

# Kinship and sociality in coastal river otters: are they related?

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Previous studies of coastal river otters (*Lontra canadensis*) in Prince William Sound, Alaska, USA, documented atypical social organization for mammals. Social groups were composed largely of males, but some males remained solitary year-round and most females were asocial. Because, in carnivores, groups are usually composed of highly related individuals but group living also provides advantages unrelated to kinship, we concurrently evaluated the role of relatedness and ecological benefits in sociality among coastal river otters. By using DNA microsatellite analysis and radiotelemetry, we were able to reject the hypothesis that social groups of otters were kin based. In addition, we found no indication of kin avoidance, as would be expected from low dispersal and high local competition. Sociality conferred no reproductive benefits or costs to otters; number of offspring and number of relatives in the population did not differ between social and solitary animals. Solitary males were not older or larger than were social males, and there was no relation between male size and number of offspring, indicating that sexual selection did not mask a potential relation between sociality and reproductive success. Among coastal river otters in this region, sociality could be explained by the benefits obtained from cooperative foraging on high-quality schooling pelagic fishes. Such benefits did not require association with kin, resulting in no selection pressure for kin-based groups. The prediction that the degree of sociality in the population will fluctuate relative to the abundance of schooling pelagic fishes merits further investigation. *Key words:* Alaska, kin selection, *Lontra canadensis*, microsatellite DNA, reproductive success, schooling pelagic fishes, sexual selection. [*Behav Ecol* 15:705–714 (2004)]

Evolution of sociality among animals has been attributed to benefits gained relative to costs. Benefits include reduced risk of predation and increased access to resources (Alcock, 1993; Alexander, 1974; Rubenstein, 1978), whereas costs include reproductive suppression, intraspecific competition for resources or reproductive opportunities, and increased potential for parasite and disease transmission (Alexander, 1974; Armitage, 1986; Packer et al., 1991; West et al., 2002; Wrangham and Rubenstein, 1986). Fitness benefits have been hypothesized to occur directly, at the level of the individual, through maximized reproductive success (Williams, 1966), or indirectly through reproductive success of related individuals (i.e., kin selection; Hamilton 1964). Although reciprocity, mutualism (Connor, 1986, 1995; Mesterton-Gibbons and Dugatkin, 1992), or ecological benefits from associations with nonkin could influence direct fitness (Gompper and Wayne, 1996; Hughes, 1998), benefits obtained from association with kin may affect both direct and indirect fitness (Gompper and Wayne, 1996; Hughes, 1998). Nonetheless, under limited dispersal and high local competition, association with kin may negatively affect both (West et al., 2002). Thus, to better understand the role of kinship in formation of groups, a concurrent evaluation of ecological benefits and relatedness is required.

In several marine mammals and carnivores, relatedness among group members is high especially when dispersal is limited (Clutton-Brock 2002; Wrangham and Rubenstein,

1986). Examples include pods of pilot whales (*Globicephala melas*: Amos et al. 1993), packs of dwarf mongooses (*Helogale parvula*: Creel and Waser, 1994; Keane et al., 1994), female groups of coatis (*Nasua narica*: Gompper 1996; Gompper et al. 1997), packs of African hunting dogs (*Lycaon pictus*: Girman et al., 1997), prides of African lions (*Panthera leo*: Packer et al., 1991), and wolves (*Canis lupus*: for review, see Gompper and Wayne, 1996). Nonetheless, in many cases ecological benefits such as counter-action against infanticide (lions: Packer et al., 1991), counter-action against cleptoparasitism (African hunting dog: Girman et al., 1997), food source manipulation (coati: Gompper, 1996), and confinement of prey (cetaceans: Herzing and Johnson, 1997) were recorded, suggesting that relatedness may not be the sole determinant of formation or maintenance of social groups in carnivores.

River otters (*Lontra canadensis*), like other mammalian species (Lott, 1991), exhibit high intraspecific variation in social systems. The degree of sociality and group composition (e.g., mixed adult groups, extended family groups, and groups with helper animals) vary among as well as within different habitats (Beckel, 1982; Melquist and Hornocker, 1983; Erickson and McCullough, 1987; Rock et al., 1994; Rostain, 2000). Recently, however, we documented a highly atypical social organization for mammals (Eisenberg, 1981; Kruuk, 1995; Lott, 1991), in river otters inhabiting marine environments of Prince William Sound, Alaska, USA (Blundell et al., 2002a). In that coastal habitat, large groups of river otters were composed mainly of males (Blundell et al., 2002a; Rock et al., 1994). Although some females briefly joined mixed-sex groups (Blundell et al., 2002a), most females and some males remained solitary year-round (Blundell et al., 2002a).

Our earlier study documented that social otters, through cooperative foraging, consumed higher proportion of school-

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ing pelagic fishes (i.e., higher-quality diet) than did solitary individuals (Blundell et al., 2002a). Nonetheless, whether the benefits of cooperative foraging are solely responsible for such unique intrapopulation variation in sociality cannot be assessed before evaluation of relatedness of individuals within groups is conducted.

Our first objective was to evaluate whether social groups of otters were composed of related individuals or represented a random collection of animals. The degree of relatedness among group members could indicate whether kinship, kin avoidance, or ecological forces independent of kinship shape group living in otters. We also explored the effect of sociality on reproductive success of individuals and whether social otters had more relatives in the population, as indices of direct and indirect fitness benefits, respectively. Finally, we investigated the interaction between sociality and morphological characters (age and size) to ensure that effects of sexual selection were not masking patterns of sociality in relation to kinship.

## METHODS

### Study area

Field research was conducted in Prince William Sound (PWS), Alaska, USA (Blundell, 2001; Blundell et al., 2002a,b) from 1996–1999. Otters were live-captured at seven sites in western PWS, spanning an area of approximately 4800 km<sup>2</sup>. Detailed descriptions of the study areas are provided in Ben-David et al. (1998) and Bowyer et al. (1995). River otters were livetrapped in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage (60°20' N, 148°10' W;  $n = 31$ ) and in 1996–1998 in Herring Bay and surrounding areas on northern Knight Island (60°30' N, 147°40' W;  $n = 39$ ). In 1998, otters were also captured at Eleanor Island (60°32' N, 147°37' W;  $n = 9$ ), Esther Passage (60°53' N, 147°55' W;  $n = 11$ ), Unakwik Inlet (60°55' N, 147°30' W;  $n = 5$ ), Wells Bay (60°55' N, 147°20' W;  $n = 8$ ), and Naked Island (60°40' N, 147°25' W;  $n = 8$ ).

### Otter capture and processing

One hundred eleven individual river otters were captured from May–July in 1996 and 1997, and from mid-April–May in 1998. For details on capture procedures, see Ben-David et al. (2002) and Blundell et al. (1999; 2002a,b). The following morphological measures were obtained from each otter: body length, total length (nose to tip of tail), baculum length, testicle width (in millimeters), and body weight (in kilograms). Age was estimated for each otter (juvenile, young adult, adult, and old adult) based on body mass and tooth wear and staining, and 7 ml blood was drawn from the jugular vein for DNA analysis and other assays for a companion study (Bowyer et al., 2003). All methods used in this research were approved by the Institutional Animal Care and Use Committee at University of Alaska Fairbanks and adhere to guidelines for animal care and use adopted by the American Society of Mammalogists (Animal Care and Use Committee, 1998).

### Radiotelemetry and sociality

Information on sociality and spatial relationships of river otters was obtained from radiotelemetry data, because behavioral observations of otters in our remote study areas were difficult to obtain (Blundell et al., 2002a,b). Fifty-five otters were surgically implanted with hermetically sealed radio transmitters (Ben-David et al., 2002; Blundell et al., 2000; 2002a,b; Bowyer et al., 2003). Otters were radio tracked from 1996–1999 in Dangerous Passage, from 1997–1999 in Herring

Bay, and from 1998–1999 at Eleanor Island ( $n = 2230$  total locations), mostly from a fixed-wing aircraft. Tracking occurred year-round, but locations were obtained with greater intensity in spring, during mating season, and in summer when weather was more conducive to regular flights.

Once a telemetered otter was located, global positioning systems (GPS) data were obtained, and radio frequencies of all other otters were checked to determine whether other individuals were present in the same location. If two or more telemetered otters were detected at the same location, the pilot took care to determine the distance between them and attempted to obtain a visual observation (94 of 2230 locations, or 4.2%). During visual observations, the presence of unmarked animals was determined. Composition of social groups was determined from telemetry locations (average of  $25.4 \pm 1.4$  locations per otter and  $416 \pm 37$  tracking days per animal) and visual sightings. Additional details on radiotelemetry procedures and determination of sociality are provided in Blundell et al. (2002a).

### Sampling density

Because we were forced to infer sociality by using indirect methods and our direct sightings were limited (4.2%; Blundell et al., 2002a), we could not be certain that a radiotagged animal did not associate with unmarked individuals. Under such conditions an animal will be designated as solitary when in effect it was social. This bias, however, would be minimal if we radiotagged a large portion of the population. To estimate the percentage of animals captured (i.e., sampling density) and radiotagged in the three study areas, we used the values of the upper and lower 95% confidence intervals of the density estimates for river otters obtained in June 1990 in nonoiled (control) areas of PWS (28 and 60 otters/100 km, respectively; Testa et al., 1994). These density estimates are similar to minimum number alive estimates obtained for Herring Bay (previously oiled; 46 otters/100 km) and Jackpot Bay (nonoiled; 26 otters/100 km) in 1997 after river otters had recovered from the effects of the *Exxon Valdez* oil spill (Bowyer et al., 2003). June estimates were used because our sampling occurred mostly in that month, and seasonal fluctuations in density estimates were reported by Testa et al. (1994). Calculations of shoreline length were obtained for each of our study areas with ARC/INFO/GIS (ESRI). Percentages of otters captured and radiotagged in each area were then calculated by dividing the number of animals captured (or radiotagged) in each study area by the minimum and maximum population estimates (Table 1).

### DNA laboratory procedures

DNA was extracted from frozen blood samples from 110 individual otters because one sample was incorrectly preserved and failed to yield DNA. Extraction was done by using a modification of a protocol described by Groves and Shields (1997). By using a library of nine polymorphic microsatellite loci (seven tetranucleotide markers—701, 715, 733, 782, 801, 818 and 829, developed for *Lutra lutra* [Dallas and Piernney, 1998; Dallas J, personal communication]—and two dinucleotide markers—Mvis075 and Mer022, developed for *Mustela vison* and *M. erminea* [Fleming et al., 1999]), we were able to obtain individual microsatellite fingerprints for each of the river otters studied. Amplifications of DNA microsatellites were done in a GeneAmp PCR System 9600 (Perkin-Elmer) thermocycler and resolved on an ABI 373S Automated Sequencer with GS350 TAMRA run as an internal size standard in each lane. Alleles were sized in base pairs and

**Table 1**  
**Estimates of density and percent of river otters captured and radiotagged in each study area in Prince William Sound, Alaska, USA, from 1996–1998**

Variable	Jackpot Bay	Herring Bay	Eleanor Island
Shoreline length (km)	172.8	138.6	88.0
No. of males captured	20	25	7
No. of males radiotagged	17	16	7
No. of females captured	11	14	2
No. of females radiotagged	8	5	2
Estimated no. of individuals in area based on minimum no. alive in 1997 (Bowyer et al., 2003)	45	64	23
Percentage captured	69.0	61.2	39.3
Percentage radiotagged	55.6	48.6	39.3
Estimated no. of individuals in area based on lower 95% CI (28 otters/100 km; Testa et al., 1994)	48	39	25
Percentage captured	64.1	100	36.5
Percentage radiotagged	51.7	54.1	36.5
Estimated no. of individuals in area based on upper 95% CI (60 otters/100 km; Testa et al., 1994)	104	83	53
Percentage captured	29.9	46.9	17.1
Percentage radiotagged	24.1	25.3	17.1

Estimates are based on upper and lower confidence intervals (CIs) for estimates of mean density of river otters in Prince William Sound in June 1990 (Testa et al., 1994) and minimum number alive estimates for 1997 (Bowyer et al., 2003).

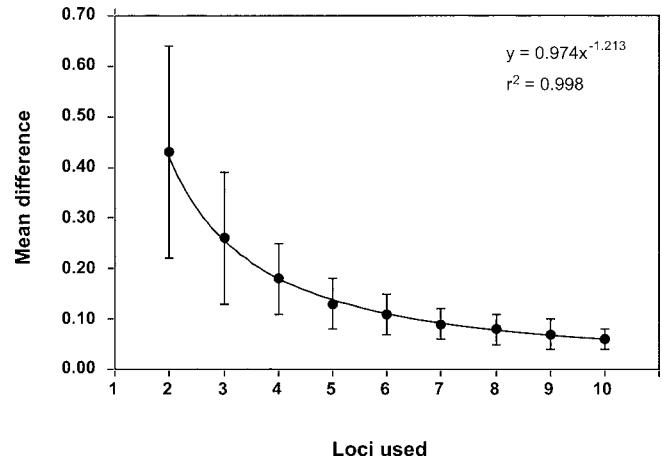
analyzed by using ABI GeneScan 3.1 and Genotyper 2.1 software (Blundell et al. 2002b).

## Data analysis

### Definition of sociality, groups, and association

Composition of otter social groups is dynamic (i.e., the same individuals do not always occur in the same groups; Blundell et al., 2002a,b); therefore, an assessment of frequency of association was not possible with respect to entire social groups. Instead of defining groups, we explored social interactions among otter dyads. We defined association as the occurrence of one otter in the same spatial location as another at the same time. Based on this definition we calculated the relative frequency ( $f$ ) of association—number of times individual  $i$  occurred with individual  $j$  divided by the total number of times individual  $i$  was located ( $f_{ij}/f_i$ ). In each study area (Table 1), we termed “associates” as any two animals that were observed at the same location (i.e., distance less than the 50-m radiotelemetry error; Bowyer et al., 2003) at the same time. Nonassociates were individuals that were never detected at the same location at the same time. Because our study areas were less than 175 km in shoreline length and home ranges of otters average 20–40 km in length (Bowyer et al., 2003), we assumed that all otters within each study area had the opportunity to interact with each other.

Because otter groups were dynamic, we also used an index of dynamic interactions (Kenward and Hodder, 1996; Kenward et al., 1993). In this metric the spatial proximity between every pair of otters through time is calculated in relation to the expected spatial distribution of locations at random. This index of association results in values ranging from  $-1$  (avoidance) to



**Figure 1**  
 A nonlinear regression between number of loci used and difference in coefficient of relatedness ( $R$ ) for river otters captured in Prince William Sound, Alaska, USA, from 1996–1998. The regression explained 99.8% of the variance ( $F_{1,7} = 3166.7$ ,  $p < .0001$ ). Error bars are standard deviation.

1 (attraction), of individuals in each dyad (RANGES V software; Kenward and Hodder, 1996; Kenward et al., 1993).

Otters were defined as solitary (or nonsocial) if they had a value of 0% relative association and a negative value of dynamic interaction with every other otter within their study area. Although this is probably a conservative definition, we elected to use it because we could not be certain that a radiotagged animal did not associate with unmarked individuals. The degree of sociality in those otters that associated with other individuals was calculated as the percentage of locations in which an otter was located with at least one more individual.

### Genetic relatedness

The coefficient of relatedness ( $R$ ) between otter dyads was calculated with program Kinship (version 1.2; Goodnight et al., 1994; Queller and Goodnight, 1989; Queller et al., 1993). Similar analyses also were performed substituting log-likelihood values for coefficient of relatedness to determine whether results differed between those two measures. The trends obtained by using  $R$  or log-likelihood did not differ; thus, only  $R$  values are reported.

To ascertain that sufficient loci were used to effectively assess relatedness, the degree of resolution in  $R$  obtained with each additional locus was determined (Girman et al., 1997). The Queller and Goodnight relatedness index ( $R$ ) changed by only 0.003 (4.3%) after nine loci (Figure 1). Therefore, inclusion of additional loci beyond the nine that were used would not improve estimates of relatedness.

The distribution of  $R$  values among all otters for which we had genetic data ( $n = 110$ ) was evaluated, without respect to sociality, to determine the overall degree of relatedness of river otters among and within populations. In addition, average relatedness was determined, independently, for otters residing in each area that had radiotagged individuals (Herring and Jackpot bays, and Eleanor Island). Relatedness was compared among telemetered populations with a one-way ANOVA. Because that analysis included numerous comparisons of  $R$  values between pairs of otters, resulting in data that were not independent, randomizations similar to Monte-Carlo simulations were conducted to minimize that bias (Manly, 1991). Code for ANOVA by randomization was written in S-Plus for Windows (version 4.5).

#### *Association and relatedness*

To test whether kinship, kin avoidance, or ecological forces independent of kinship shape group living in otters, we determined the average relatedness of animals with which a telemetered otter associated (i.e., associates), and average relatedness of otters with which a telemetered individual did not associate (i.e., nonassociates) within each of the three study areas (Table 1). Sociality of river otters was analyzed in yearly increments because in PWS group composition changes seasonally and among years, as a result of varying ecological or reproductive conditions (Blundell et al., 2002a,b). To determine whether sex, area, or year influenced group composition, a three-way ANOVA by randomization was conducted to compare average relatedness of an otter to its associates and nonassociates. Because power to detect differences among areas and between sexes was low, separate one-way ANOVAs by randomization also were conducted for each sex to compare the average relatedness of associates and nonassociates among areas. Finally, a paired *t* test by randomization was conducted to assess whether the relatedness of otters with which an individual associated differed from the average relatedness of animals with which it did not associate. Appropriate power calculations were conducted for non-significant *p* values for all statistical analyses (Zar, 1994).

#### *Association and relatedness of otter dyads*

We assessed dyad interactions with four different indices of association: (1) relative frequency (*f*) of association, (2) dynamic interactions, (3) overlap of 95% home ranges obtained with fixed kernel analyses and the reference smoothing parameter (Blundell et al., 2001; RANGES V software; Kenward and Hodder, 1996), and (4) overlap of 50% home ranges obtained with fixed kernel analyses and least-squares cross-validation (LSCV) smoothing (Blundell et al., 2001; RANGES V software; Kenward and Hodder, 1996). Although the overlap of home ranges may not indicate social association, in Eurasian otters (*Lutra lutra*) inhabiting marine habitats, females who forage individually defend a group territory (Kruuk, 1995). In that system, Kruuk (1995) observed that related females had overlapping home ranges that were defended by all members against outsiders through scent marking behavior. By evaluating several measures of association derived in different manners, potential for bias was reduced, thereby increasing confidence in our conclusions.

To test whether otters that were closely associated with each other were also close kin, we used Mantel tests (Lugon-Moulin et al., 1999; Manly, 1991; Smouse et al., 1986) to compare matrices of association indices with degree of relatedness (*R*), with Multreg software (available from J. Goudet). Matrices of home-range overlap, dynamic interactions, and relative frequency of association between dyads were individually correlated with a matrix of the coefficient of relatedness between dyads. A total of 10,000 randomizations were conducted at each comparison.

#### *Sociality and relatedness*

In the event that otters that spent more time in social groups were more likely to associate with related individuals, and solitary otters lived alone because they had no relatives in the population with which to socialize, analyses were performed assessing average relatedness by degrees of sociality. Degree of sociality was categorized similar to that presented by Blundell et al. (2002a) as solitary, low sociality (up to 10% of locations the animal was found with at least one other individual), moderate sociality (11–50% of locations are social), and highly social (more than 50%). Relatedness of each social otter to all telemetered otters in their respective population was assessed

with a one-way ANOVA by randomization, comparing mean relatedness for otters in each category of sociality. That analysis, however, did not indicate the degree of sociality and relatedness among individuals with which an otter interacted. Accordingly, relatedness of associates also was assessed with a one-way ANOVA by randomization, comparing average relatedness of associates in the low, medium, and high categories of sociality (Blundell et al., 2002a).

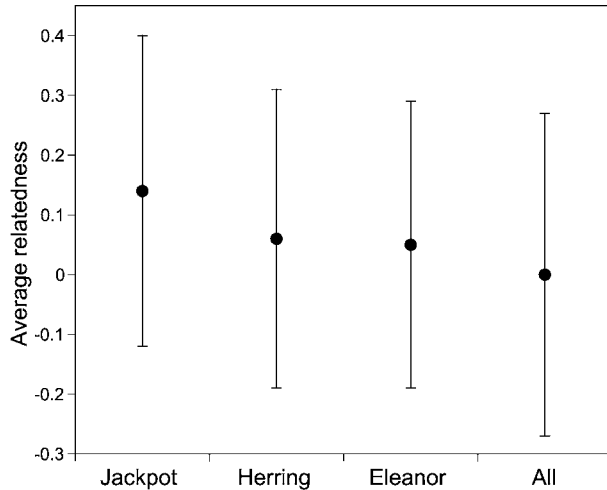
#### *Parentage*

Parentage was assigned with CERVUS software (Marshall et al., 1998; Slate et al., 2000), which uses a likelihood model and Monte-Carlo simulations to assess multiple candidate parents. In the present study, there were no known parent-offspring relationships; consequently, parentage was determined based upon the most likely assignment of offspring to candidate parents. Only those otters that were obviously young were considered as potential offspring. River otters are relatively long-lived (13 years in the wild; Docktor et al., 1987) and most reproduce as 2-year-olds (Docktor et al., 1987; Hamilton and Eadie, 1964); thus, our approach likely excluded some adults from the analysis that may have been offspring of other resident adults. Because we had only crude estimates of age for most otters we captured, we could not reliably distinguish between ages of adults with sufficient accuracy to determine that potential parents were at least 2–3 years older than potential offspring. Therefore, we chose a conservative route, assigning parentage only for those otters that were too young to be parents and considering all other otters as potential parents. Because our samples were heavily male biased (*n* = 75 male otters, *n* = 35 females), candidate fathers were assessed before evaluating candidate mothers.

To determine whether association with a group had a reproductive benefit, the relation between otter sociality (i.e., average percentage of locations that were social for each otter; Blundell et al., 2002a) and number of putative offspring identified for each individual was evaluated for each sex separately. Because there were several years of telemetry data for some individuals, and the extent of sociality varied among years, the average sociality among years was calculated for each otter. The correlation (Spearman's  $\rho$ ) between average sociality and number of offspring was assessed because identifying which year of social data might pertain to the putative offspring identified was not possible. In addition, to assess whether group size influenced reproductive success for males, the correlation of number of offspring and average group size for each social otter was determined with SPSS for Windows (version 7.0; SPSS, 1995).

#### *Number of relatives in the population*

The mean proportion of individuals related to each otter at increasing levels of relatedness (*R*) was used to determine whether number of relatives in the population differed between social and nonsocial otters. We used standard subdivisions of *R* values (Avise, 1994; Hartl and Clark, 1997) to divide our relatedness index into six discrete categories ( $R < .009$ , .01–.124, .125–.24, .25–.49, .5–.69,  $> .7$ ) in a manner similar to that of Kapsalis and Berman (1996). We did not have genetic samples from a reference group of otters of known relationships with which to calibrate the relatedness coefficient (de Ruiter and Geffen, 1998; Girman et al., 1997). Therefore, we do not suggest that an *R* value of .5 necessarily implies a full sibling or parent-offspring relationship (Avise, 1994; Hartl and Clark, 1997), only that increasing *R* values indicate increasing degrees of relatedness (i.e., constitute a relatedness index). The proportion of individuals (i.e., number of individuals per relatedness category/total number



**Figure 2**  
Coefficient of relatedness (mean  $R \pm SD$ ) for all river otters captured in Jackpot Bay ( $n = 31$ ), Herring Bay ( $n = 39$ ), and Eleanor Island ( $n = 9$  otters) and the  $R$ -value for all otters captured in the present study (seven areas,  $n = 110$  individuals). Error bars are standard deviation. Average relatedness differed among telemetered populations ( $F_{2,2473} = 32.3$ ,  $p < .001$  ANOVA by randomization); otters residing in the Jackpot Bay area were more highly related ( $p = .02$  Scheffe post hoc comparisons) than were otters in Herring Bay or Eleanor Island, which did not differ in average relatedness ( $p = .9$  Scheffe).

of individuals sampled in the population) was calculated to adjust for differences in sampling density for each area.

To test whether sociality increased the reproductive success of relatives (i.e., social otters will have a higher proportion of related individuals in the population), we used a two-way ANOVA by randomization to compare social and nonsocial otters with respect to the proportion of related individuals occurring in each category of relatedness. That analysis was conducted twice: to assess the number of relatives for each otter among otters in the population in which the telemetered individual resided; and among all otters for which we had genetic data, to allow for dispersal of related individuals.

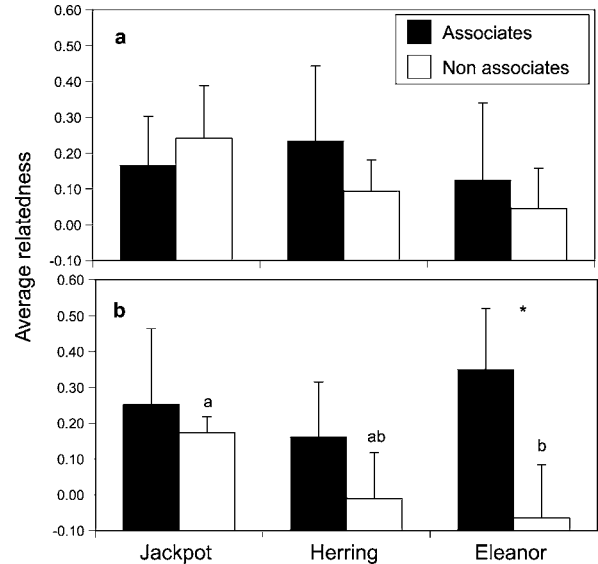
#### Effects of age and size on sociality and reproductive success

A one-way ANOVA was used to determine whether percentage of social locations differed between age classes (young adult, adult, and older adult) for both sexes, and a chi-square analysis was performed to assess whether sociality (i.e., social or nonsocial) differed by age class. To determine whether social organization in male otters was associated with sexual selection for larger males, multivariate analysis of variance (MANOVA; SPSS 7.0) was conducted to evaluate differences in morphological characters (weight, body length, weight to total length ratio, baculum length, and testicle width) between social and nonsocial male otters considered as candidate parents. To determine whether larger males had higher reproductive success, we used a multiple linear-regression with size parameters as independent variables entered simultaneously and number of offspring per individual (square-root transformed) as the dependent variable.

## RESULTS

### Sampling density

A greater percentage of otters was captured in Herring Bay (46.9–100%) and Jackpot Bay (29.9–69%) compared with Eleanor Island (17.1–39.3%) (Table 1). Similarly, the propor-



**Figure 3**  
Average relatedness (mean  $R \pm SD$ ) of radiotagged otters in Prince William Sound, Alaska, USA (1996–1999) to river otters with which they associated (i.e., associates) and with which they did not associate (i.e., nonassociates). There was no difference for any analysis of relatedness of associates or nonassociates for male otters (a), but the relatedness of female otters (b) differed by area for nonassociates. Different letters indicate significant differences between areas. An asterisk represents a difference between associates and nonassociates.

tion of the estimated density of otters that were radiotagged in Herring Bay (25.3–54.1%) and Jackpot Bay (24.1–55.6%) were greater compared with Eleanor Island (17.1–39.3%) (Table 1). These differences in sampling densities reflect the lower trapping effort in Eleanor Island. In that area, trapping occurred only in 1998 compared with trapping in 1996 and 1997 in Jackpot Bay and 1996–1998 in Herring Bay. The trapping effort in Eleanor Island resulted in the capture of nine individuals (Table 1), and therefore, results from this area should be interpreted with caution.

### Genetic relatedness

Relatedness among river otters was generally low and the average  $R$  value was higher within telemetered populations than among all otters for which genetic data were available (Figure 2). Average relatedness differed among telemetered populations; otters residing in the Jackpot Bay area were more highly related than were otters in Herring Bay or Eleanor Island (Figure 2).

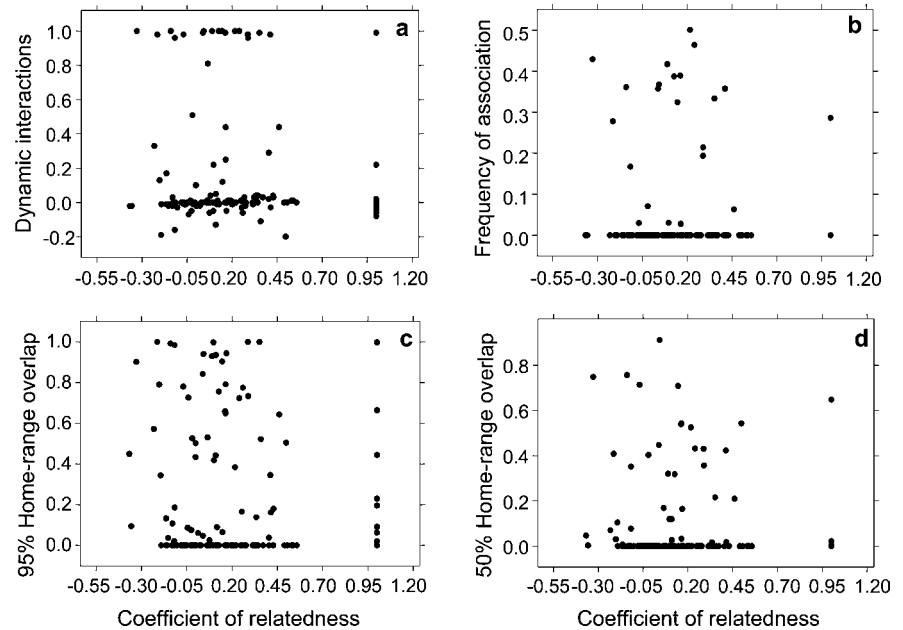
### Association and relatedness

A three-way ANOVA by randomization detected no difference among areas ( $F_{2,64} = 0.10$ ,  $p = .91$ ), among years ( $F_{3,64} = 0.35$ ,  $p = .79$ ), or between sexes ( $F_{1,64} = 1.9$ ,  $p = .18$ ) in the average relatedness of associates (Figure 3). There was a significant difference in mean relatedness of nonassociates among areas ( $F_{2,64} = 3.3$ ,  $p = .04$ ) (Figure 3), but not among years ( $F_{3,64} = 0.39$ ,  $p = .75$ ) or between sexes ( $F_{1,64} = 0.02$ ,  $p = .9$ ).

In separate analyses by sex, no difference among areas occurred in average relatedness of associates ( $F_{2,56} = 0.64$ ,  $p = .52$  ANOVA by randomization) or nonassociates ( $F_{2,56} = 1.39$ ,  $p = .26$  ANOVA by randomization) for male river otters (Figure 3). Similarly, there was no difference among areas in mean relatedness of otters that females associated with ( $F_{2,9} = 0.96$ ,  $p = .46$  ANOVA by randomization), but a difference was

**Figure 4**

Relation between relatedness ( $R$ ) and indices of association for otter dyads for Herring Bay ( $n = 17$  otters), Prince William Sound, Alaska, USA, in 1998. (a) Dynamic interactions indicate proximity of temporal-spatial locations; negative values indicate avoidance, zero indicates not different from random, and increasing positive values indicate more time spent in association (1 = always together). (b) Frequency of association is a relative measure of the number of times otter  $i$  was located with otter  $j$  divided by total number of locations for otter  $i$  ( $f_{ij}/f_i$ ). The percentage of overlap of 95% (c) and 50% (d) home ranges indicate the spatial relationship of otters. There was no correlation between relatedness and any index of association in any year or study area. As an example, data from Herring Bay, 1998, are shown here because a larger number of otters in that year offered greater potential of demonstrating any correlation between relatedness and indices of association.



detected among areas in average relatedness of nonassociates ( $F_{2,9} = 7.2$ ,  $p = .02$  ANOVA by randomization) (Figure 3). Mean relatedness of nonassociates for females was similar between Eleanor Island and Herring Bay ( $p = .7$ , post hoc Scheffe), and between Herring and Jackpot bays ( $p = .07$ , post hoc Scheffe), but Jackpot Bay and Eleanor Island differed ( $p = .01$ , post hoc Scheffe) (Figure 3). A paired comparison, by individual, of mean relatedness of associates compared with nonassociates noted no difference for male otters ( $t_{32} = 1.8$ ,  $P = .08$ ) (Figure 3); power to detect a difference was high (power = 0.91). For female otters, mean relatedness of associates differed from that of nonassociates ( $t_9 = 2.6$ ,  $P = .03$ ); but nonassociates were less related than were associates only at Eleanor Island (Figure 3).

#### Association and relatedness of otter dyads

Degree of relatedness within pairs of individuals did not affect spatial or temporal interactions. There was no correlation between any of the association indices and genetic relatedness (Figure 4). There was variation among study areas and years, but randomization probabilities for all indices ranged from 0.15–1.0 and the highest  $r^2$  equaled .08.

#### Sociality and relatedness

Degree of sociality did not have an effect on whether an otter was more likely to socialize with relatives (Figure 5). When mean coefficient of relatedness of otters in each category of sociality (none, low, moderate, and high) was compared among all telemetered otters in the resident population, there was no difference in the mean relatedness among otters with which an individual had the potential of associating (Figure 5a). Similarly, when mean relatedness of only those individuals with which otters actually associated was evaluated, there

also was no difference in level of relatedness among categories of sociality (Figure 5b).

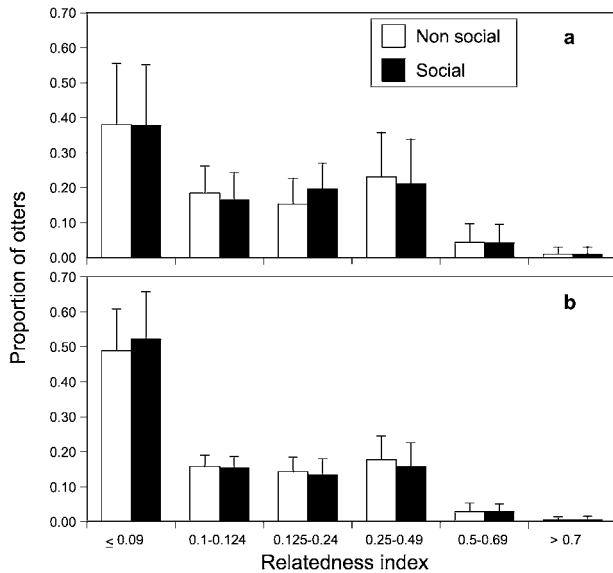
#### Parentage

Parentage was assigned for all 53 young otters. LOD scores (logarithm of the likelihood ratio) ranged from 0.79–8.03 (mean = 3.2, SD = 1.5). Delta values (difference in LOD scores between most likely and second most likely parent) ranged from 0.34–5.35 (mean = 1.75, SD = 1.34). A total of 67.3% of parent-offspring trios were assigned at 95% confidence level, and additional 32.7% were assigned with 80% confidence. Offspring were assigned for 29 of 35 males and 20 of 22 adult females. Twenty-one candidate fathers and 12 candidate mothers were radiotagged individuals. There was no correlation between number of putative offspring and proportion of locations spent social for either sex (Figure 6). Similarly, there was no correlation ( $r_s = .31$ ,  $p = .17$ , Spearman's  $\rho$ ) between number of offspring and average group size among telemetered male otters considered as candidate parents (overall mean group size mean = 2.9, SD = 1.1).

#### Number of relatives in the population

The mean proportion of relatives in each relatedness category did not differ among resident populations between social and nonsocial otters (Figure 7a). Similarly, there was no difference between social and nonsocial otters in mean proportion of relatives in each relatedness category among all otters for which we had genetic data (Figure 7b), indicating that association with a group conferred no advantage with respect to number of relatives. Independent of sociality, the proportion of relatives occurring in each category of relatedness was significantly different for both analyses (i.e., most otters were not related) (Figure 7).





**Figure 7**  
Mean proportion ( $\pm$ SD) of relatives in each relatedness category, between social and nonsocial otters, among resident populations (a) and among all populations (b). There was no difference in mean proportion of relatives per category between social and nonsocial otters in resident populations ( $F_{1,635} = 0.0006$ ,  $p = .99$ , ANOVA by randomization) (a), or among all populations ( $F_{1,641} = 0.0015$ ,  $p = .97$ , ANOVA by randomization) (b), but the proportion of relatives in each category of relatedness was significantly different for both analyses ( $F_{5,635} = 152.0$ ,  $p < .001$ ) (a and b).

season of up to 25 km beyond the boundaries of their normal home ranges (Blundell et al., 2000b). When considering the average length of shoreline that constitutes the home ranges of otters in our area (12–16 km for females; 35–40 km for males; Bowyer et al., 2003), it seems that dispersal distances, especially for males, are short. Given that males in this population are more likely to be social than are females, and males dispersed short distances, it is unlikely that the low degree of relatedness among group members is a by-product of dispersal patterns.

Our results indicated no obvious cost or benefit to sociality in terms of reproductive success. Group size and percentage of sociality (Figure 6) were unrelated to number of putative offspring, and social and nonsocial animals appeared to have similar number of relatives in the population (Figure 7). In contrast to many studies in which larger males had greater reproductive success (Cooper and Vitt, 1993; Haley et al., 1994; Lewis et al., 2000; Weatherhead and Boag, 1995), in our system, body size had no apparent bearing on number of offspring produced by male river otters (Table 2). In addition, size and age had little influence on whether an otter was social or solitary.

We expected that sexual selection would influence reproductive success of individuals, likely masking the potential benefits of sociality. In other words, if solitary males were larger they would have been able to obtain reproductive opportunities without the aid of cooperation from group members. This would have reduced our ability to detect differences in number of offspring between social and nonsocial males. That solitary males were not older or larger than social males, and there was no relation between male body size and number of offspring, suggests that size and age were not the cause for the lack of relation between sociality and reproductive success. Clutton-Brock (1988) concluded,

**Table 2**

**A comparison of morphological and reproductive features among male river otters in Prince William Sound, Alaska, USA, with respect to sociality**

Variables	Social ( $n = 14$ )	Nonsocial ( $n = 7$ )
Body length (mm)	812.1 $\pm$ 47.6	842.7 $\pm$ 44.0
Weight (kg)	9.6 $\pm$ 0.8	10.6 $\pm$ 0.6
Weight/length ratio (weight/total length $\times$ 1000)	7.3 $\pm$ 0.6	7.8 $\pm$ 0.5
Testicle width (mm)	53.8 $\pm$ 6.3	53.0 $\pm$ 5.4
Baculum (mm)	118.6 $\pm$ 14.3	120.7 $\pm$ 11.4
Number of offspring	1.9 $\pm$ 1.3	1.3 $\pm$ 1.1

Values are mean  $\pm$  SD. Overall model  $p$  value for the MANOVA assessing sociality and morphological characters was not significant ( $p = .35$ ). Otters included in this analysis were adult males considered as candidate parents.

however, that phenotypic characters such as size are unlikely to be the sole factors determining mating success. Therefore, it is possible that other attributes of males, as yet unidentified, could have influenced reproductive success among coastal river otters. The relation between reproductive success and male attributes such as foraging efficiency or rates of scent-marking behavior merit further investigation.

How can we explain the occurrence of sociality in coastal river otters? Blundell et al. (2002a) suggested that benefits of group association for otters in PWS included cooperative foraging to increase individual capture success when preying upon schooling pelagic fishes. Large schools of pelagic fishes enter the nearshore system, in which otters forage (Ben-David et al., 1996; Bowyer et al., 1994), after the cessation of the mating season (Blundell et al., 2002a). When available in the nearshore environment, pelagic fishes aggregate in such abundance (Brown et al., 1999; Groot and Margolis, 1991; Maniscalco et al., 1998) that intraspecific competition is nil because rich patches of prey cannot be exploited in a single feeding (Blundell et al., 2002a). Although a group of predators may work together to contain a school of fishes (Norris and Schilt, 1988), each group member forages as an individual, capturing its own prey (Packer, 1988). Such low local competition does not require kin avoidance, despite short-range dispersal in males (West et al. 2002). Also, because sociality conferred no reproductive costs to otters, association with kin for cooperative foraging on high-quality food was not imperative, and thus, there is no selection pressure for formation of kin-based groups.

Moreover, timing of prey availability further eliminates the need for kin-based social groups among male otters. Schooling pelagic fishes usually arrive in the nearshore environment at the end of the otter mating-season (Blundell et al., 2002a). Several male otters have been observed to leave social groups for the duration of the mating season, later rejoining the group before the arrival of pelagic fishes (Blundell et al., 2002a,b). Female river otters likely have fewer opportunities to take advantage of cooperative foraging because they attend to altricial offspring during the availability of schooling fishes (Blundell et al., 2002a). Nonreproductive females joined male groups during that time (Blundell et al., 2002a), providing further support for the conclusion that group formation in coastal river otters is driven by the benefits of cooperative foraging on a seasonally available high-quality food.

The occurrence of solitary males among coastal river otters remains a mystery, however. If sociality results in a better-

quality diet and does not have a cost in terms of reproductive success, we would expect all males to be social (Blundell et al., 2002a). This is especially true given the observation that unlike Eurasian otters (Kruuk, 1995), male river otters in PWS are not territorial (Ben-David M, Blundell GM, Kern JW, Maier JAK, Brown ED, Jewett SC, in preparation). Our data and the observations on captive male river otters (Hansen H, Ben-David M, Groves P, Maier JAK, in preparation) indicate that two behavioral strategies occur among wild coastal otters. Animals belonging to the first strategy join social groups that cooperatively forage on pelagic fishes. Animals of the alternative strategy are those that lead a solitary life and forage on intertidal/demersal fishes (Blundell et al., 2002a).

High intraspecific variation in sociality occurs in numerous vertebrate species (Lott, 1991). Such variation usually arises because of different ecological conditions, demography, or strategies of conspecifics (Hofer and East, 1993; Lott, 1991; Zabel and Taggart, 1989). Nonetheless, to the best of our knowledge, the occurrence of two parallel social strategies in the same population under the same ecological conditions is not common. One of few examples for such phenomenon is the multiple behavioral strategies related to dietary preferences in killer whales (*Orcinus orca*: Saulitis et al., 2000). In river otters, animals adopting either foraging strategy have similar body size and weight (Table 2), and comparable reproductive success (Figure 6). Thus, both strategies can persist in the population. This behavioral model implies that the prevalence of each strategy will fluctuate through time in relation to the abundance and distribution of schooling fishes.

In conclusion, our data lead to the rejection of the hypothesis that otter social groups are kin based. In addition, we found no indication for kin avoidance, as would be expected from low dispersal and high local competition. Sociality conferred no reproductive costs or benefits to otters because number of offspring and number of relatives in the population did not differ between social and solitary animals. In this population, association with kin for cooperative foraging on high-quality food was not imperative, and thus there is no selection pressure for formation or maintenance of kin-based groups. The prediction that the degree of sociality in this population will fluctuate relative to the abundance of schooling pelagic fishes merits further investigation.

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