customary home range until just prior to mating season, whereupon he returned to that new area until mating season was over. The remaining five otters (55.6% of breeding dispersers) temporarily expanded their ranges beyond the bay in which their home range occurred for the rest of the year (Fig. 5). Four of those otters had significant shifts in space use ($P \leq 0.008$, MRPP). One otter, which travelled $\approx 25$ km south of his customary home range during the mating season, did not exhibit a significant shift in spatial distribution ($P = 0.17$, MRPP), likely because only one location was detected outside the normal area (Fig. 5).

Isolation by distance

Relatively large bodies of open water did not appear to constitute a barrier to dispersal for coastal river otters. With telemetry data, we recorded open-water crossings of $\approx 6.5$ km, and assignment tests indicated that otters of both sexes crossed bodies of water in which the shortest open-water distance was $\approx 13$ km (Fig. 1).

When data from both genders were analysed collectively, there was a significant positive correlation (Table 6) between most measures of genetic distance (except $D_{LR}$ and $D_{fs}$) and both measures of geographical distance (linear distance and otter distance). A separate analysis by gender noted significant positive correlation between all measures of genetic and geographical distances (with the exception of $D_{fs}$) for males, but not for females (Table 6; Fig. 6). The insignificant correlation obtained with $D_{fs}$ may be associated with small sample sizes in some study areas. The $D_{fs}$ measure of distance makes use of unique alleles, which often are among the rare alleles in a population. For those under-represented populations, $D_{fs}$ lacks power and may generate erroneous distance estimates.

Discussion

Various aspects of social structure, in particular mating system, dispersal patterns and group size, influence the genetic structure of populations (Chesser 1991; de Jong et al. 1994). Results from our tests of linkage disequilibrium, $F$-statistics, multidimensional scaling of Euclidean distances (Fig. 2) and minimum spanning trees (Fig. 3) indicate that

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we sampled genetically distinct subpopulations (Table 3) with moderate levels of genetic differentiation among loci, and evidence of gene flow among sites (Fig. 4).

That we established clear differentiation between study areas with multidimensional scaling based upon Euclidean distances and allelic frequencies (Fig. 2), as well as with minimum spanning trees of standardized values of $R_{ST}$ and $F_{ST}$ (Fig. 3), indicates that genetic structure exists between study sites within the area we sampled in Prince William Sound. Those results may represent source-sink or metapopulation dynamics (Pulliam 1988; Hanski & Gilpin 1991). For example, Unakwik Inlet is uniquely aligned on dimension 1 (Fig. 2) and is the centre point for both minimum spanning networks (Fig. 3). That area offers one of the few known spawning areas in Prince William Sound for lipid-rich Eulachon (Thaleichthys pacificus, MB-D personal observation), potentially drawing otters from surrounding populations. In addition, there was evidence that Unakwik Inlet may have been subject to greater trapping pressure (i.e. higher mortality) than other areas (GMB & MB-D, personal observation) commensurate with a sink population, however, further investigations are necessary to elucidate metapopulation dynamics.

Recolonization from source populations following local extirpation requires that both sexes disperse (Hanski & Gilpin 1991). Factors that determine which sex disperses are generally attributed to gender differences in the potential for reproductive success due to local competition for resources or mates (Greenwood 1980; Shields 1987; Perrin & Mazalov 2000), and demographics of the source population.

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may differentially affect dispersal rates for each gender (Aars & Ims 2000). Assignment tests (i.e. misassigned individuals) indicated that male and female river otters had an equal, but low, probability of natal dispersal, although we caution that sample size for females was small. Likewise, our telemetry observations noted similar low rates of natal dispersal for both genders, in agreement with results reported by Melquist & Hornocker (1983), in which dispersal of telemetered individuals from the natal area was observed for both male and female Lontra canadensis in a freshwater environment.

Although natal dispersal was similar between genders, differences in movement patterns and potential for gene flow were detected with telemetry tracking that were indicative of a male-biased dispersal facilitated by breeding dispersal. Thirty per cent of 40 male otters that were radiotracked showed some form of dispersal. Of that dispersal, 22.5% (9 of 40) occurred through apparent breeding

Table 6 Correlation coefficients (and P-values in parenthesis) based on mantel tests between genetic and geographical distances for river otters captured in Prince William Sound, Alaska, USA, from 1996 to 1998

<table>
<thead>
<tr>
<th>Genetic distance</th>
<th>All otters</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Otter distance*</td>
<td>Linear distance</td>
<td>Otter distance*</td>
</tr>
<tr>
<td>F_{ST}^* (P)</td>
<td>0.578 (0.005)</td>
<td>0.577 (0.003)</td>
<td>0.533 (0.009)</td>
</tr>
<tr>
<td>R_{ST}^* (P)</td>
<td>0.502 (0.023)</td>
<td>0.490 (0.030)</td>
<td>0.543 (0.036)</td>
</tr>
<tr>
<td>Nei’s‡ (P)</td>
<td>0.561 (0.006)</td>
<td>0.550 (0.006)</td>
<td>0.512 (0.024)</td>
</tr>
<tr>
<td>D_{ST}§ (P)</td>
<td>0.564 (0.106)</td>
<td>0.406 (0.052)</td>
<td>0.457 (0.036)</td>
</tr>
<tr>
<td>D_{FS}¶ (P)</td>
<td>0.473 (0.045)</td>
<td>0.401 (0.073)</td>
<td>0.484 (0.020)</td>
</tr>
</tbody>
</table>

*Otter distances were estimated by calculating the most direct route between study areas in which open-water crossings were measured between the closest possible landmasses. †Standardized R_{ST} (Goodman 1997). ‡Nei’s unbiased distance (Nei 1978). §Genotype likelihood ratio distance (Paetkau et al. 1997). ¶Fuzzy set similarity – proportion of shared alleles divided by proportion of unique alleles (Dubois & Prade 1980).

Fig. 6 A test of the hypothesis of isolation by distance for male and female river otters in Prince William Sound, Alaska, USA. Results were significant for males, but not for females (Table 6). Distance measures shown here are those that showed lowest P-values among the measures of genetic distance evaluated (Table 6).
dispersal (Fig. 5); however, we cannot assess whether breeding dispersal constituted effective dispersal (i.e. resulted in reproductive success). Some males temporarily shifted to a new area, whereas others expanded their home ranges during mating season. A range expansion during mating season maintains the potential for reproductive success within the resident area as well as increasing the potential for contributing to gene flow beyond the normal range of movements for an otter outside of mating season (Fig. 5). Both forms of breeding dispersal, in combination with natal dispersal indicate male-biased dispersal among these coastal river otters, potentially facilitating gene flow with natal dispersal indicate male-biased dispersal among these coastal river otters, potentially facilitating gene flow to nearby populations.

A comparison of F-statistics between genders substantiated male-biased dispersal strategies noted with telemetry observations. Females had higher $F_{is}$ values than males (Table 4), probably because most females did not disperse, thus are more likely to share common ancestors. Females likely had higher $F_{is}$ values because most females that did disperse moved farther than males (Fig. 4). In contrast, males experienced higher rates of gene flow over short distances via both breeding (Fig. 5) and natal dispersal (Fig. 4). Therefore, the potential for common ancestry among males is lower among different individuals within subpopulations ($F_{is}$) and across all populations ($F_{st}$) at the relatively small geographical scale in which we sampled. Similarly, females had higher $F_{is}$ values than males (Table 4) indicating higher genetic differentiation for females, as would be expected if females showed philopatry and gene flow among males was higher.

In further support of the hypothesis of male-biased dispersal, a greater number of effective migrants per generation was detected with private alleles analyses for males compared with females. Similarly, for Herring and Jackpot bays, females were more closely related to females within a site than to males (Table 5) and relatedness among male otters within a study area was considerably lower than relatedness among females, both of which are consistent with a hypothesis of male-biased dispersal. Similarly, if during our 5 calendar days of sampling each area in 1998, we primarily captured transient individuals (i.e. otters most vulnerable to capture because of lack of familiarity with the area), transients arriving from other areas would not be more related within areas than expected by chance. The high similarity in relatedness of male otters within and between areas in 1998 (Table 5) likely indicates movements of males between populations consistent with male-biased dispersal. In addition, some areas sampled in 1998 (e.g. islands) may support only small resident populations, or may be subject to high population turnover as a result of mortality within a site. Each of those possibilities might result in a propensity toward transient otters, resulting in the patterns of relatedness that we observed within and between areas (Table 5).

That we did not detect significant differences in relatedness values within and between study areas for females in 1998 (Table 5) may be a result of sample size (Table 1). An incomplete sampling of gene frequencies from a population would make an accurate assessment of relatedness within that population more difficult and likely limited our ability to assess relatedness of females in that year.

Theoretically, sex-biased dispersal may result in local differences in gene frequencies between genders, and random mating in such a population should result in an excess of heterozygotes (i.e. negative $F_{is}$ values; Prout 1981); a pattern opposite of our observations. Various factors influencing population structure, however, could have contributed to decreasing our ability to analyze relatedness of females in that year.

Rates and distances of dispersal are main factors in geographical differentiation at small spatial scales (Forbes & Hogg 1999), and probability of recolonization of extirpated populations is determined by insularity of the extirpated population and potential dispersal distances of the species (Hanski & Gilpin 1991). Assignment tests indicated a bimodal distribution to dispersal distances (Fig. 4) for coastal river otters consistent with the results from tests of isolation by distance. Most males moved only short distances, but when females dispersed, most dispersed to distant study sites (Fig. 4). Similarly, male otters showed significant isolation by distance (Fig. 6), likely because dispersing males did not travel far (Fig. 4). Contrary to our hypothesis, there was no significant isolation by distance for females (Fig. 6). This may be due to small sample sizes for females (Table 1) or possibly because dispersing females travelled farther than males (Fig. 4) and many may be moving beyond the spatial scale of our genetic sampling (Fig. 1). More genetic data for female river otters are needed to definitively determine whether isolation by distance does in fact occur among females, however, different dispersal distances between genders are consistent with sociality and spatial relationships that we observed among coastal river otters.

Blundell et al. (2002) noted that males were highly social, but most females remained solitary. Solitary females tended to occupy exclusive home ranges, but the home ranges of solitary males and groups of males overlapped each other.
as well as the home ranges of females (Blundell et al. 2000). The high sociality and apparent lack of territoriality among male otters would enable dispersing males to relocate to nearby populations, but dispersing females likely would need to travel greater distances to locate available habitat in which to establish an exclusive home range.

Conclusions

Our data provided evidence for male-biased dispersal among coastal river otters, but not in the manner typical of most mammals (Greenwood 1980). Sociality influenced the genetic structure of populations, and gender differences in sociality and spatial relationships resulted in different dispersal distances. Our study indicated that, for coastal river otters, males had greater potential for contributing to gene flow among close populations via both breeding and natal dispersal, but both genders exhibited equal, low probability of natal dispersal, and females in particular may travel 60–90 km during dispersal (Fig. 4).

Given the susceptibility of otters to effects of environmental pollution (Mason 1989; Serfass et al. 1993; Latrivié & Walton 1998), a local extinction caused by anthropogenic factors may be difficult to remedy with natural recolonization unless the extinction occurred on a relatively small spatial scale. In general, fecundity in female mustelids is reduced as a result of exposure to pollutants (Bleavins et al. 1980; Moore et al. 1999), but males are less affected (Bleavins et al. 1980). Therefore, following environmental remediation of an extirpated area (i.e. removal of the pollution source), immigrating females could potentially originate from an area beyond the scale of environmental effect, and male otters likely would immigrate from neighbouring areas into an unoccupied zone via both breeding and natal dispersal. Although male otters could arrive relatively rapidly, immigration of females would be delayed as a result of low rates of natal dispersal. Further studies are needed, but the initial data indicate that natural recolonization of coastal river otters following local extinction might be a slow process and may be substantially delayed unless viable populations were available nearby (i.e. within 60 km; Fig. 4).

Rates of dispersal from source populations, distances dispersed and immigration into sink populations are influenced by demographics, density dependence and associated habitat saturation (Aars & Ims 2000; Kokko & Lundberg 2001). Rates of immigration of otters into vacated habitat during a recolonization event may differ from dispersal movements we documented among areas with established populations. Empirical studies are therefore recommended to compare immigration of otters into occupied vs. unoccupied habitat to further assess the potential for natural recolonization of extirpated populations of river otters. Additional exploration of the potential for recolonization among otters is also recommended via development of a quantitative spatial model incorporating sex-biased dispersal, dispersal distances and the effects of habitat saturation and delayed implantation on dispersal and gene flow, respectively.

Studies such as ours are useful for establishing the geographical scale for contemporary and historical patterns of gene flow (Avise 1994; Forbes & Hogg 1999). These data may be useful for modelling exercises to establish the appropriate size of conservation units, as well as determining geographical distances for source populations for translocation to avoid the potential for outbreeding depression or disruption of local adaptations (Hedrick & Miller 1992; Frankham 1995; Forbes & Hogg 1999). Species with evidence of high gene flow among populations may be more appropriate for consideration for translocations (Forbes & Hogg 1999). Because of the isolation by distance that we noted for male otters and limited gene flow for females, we recommend that translocation of river otters should be undertaken with extreme caution to avoid loss of genetic diversity within the species.

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SEX-BIASED DISPERSAL IN COASTAL RIVER OTTERS


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