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Sociality in river otters: cooperative foraging or reproductive strategies?

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We evaluated factors influencing social organization in coastal river otters (*Lontra canadensis*) to test two hypotheses: group formation is an antipredation strategy, or, alternatively, group information is related to cooperative foraging. Data on group size, group composition, and sociality were obtained through radiotracking 55 otters in Prince William Sound, Alaska, USA, from 1996 through 1998. For males, larger groups occurred after the mating season and concurrent with availability of schooling pelagic fishes. Stable isotope analysis revealed that otters social in >10% of their locations had diets significantly higher in rapidly swimming pelagic fishes than did less social otters, regardless of gender. In addition, otters that were more social had significantly smaller home ranges than did less social otters, an observation consistent with increased foraging efficiency through cooperative foraging. Discounting associations of females with young of the year, approximately 47% of females and only 24% of males were asocial. Among social otters, males were social in 46% of their locations and 63% of that time occurred in all-male groups. Females were only social in 26% of locations and were in mixed-sex groups 78% of that time. We hypothesize that the time-consuming task of raising offspring prevents females from joining foraging groups. When not raising young, females may join males to cooperatively forage for better-quality prey (pelagic fishes), which would be more difficult to acquire as a solitary forager. *Key words:* Alaska, *Lontra canadensis,* predation risk, river otters, schooling pelagic fishes, sexual dietary partitioning, sexual dimorphism, social organization, stable isotopes. *[Behav Ecol 13:134–141 (2002)]*

Avoidance of predators and successful acquisition of food have been proposed as two main hypotheses for formation of social groups (Alexander, 1974; Gittleman, 1989; Wrangham and Rubenstein, 1986). Ecological and behavioral constraints may affect the genders differently, however, because of dissimilarity in reproductive strategies (Bleich et al., 1997). To understand the evolution of social organization, social relationships and reproductive status of individuals should be considered independently for each gender (Wrangham and Rubenstein, 1986).

Mustelids are among the least social carnivores (Gittleman, 1989), but considerable variation occurs among Lutrinae. Otter social behavior includes solitary individuals (*Lutra lutra* in marine environments; Kruuk and Moorhouse, 1991), monogamous pairs (*Lontra felina*; Ostfeld et al., 1989), ''family parties'' (*Lutra maculicollis;* Proctor, 1963:101) family groups with solitary males (*Lontra canadensis* in a freshwater system; Melquist and Hornocker, 1983), male groups (*Aonyx capensis*; Arden-Clarke 1986), and mixed-gender groups (*Pteronura brasiliensis*; Duplaix, 1980).

Coastal river otters (*L. canadensis*) in Prince William Sound (PWS), Alaska, USA, exhibit high variability in social organization. Recent studies documented the occurrence of solitary individuals (Blundell et al., 2000), as well as large groups of up to 18 individuals (Blundell et al., 2000; Rock et al., 1994; Testa et al., 1994). In addition, scent marking at communal latrines (Ben-David et al., 1998; Bowyer et al., 1995; Testa et al., 1994) and helping behavior have been reported in this population (Rock et al., 1994). In the present study, we explored hypotheses to explain sociality in coastal *L. canadensis.*

In PWS, river otters have access to two major types of prey: schooling pelagic fishes are available seasonally (Ben-David et al., 1998; Brown et al., 1999; Dean et al., 2000) and have high energy density. Alternatively, intertidal-demersal organisms such as Cottidae, Hexagrammidae, and crustaceans are easier to capture but are lower in quality (Anthony et al., 2000; Bowyer et al., 1994). Formation of groups and cooperative foraging (or ''by-product mutualism''; Connor, 1986) among aquatic predators may increase individual capture success of schooling fishes (Baird and Dill, 1995, Götmark et al., 1986; Norris and Schilt, 1988). Under such conditions, we predict that more social otters would have diets higher in better quality pelagic fishes, compared with otters that exhibit low levels of sociality. Further, we hypothesize that if sociality enhances foraging success, group size will change seasonally, tracking the seasonal changes in availability of schooling pelagic fishes in the nearshore environment. In addition, increased foraging efficiency as a result of cooperative foraging should be negatively related to home range or territory size (Herrman, 1994; Woodroffe and MacDonald, 1993), and we predict that otters exhibiting higher degrees of sociality will have smaller home ranges.

Alternatively, otters inhabiting marine environments occupy a long, narrow stretch at the marine–terrestrial interface (Arden-Clarke, 1986; Blundell et al., 2001; Bowyer et al, 1995; Kruuk and Moorhouse, 1991) that may be difficult to defend (Kruuk, 1989). If so, formation of large groups may facilitate the defense of group territories. Under such conditions, we predict that social otters would have larger home ranges compared with less social animals.

Hypotheses for explaining sociality in coastal river otters also can be derived from the different ecological constraints and reproductive strategies of genders. Sexual dimorphism (Moors, 1980) may afford larger male otters superior swimming abilities (Fish, 1994), facilitating the capture of rapidly swimming prey. Under such conditions, we hypothesize that diets of males would be composed of more pelagic fishes than would diets of females.

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Differences between genders in reproductive strategies (Wrangham and Rubenstein, 1986) also may influence degree of sociality in river otters. Male–male competition for reproductive opportunities likely would be the main constraint on sociality and cooperative foraging for male otters (Le Boeuf and Reiter, 1988) because *L. canadensis* males do not participate in rearing offspring (Melquist and Hornocker, 1983; Rock et al., 1994). Nonetheless, the short mating season in Alaska (~1 month; Blundell GM, personal observation; Woolington, 1984), will influence sociality in males for only a brief period. In contrast, females spend much of the year raising young and are spatially restricted in their movements during that time (Noll, 1988), and females with offspring may avoid foraging in mixed-gender groups because of the risk of infanticide (Alcock, 1993; Packer and Pusey, 1984; Kruuk H, personal communication, for infanticide in *L. lutra*). Thus, we hypothesize that males will spend more time in social groups than females, and male group size will decrease before and during mating season. Alternatively, formation of male coalitions may increase male reproductive success (Packer et al., 1991; Witt et al., 1981). Under such conditions, we would expect group size for males to increase or remain large during the mating season.

Many of the hypotheses we discuss are not mutually exclusive and often result in similar predictions, making critical tests difficult. Therefore, we use a weight-of-evidence approach in evaluating the importance of different ecological factors in influencing sociality in coastal river otters.

METHODS

Study areas

Our study areas are located in western Prince William Sound, Alaska, USA, spanning an area of approximately 4800 km^2. Detailed descriptions of the study areas and a map are provided in Ben-David et al. (1998) and Bowyer et al. (1995). Fieldwork was conducted in 1996 and 1997 in Jackpot, Ewan, and Paddy bays along Dangerous Passage (60°20′ N, 148°10′ W), and in Herring Bay and surrounding areas on northern Knight Island (60°23′ N, 147°40′ W). In 1998, our study areas included Herring Bay, Eleanor Island (60°32′ N, 147°37′ W), Esther Passage (60°53′ N, 147°55′ W), Unakwik Inlet (60°55′ N, 147°30′ W), Wells Bay (60°55′ N, 147°20′ W), and Naked Island (60°40′ N, 147°25′ W).

Live capture of otters

We live-captured 111 individual river otters from May through July in 1996 and 1997, and from mid-April through May in 1998, with no. 11 Sleepy Creek double-jaw leg-hold traps or with Hancock traps (Blundell et al., 1999). A subset of otters ($n = 55$) from three of our study areas (Dangerous Passage, northern Knight Island, and Eleanor Island) were equipped with radiotransmitters (Blundell et al., 2000). Further details on capture and handling are provided in Blundell et al. (1999). All methods used in this research were approved by the Institutional Animal Care and Use Committee at University of Alaska-Fairbanks and adhere to the Animal Behavior Society/Association for the Study of Animal Behavior guidelines for ethical treatment of animals.

Radiotelemetry and sociality

Radiotracking was conducted either from a boat (1996), or from a small, fixed-wing aircraft (1997–1998). Tracking by boat occurred 2–3 times/week in July and August. Aerial tracking occurred approximately every 4 days from mid-April through mid-June to monitor shifts in activity around the mating season. Thereafter, tracking was conducted weekly until September and every 2–3 weeks during winter. We radiotracked 12 otters in 1996 (mean = 19.7 locations per otter, SE = 1.4), 18 otters in 1997 (mean = 25.5 locations, SE = 1.0), and 34 otters in 1998 (mean = 25.4 locations, SE = 1.4) over periods ranging from 41 to 994 days (mean = 416 days, SE = 37). Further details regarding collection of telemetry data are provided in Blundell et al. (2000).

Once a telemetered otter was located, global positioning system data were obtained and the radio frequencies of all other otters scanned to determine whether other individuals were present in the same location. During visual observations, presence of unmarked animals was determined. On two occasions, group association as determined by the pilot (i.e., number and identity of radiotagged otters) was verified as accurate by an independent observer on the ground.

Radiotelemetry estimates of sociality likely represent underestimates because visual observations were infrequent and telemetered otters may have been traveling with unmarked animals. In visual sightings (83 of 1972 locations), large groups occasionally included unmarked individuals, but most small groups contained only radiotagged otters, and the occurrence of solitary individuals was confirmed. Thus our telemetry observations characterizing sociality correspond to minimum group size. Assessment of sociality in female otters does not reflect the association of a female with her offspring of that year.

Diet and morphometrics

Fur samples (under fur and guard hair) were collected from otters for diet analysis with stable isotope ratios (Ben-David et al., 1998). River otters fully shed and replaced under fur from May through August and shed and replace guard hair from August to November (Ben-David et al., 2000; Ben-David M, personal observation), allowing for an assessment of seasonal diets. Details on protocols for stable isotope analysis are provided in Ben-David et al. (1998).

We collected morphometric data from captured otters, including body mass (nearest 0.1 kg); and body length, tail length, and total length (nearest 1 mm). In 1997–1998, we also measured interdigital spread of the right hind foot to the nearest 0.1 mm. Age of otters (pup, young adult, adult, and old adult) was estimated based on body size and tooth wear and staining.

Data analyses

Group size

We determined minimum group size for otters based on telemetry and visual observations. For each otter, the total number (telemetered + unmarked, if visual observation) of otters in the group was recorded for each observation. To test whether group size varied with the availability of schooling prey for each gender, we used a two-way ANOVA (Zar, 1996), with month and gender as main effects, age as a random factor, and average group size as the dependent variable. We followed with post-hoc Scheffe multiple comparisons among months and ages. We used data on the availability of pelagic fishes from Brown et al. (1999) and Groot and Margolis (1991).

Sociality

Because some otters foraged in the freshwater system (Blundell et al., 2000), we used data only from otters located in the marine system >70% of the time. We used each year of telemetry data for each otter as an independent sample. Accordingly, 55 otters sampled across 3 years yielded 70 instances that were used for our analyses of sociality.

For each otter, we calculated proportion of social locations (occurrence with at least one additional otter). To test the null hypothesis that sociality did not differ between genders, we conducted a Kolmogorov goodness-of-fit test for continuous data (Zar, 1996). For that test, we calculated the cumulative proportion of females and males occurring at each measured percentage of social locations and the maximum difference in cumulative frequency between genders compared to a critical value for that test. For social otters, we explored gender differences in proportion of social locations with a one-way ANOVA. We also conducted a chi-square analysis to compare, by gender, the proportion of social otters that occurred in mixed-sex groups (Conover, 1980).

Diet

To determine whether isotopic signatures of intertidal-demersal fishes, pelagic fishes, and freshwater fishes differed significantly, we employed the K nearest-neighbor randomization test (Rosing et al., 1998). We used a two-way multivariate analysis of variance (MANOVA; Johnson and Wichern, 1988) with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables to compare diets of otters between season and gender.

Our sample size was smaller when stable isotopes were paired with telemetry data for each individual because only the year of spatial data that most closely corresponded to the year of dietary data was used. Consequently, we considered two categories of sociality (low $\leq 10\%$, and high $> 10\%$ social locations) for comparison of diet and sociality. We used one-way ANOVA with degree of sociality and gender as independent variables, otter as a random factor, and $\delta^{13}C$ as the dependent variable. We excluded $\delta^{15}N$ from this analysis because carbon signatures more clearly distinguish between prey groups in our system. We followed that analysis with a Wilcoxon test to determine whether seasonal changes occurred in diets of otters, for both low and high categories of sociality.

Home-range size and sociality

Home ranges were estimated with fixed-kernel analyses and the reference smoothing parameter (Blundell et al., 2001). We obtained home-range contours for 95% isopleths for each otter in each year with RANGES V (Kenward and Hodder, 1996). Because otters generally confine their movements to the shoreline, we measured kilometers of shoreline within those home-range contours (Blundell et al., 2001; Sauer et al., 1999) with the geographic information system (GIS) ARC/INFO (ESRI, Redlands, California, USA).

To test whether more social otters had smaller home ranges, we regressed home-range size on percentage of social locations, entering sociality (% social locations) as the independent variable and home-range size (km shoreline) as the dependent variable in a regression analysis. To meet assumptions of curve fitting in some regression models, we eliminated values of zero from sociality data by adding 0.01 to all measures of percent social locations. We conducted the analysis without respect to gender, assuming that within a social group both genders will experience the same conditions.

Morphometrics

To determine the degree of sexual dimorphism in our otters, we used MANOVA to compare morphometric measurements between genders and included age as a covariate to control for effects of age on size. We used the ratio of weight to total length to assess overall sexual dimorphism and compared body length, tail length, interdigital spread, and body weight between sexes.

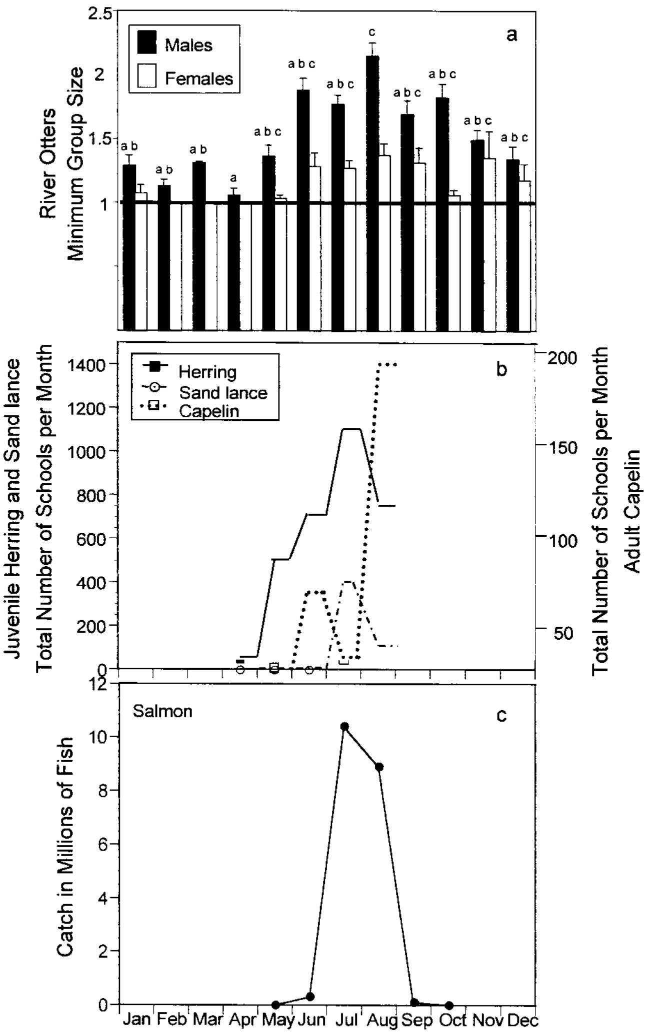

Figure 1

Mean minimum size of groups for river otters inhabiting Prince William Sound, Alaska, from 1996 to 1998 (a) in relation to availability of surface schools of pelagic fishes in the nearshore environment (b; adapted from Brown et al., 1999), and the period of salmon availability (c) in south-central Alaska and Prince William Sound (adapted from Groot and Margolis, 1991). Average minimum group size differed among months for male otters (overall model and month $p < .001$, ANOVA), but not for females (overall model $p = .13$, month $p = .18$, ANOVA). Horizontal line represents minimum possible group size (1 animal); bars indicate gender. Different letters above bars indicate significant differences among months for male otters at $\alpha = 0.05$; similarity within month clusters for males was a: $p = .11$; b: $p = .11$; c: $p = .054$ (ANOVA, Scheffe multiple comparisons).

RESULTS

Group size

Average minimum group size in all years differed among months for male but not female otters (Figure 1). Male group size corresponded to availability of pelagic fishes (Figure 1). Groups composed of up to nine individuals were sighted from late May until mid-September, whereas groups of fewer than four individuals were not observed after early September. Group size differed by age class for males ($p = .002$, ANOVA), with juveniles occurring singularly or in smaller groups more often than older animals. Group size did not differ among age classes for females ($p = .8$, ANOVA), and the interaction

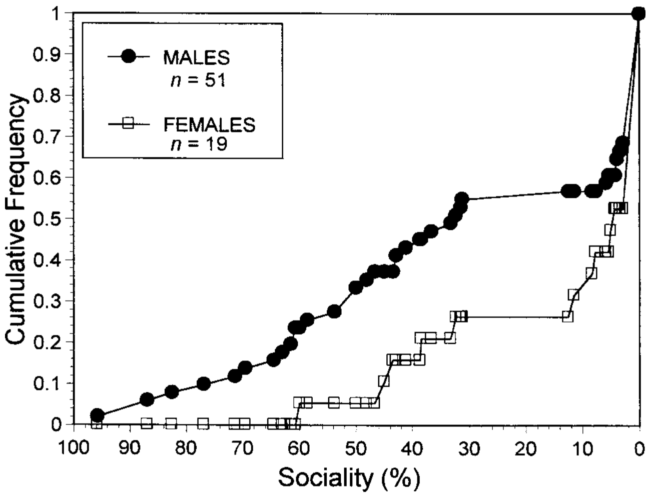

Figure 2
A comparison of the prevalence of sociality (percentage of social locations for each otter per year) in male and female coastal river otters in Prince William Sound, Alaska. For each sex, the cumulative proportion of otters as a function of decreasing sociality (i.e., percentage of social locations) is presented. A significantly larger proportion of male otters occurred in the higher ranges of percent social locations ($D_{max} = 0.3199$, $p < .001$; Kolmogorov-Smirnov goodness-of-fit test for continuous data).

between age class and month was not significant for either sex ($p > .5$, ANOVA). In the overall model, month, gender, and age were significantly different ($p < .001$, ANOVA); interactions did not differ ($p > .24$, ANOVA). Because group size differed by age class only for juvenile males and juvenile males were few (6% of 64), we did not consider effects of age in further analyses.

Sociality

Males were significantly more social than females; only 24.4% of male otters were solitary, compared with 47.4% of females. A significantly larger proportion of male otters occurred in the higher ranges of percent social locations (Figure 2; $D_{\max} = 0.3199$, $p < .001$; Kolmogorov-Smirnov goodness-of-fit test for continuous data). Approximately 55% of males were social for ≥30% of their telemetry locations each year, compared with only 26% of females (Figure 2). When only social otters were considered, male otters (mean = 45.7%, SE = 4.6%) were social for a significantly larger proportion of their locations per year compared with females (mean = 25.6%, SE = 6.5%, $p = .03$, ANOVA). Additionally, males occurred in mixed-gender groups only 37.5% of the time ($n = 32$), whereas social females were in mixed-gender groups in 77.8% of their locations ($n = 9$; $p = .003$; χ^2 test).

Diet

Herring and adult salmon and sand lance and juvenile salmon had overlapping isotopic ratios ($p = .55$, and .76, respectively; K nearest-neighbor). When pooled by groups, intertidal and demersal fishes, pelagic fishes, and freshwater fishes all had significantly different isotopic values (Figure 3). Diets of male and female otters were significantly different during spring and early summer (Figure 4a). That difference became more pronounced later in the summer and in the autumn (Figure 4b). During that latter period, more males than females shifted to include pelagic fishes in their diet, as indicated by more depleted signatures of both $\delta^{13}C$ and $\delta^{15}N$ (Figure 4b). Eleven of 34 females (32%) changed their diet, compared with 43% of 82 males. The overall model of sex by season (hair type) was significant ($p < .001$ for $\delta^{13}C$ and $\delta^{15}N$, MANOVA). No difference occurred in $\delta^{13}C$ by season ($p = .8$) but $\delta^{15}N$ differed seasonally ($p < .001$). Values for each isotope differed between genders ($p < .002$), but the interaction between season and sex was not significant for $\delta^{13}C$ or $\delta^{15}N$ ($p > .1$).

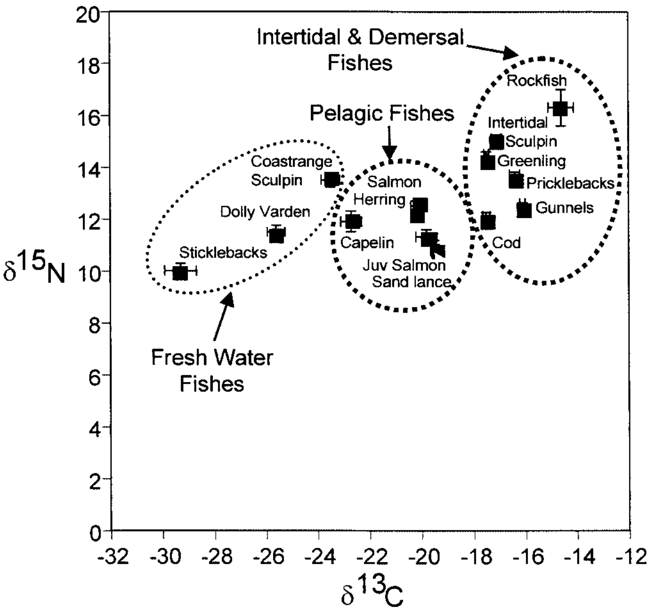

Figure 3
Stable isotope values for fish tissues collected in Prince William Sound, Alaska, obtained from companion studies (Ben-David M et al., 1998; Hirons A, Institute of Marine Sciences, University of Alaska Fairbanks; Kline TC, Prince William Sound Science Center, Cordova, Alaska). When pooled by groups (indicated by ovals), intertidal and demersal fishes, pelagic fishes, and freshwater fishes all had significantly different isotopic values ($p < .05$; K-nearest randomization test). Sample sizes (and scientific names) are as follows: coastrange sculpin (*Cottus aletuticus*; $n = 9$), dolly varden (*Salvelinus malma*; $n = 9$), stickleback (*Gasterosteus aculeatus*; $n = 14$), salmon (*Oncorhynchus gorbuscha* ; $n = 43$), herring (*Clupea pallasi*; $n = 15$), capelin (*Mallotus villosus*; $n = 19$), sand lance (*Ammodytes hexapterus*; $n = 22$), juvenile salmon (*Oncorhynchus sp.*; $n = 10$), rockfish (*Sebastes sp.*; $n = 2$), intertidal sculpin (*Cottidae*; $n = 12$), greenling (*Hexagrammos decagrummus*; $n = 61$), pricklebacks (*Stichaedae*; $n = 10$), gunnels (*Pholis laeta*; $n = 44$), and cod (*Gadidae*; $n = 6$).

Analysis of diet, as represented by isotopic ratios of under fur and guard hair, in relation to sociality, revealed that values of $\delta^{13}C$ were significantly different between categories of sociality, but not between genders (overall model $p = .02$; sociality $p = .02$; gender $p = .8$, ANOVA). Significant differences occurred in diet between sociality categories for spring–summer (low sociality, average $\delta^{13}C = 14.58 \pm 0.01$ SE, $n = 25$; high sociality, average $\delta^{13}C = 15.16 \pm 0.02$ SE, $n = 32$; $p = .006$; ANOVA). Similarly, significant differences occurred in summer–autumn (low sociality, average $\delta^{13}C = 14.55 \pm 0.02$ SE, $n = 25$; high sociality, average $\delta^{13}C = 15.35 \pm 0.04$ SE, $n = 32$; $p = .004$; ANOVA), indicating that those animals with lower levels of sociality had diets composed primarily of intertidal fishes during both seasons, and highly social animals had $\delta^{13}C$ signatures consistent with an increased pelagic component in the diet. No significant difference existed between seasons within sociality categories (low sociality, $p = .255$; high sociality, $p = .16$; Wilcoxon tests).

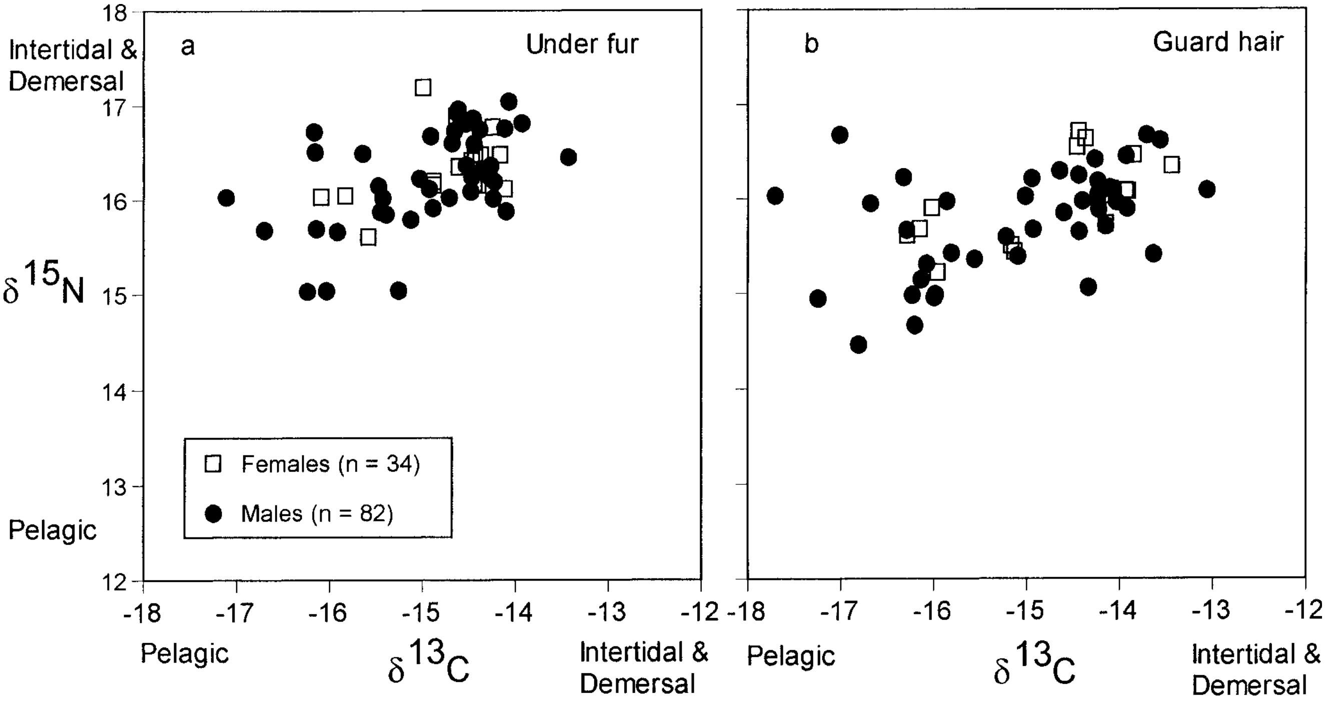

Figure 4

Stable isotope ratios indicating seasonal diets of male and female river otters in Prince William Sound, Alaska. Stable isotope signatures of hair samples represent the diet consumed at the time of hair replacement. Although diets of male and female otters were significantly different during the spring and early summer season (a, under fur: overall model $p = .026$; MANOVA, $\delta^{13}C$ $p = .007$; $\delta^{15}N$ $p = .228$), this difference became more pronounced later in the summer and fall (b, guard hair: overall model $p = .004$; MANOVA, $\delta^{13}C$ $p = .004$, $\delta^{15}N$ $p = .004$).

Sociality and home-range size

Sixty-nine otters had sufficient telemetry locations (Blundell et al., 2001) with which to calculate home-range size (mean = 23.6 locations, SE = 0.9). There was a significant negative correlation between home-range size and sociality (Figure 5; $r = -.239$, $p = .05$ Pearson). A regression model with a logarithmic curve fit was significant (Figure 5; $T = -2.38$, $p = .02$).

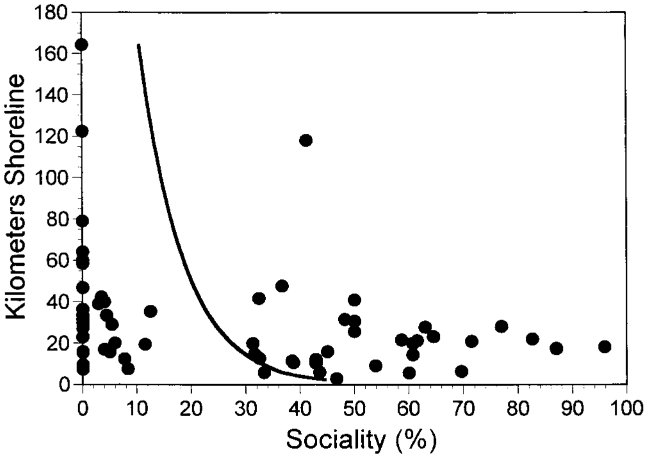

Figure 5

A comparison of home-range size (length of shoreline contained within 95% isopleths of fixed-kernel estimates of home ranges) and percentage of social locations for coastal river otters in Prince William Sound, Alaska. The regression model fitting a logarithmic curve (shown) was significant ($T = -2.38$, $p = .02$).

Morphometrics

Male otters ($n = 81$) were significantly ($p = .04$, overall model MANOVA) larger than females ($n = 35$), but dimorphism was not pronounced. The weight:length ratio of male otters (mean ± SE, 7.3 ± 0.1) was only 10.8% greater than that of females (6.4 ± 0.14; $p < .001$). Males (9.2 ± 0.2 kg) weighed an average of 1.1 kg more than females (9.2 ± 0.2 kg; $p < .001$), but body length did not differ between genders (males: 773 ± 10.2 mm, females: 774 ±7.1 mm; $p = .99$). Tail length (males: 500 ± 10.5 mm, females: 472 ± 7.0 mm) and interdigital spread (males: 93.3 ± 0.8 mm, females: 91.3 ± 1.4 mm) were significantly larger for males than for females ($p < .03$ and $p < .001$, respectively).

DISCUSSION

Our data support predictions associated with the hypothesis that group formation facilitates cooperative foraging, at least for male otters. Group size in males increased between May and October and decreased thereafter, tracking the availability of schooling pelagic fishes in the nearshore environment (Figure 1), supporting the hypothesis that sociality was a foraging strategy. More social individuals had smaller home ranges, suggesting greater efficiency in foraging (Figure 5). In addition, a higher incidence of pelagic fishes in diets of more social otters indicates that social otters may be cooperatively foraging.

Sexual dietary partitioning (Figure 4) in otters may reflect differential swimming abilities between genders. Sexual dimorphism among river otters was subtle, but higher body mass may confer superior swimming ability to males. We hypothesize that larger body mass in males is likely a result of greater skeletal muscle mass distributed along a frame similar in length to that of females. Such structure, together with larger feet, may provide males with greater undulating power and propulsion (Fish, 1994), potentially increasing their swimming speed or efficiency. Nonetheless, a school of pelagic fish moves rapidly and erratically as a polarized unit, or sometimes splits into several schools, thereby confusing a solitary predator and inhibiting capture success (Norris and Schilt, 1988). Therefore, sexual dimorphism may not be sufficient to explain sexual dietary partitioning in coastal river otters without the formation of groups.

Norris and Schilt (1988) observed that fishes receiving simultaneous cues from multiple predators were unable to respond with polarized or evasive movements, leading to a decrease in interfish distance (Major, 1978) and greater capture success for individuals foraging in a group, compared with solitary foragers (Götmark et al., 1986; Norris and Schilt, 1988). Rich, ephemeral patches of schooling fishes occurring in the nearshore environment in PWS (Brown et al., 1999; Groot and Margolis, 1991) cannot be exploited at a single feeding; thus costs of defending the resource would exceed benefits (Krebs and Davies, 1993), and unequal competitors can fare equally well in capture success (Rita et al., 1996). That male otters exhibited higher sociality than females (Figures 1 and 2), that female otters joined male groups, and that sociality influenced the consumption of pelagic fishes regardless of gender indicate that sexual dimorphism may not be a critical factor in foraging strategies of otters. Cooperative foraging by coastal river otters on schooling fishes, however, should result in increased access to better quality prey—a benefit that likely would be afforded to all group members, regardless of gender or swimming ability.

Foraging in groups would be beneficial to river otters because successful evasion of predation by schools of fishes is inversely proportional to the number of predators in the group (Götmark et al., 1986; Pitcher and Parrish, 1993). Although foraging behavior was not directly observed in this study, observations in which otters cooperated to drive fish toward shore or toward one another were reported in freshwater habitats for *L. canadensis* (Sheldon and Toll, 1964; Serfass, 1995) and for *L. perspicillata* (Kruuk et al., 1994).

The weight of evidence indicates that sociality in coastal river otters may be a foraging strategy, but we cannot critically evaluate hypotheses concerning predation. Nonetheless, an increase in group size solely to avoid predation is not likely to have resulted in differential diets between otters with varying degrees of sociality. Increased foraging efficiency and antipredator strategies might be jointly employed, however, to allow more social otters to forage for pelagic fishes farther offshore, potentially facing greater risk of predation. Blundell et al. (2001) evaluated data collected during behavioral observations of river otters in PWS in 1991 (Rock et al., 1994) and reported that otters foraged an average of 5.1 m from shore (n = 119, SE = 0.9, range 1–80 m). For those data, there was a negative correlation between group size (mean = 4.1, SE = 0.2, range 1–8 otters; unpublished data) and distance from shore ($r = -.2$, $p = .01$; unpublished data); thus larger group size among coastal river otters did not appear to promote foraging farther from shore.

Predation risk for river otters is difficult to assess. Potential predators include killer whales (*Orcinus orca*), sea lions (*Eumetopias jubatus*), seals (*Phoca vitulina*), salmon sharks (*Lamna ditropis*), terrestrial carnivores (e.g., wolves, *Canis lupus*), and, for young otters, bald eagles (*Haliaeetus leucocephalus*). With the exception of minor predation by wolves (Kohira and Rexstad, 1997), no other predation events have been reported for river otters. Information on transient killer whales, which prey on marine mammals (Baird and Dill, 1995), indicates there is little change in their occurrence by season in PWS (Saulitis et al., 2000). Thus, the evidence suggests that predation pressure for river otters is low and not likely to vary seasonally. Seasonal variation in group size for male otters (Figure 1) provides further evidence that sociality likely is not an antipredator strategy for that gender.

Besides risk of infanticide, predation risk may impose some limitations on sociality for reproductive females. In ungulates, females with young sometimes choose a lower quality habitat and thus a lower quality diet to reduce predation risk (Bleich et al., 1997). Similarly, avoidance of social groups may limit opportunities for cooperative foraging in female river otters with young, resulting in a lower quality diet for females. River otter neonates are kept in natal dens for approximately 8 weeks (Noll, 1988), followed a postemergence period several months long (Melquist and Hornocker, 1983), during which the movements of a female remain restricted compared with the size of her predenning home range (Noll, 1988). Therefore, between parturition in early May (Noll, 1988) and October, the period of availability of schooling fishes (Figure 1), reproductive females might initially have difficulty in locating a group of cooperatively foraging otters and then, during postemergence, actively avoid such groups. Consequently, options for cooperative foraging while raising offspring likely would be limited for reproductive females, resulting in the sexual dietary segregation we observed (Figure 4).

Although little is known about the mating system for coastal river otters, our data indicate that sociality in males cannot be attributed to male mating coalitions (Packer et al., 1991; Witt et al., 1981). Group size significantly declined before and during the mating season (Figure 1), providing no support for that hypothesis. Conversely, that observation supports the hypothesis that males may compete for reproductive opportunities. In Alaska, the mating season for river otters occurs in May (Blundell GM, personal observation; Noll, 1988; Woolington, 1984) before the arrival of large numbers of pelagic fishes (Figure 1). Data on testicle width, testosterone secretion, and increased aggression between individuals in captive male otters (Ben-David M, unpublished data) indicated that timing of male–male competition for mates occurs in late March to late May, before the increase in pelagic fishes (Figure 1). Thus, during the period when aggression (i.e., costs of sociality) would be escalated between males, benefits of sociality (cooperative foraging) are limited. Why some males appear to remain solitary year-round, however, is unclear and merits further investigation.

Although we were unable to directly evaluate the role of risk of predation or infanticide, our data provide considerable evidence that cooperative foraging is a key factor influencing social organization of coastal river otters. We suggest that the higher incidence of pelagic fishes in diets of male otters is not a result of sexual dimorphism and superior swimming ability; rather, it is a benefit of sociality. Furthermore, we suggest that otters may switch strategies from social to nonsocial, depending on the time of year, prey availability, their gender, and their reproductive status. During years in which a female is not raising offspring, her best strategy is to join a group to take advantage of the benefits of cooperative foraging and the associated increased access to a better quality diet that would be difficult to obtain as a solitary forager.

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