Ethology

Social Networks and the Formation and Maintenance of River Otter Groups

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Received: June 24, 2008
Initial acceptance: August 18, 2008
Final acceptance: November 15, 2008
(L. Ebensperger)

doi: 10.1111/j.1439-0310.2009.01624.x

Abstract

Many studies have evaluated why male mammals form social groups; few however have investigated how these groups are formed and maintained. We observed behavioral interactions of 15 male river otters (*Lontra canadensis*) captured in Prince William Sound (PWS), Alaska, and held in captivity for 10 mo. Because the otters were captured in various areas and differed in age and relatedness, we were able to test how kinship and age influenced social interactions. We also explored how kinship, age and social interactions in captivity related to geographic spacing after the otters were released back in PWS. In 284 h of observations, the otters exhibited more positive than negative interactions. Social network models indicated that in the early stage of captivity, there were more links among individuals than in the late stage. In the late-stage period, older animals that had higher testosterone levels exhibited increased social distance and lower information centrality (a network connectivity metric). Social distance was not related to genetic distance, nor did it relate directly to age, although both social distance and age were correlated with post-release geographic distance. Thus, the formation of male groups in coastal river otters is largely influenced by familiarity and past experience, rather than kinship. The maintenance of groups, especially during the mating season, is a function of reproductive status and age, with older animals withdrawing from the social network during that time. What other phenotypic characters may contribute to the formation and maintenance of river otter groups merit future exploration.

Introduction

Male social congregations (*sensu* Parish et al. 1997) outside of the breeding season have been documented in ungulates, whales, seals, primates, and carnivores (Ruckstuhl & Neuhaus 2000; Begg 2001; Blundell et al. 2002a,b). Several hypotheses have been proposed to explain why males form social congregations or coalitions. These include increased mating success, territorial defense, predator detection and avoidance, and cooperative foraging. For example, in elk (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*), male bachelor-groups are thought to facilitate increased predator detection and avoidance, and decreased competition with females for forage throughout the year except during the rut (Geist & Petocz 1977; Berger 1978; Lawson & Johnson 1982; Peek 1982). Red howler monkeys (*Alouatta seniculus*) form male coalitions in order to increase mating success and compete for reproductive females (Pope 1990). Male lions (*Panthera leo*) form coalitions in order to compete jointly for opportunities to join and defend female prides (Packer & Pusey 1982; Packer 1986; Waser 1996). In other species, such as the slender mongoose (*Herpestes sanguineus*) and the cheetah (*Acinonyx jubatus*), male social groups of both related and unrelated individuals may form for the benefits of cooperative hunting, reproductive access to females, and territorial defense (Caro & Collins 1987; Waser et al. 1994; Gompper & Wayne 1996).

While many studies have evaluated the costs and benefits of group formation in mammalian males, or the 'why,' few have investigated how males form and maintain social groups. In many cases, clustering of individuals results when dispersal costs are high (Clutton-Brock 2002). Indeed, cooperation appears more extensive among individuals of the sex that is less likely to disperse (Wrangham & Rubenstein 1986). In carnivores, when dispersal is low and cooperation among relatives results in increased direct or indirect fitness, male social groups will likely be kin based, and coalitions that consist of strangers are expected to be smaller and less stable (Macdonald & Moehlman 1982). For example, male coalitions in lions tend to consist of closely related individuals, especially in larger, more permanent ones (Spong et al. 2002). Larger coalitions of male lions composed of kin have higher reproductive success because they can gain access to larger prides and control those prides for longer periods (Bygott et al. 1979; Packer 1986). Packer et al. (1991) hypothesized that male lions are more willing to forego reproductive opportunities if doing so increases reproductive potential in a close relative. In primates, such as red howler monkeys, the amount of cooperation within sexes is closely correlated with the tendency for kin to live together (Wrangham & Rubenstein 1986; Clutton-Brock 2002). Under such conditions, male social groups may form from interactions among relatives. Recent molecular studies, however, have shown that cooperation between unrelated individuals is common (Gompper & Wayne 1996; Blundell et al. 2004), as seen in the slender mongoose and lion male coalitions composed of fewer individuals (Packer et al. 1991; Waser et al. 1994).

Clustering and formation of male groups may occur when cooperation among familiar individuals offers benefits, regardless of kinship (Spong et al. 2002). As group size increases, foraging success, growth, fitness, and survival may increase and risk of predation decrease for related and unrelated individuals in groups as seen in the meerkat (*Suricata suricatta*; Clutton-Brock 2002). Similarly, in slender mongooses related and unrelated males that are found in close spatial proximity may assist each other in defense of territories, may play together and also feed and den together (Waser et al. 1994). In adult male Savanna baboons (*Papio cynocephalus cynocephalus*), formation of coalitions is hypothesized to depend in part on shared residence in a group, close spatial proximity, and associated affiliative relationships (Noë & Sluijter 1995).

Alternatively, sexually immature individuals may form social groups because they lack the opportunity to breed. In such cases, males of similar age are more likely to form subadult bachelor-groups irrespective of kinship or familiarity in order to increase protection from predators, optimize foraging efficiency, or practice fighting skills and establish social hierarchies, as seen in ungulates (Geist & Petocz 1977; Lawson & Johnson 1982; Peek 1982; Ruckstuhl & Festa-Bianchet 2001). Similarly, male squirrel monkeys (*Saimiri oerstedii*) are philopatric and maintain strong interactions with same age-cohort males to support future mate competition (Boinski et al. 2005).

Here we test how kinship, familiarity, and age influence social interactions and group formation and maintenance among river otters (*Lontra canadensis*). River otters exhibit high variability in social organization, likely as a function of resource availability. For example, in most freshwater systems, river otters are largely solitary (Stevens & Serfass 2008) and females, especially, may exhibit intrasexual territoriality (Melquist & Hornocker 1983; Spinola et al. 2008). Nonetheless, small groups of river otters (two to four individuals) have been observed in freshwater systems, especially during and following the breeding season (Melquist & Hornocker 1983; Crait et al. 2006; Spinola et al. 2008; Stevens & Serfass 2008). In contrast, coastal river otters in Prince William Sound (PWS), Alaska, USA, form large social groups of up to 18 individuals, most of which are males (median group size 6, range 2–18; Rock et al. 1994; Blundell et al. 2000, 2002a). In that environment, most females and few males remain solitary year round (Blundell et al. 2004). Unlike many social species in which males defend areas against other males (Wrangham & Rubenstein 1986), male river otters seem to be non-territorial (Ben-David et al. 2005; Gorman et al. 2006) and newly dispersing males may join established male groups (Blundell et al. 2002b). Otter group sizes in PWS increase between May and October concurrently with the seasonal migration of schooling pelagic fishes and decline before and during the mating season (Blundell et al. 2002a). Thus, the seasonal and annual changes in group composition of coastal river otters in PWS (Blundell et al. 2002a,b) provide an opportunity to assess the mechanisms that underlie formation and maintenance of male groups in these carnivores.

Because river otters are difficult to observe in the wild, we studied the behavioral interactions among 15 male river otters that were captured in coastal habitats in PWS and brought into captivity for 10 mo (Ben-David et al. 2000, 2001, 2002; Rostain et al. 2004). Because the animals were captured in four different areas within PWS, were of various ages, and had different levels of relatedness, we were able to test how kinship, familiarity, and age influenced social interactions. After the captive period, the otters were released back into PWS (Ben-David et al. 2002). This allowed us to explore how kinship, familiarity, age, and social interactions in captivity influenced post-release spatial proximity. Although behavioral interactions within river otter social groups are largely positive (Beckel 1982, 1991; Melquist & Hornocker 1983; Rock et al. 1994; Rostain et al. 2004) and actual fights are rare (Kruuk 1995; Rostain et al. 2004), we hypothesized that otters that are more closely related would have a higher number of positive social interactions than otters that are unrelated. In addition, we expected that animals captured in the same area would have more positive interactions due to prior familiarity than animals whose capture sites were in different areas, regardless of kinship. Also, we predicted that male otters of similar age would be more likely to interact with each other than with animals of other age groups, regardless of familiarity or kinship. Finally, we hypothesized that males with a prior history of positive interactions would remain in closer proximity following release than would animals that had fewer previous social interactions.

Methods

Study Animals

We conducted behavioral tests on 15 adult male otters that were live-captured in four different geographic areas in northwestern PWS, Alaska, USA, in spring 1998 (Fig. 1). Those animals were trapped from the population studied by Blundell et al. (2002a,b). Of the 15 river otters, three were caught in Esther Passage (EP05, EP06, EP07), four at Naked Island (NI01, NI02, NI03, NI06), three in Unakwik Inlet (UI02, UI03, UI05), and five in Wells Bay (WB02, WB04, WB05, WB06, WB07). Only adult males were used in this study because of the need to avoid separating females from young that could have

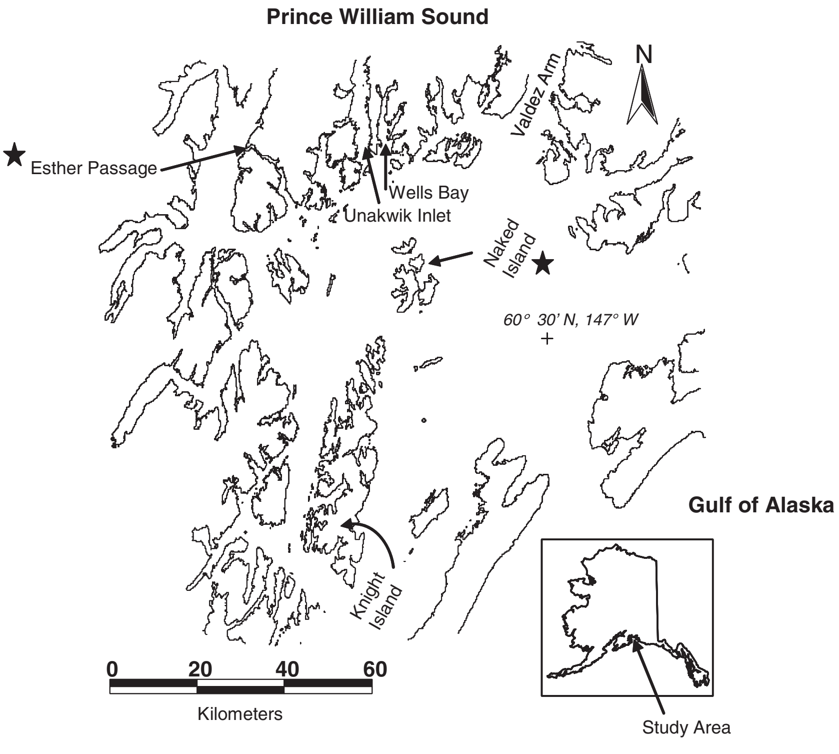

Fig. 1: Locations in Prince William Sound, Alaska, USA, where 15 adult male river otters were live captured in 1998 at Esther Passage, Unakwik Inlet, Naked Island, and Wells Bay and transported to the Alaska Sealife Center, Seward, Alaska, via air. Stars indicate release locations in Mar. 1999. Stars represent release locations.

been sequestered in natal dens. Also, males are more social than females and are less likely to engage in intra-sexual aggression (Blundell et al. 2002a,b).

Animals were held in captivity at the Alaska Sealife Center (ASLC) in Seward, Alaska, from May 1998 to Mar. 1999, for a study on the effects of hydrocarbons on physiology (Ben-David et al. 2000, 2001, 2002). The otters were housed together in a 90-m^2 area with one large and four smaller salt-water pools, and were fed frozen fish supplemented with live prey, vitamins and minerals. For more details on conditions in captivity see Ben-David et al. (2000, 2001) and Rostain et al. (2004). All methods used in this research were approved by the Institutional Animal Care and Use Committees at the University of Alaska Fairbanks and ASLC (Nos. 97-14 and 98-002, respectively) and trapping permits were issued by the Alaska Department of Fish and Game (98-001). All procedures adhere to the guidelines for animal care and use adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998) and the *Guidelines for the Use of Animals in Research*.

Behavioral Interactions

To evaluate the social interactions of the 15 captive male otters, we identified and recorded 14 social behaviors (Table 1). The otters were observed during two stages of captivity: early-stage, from May 27, 1998 to Aug. 8, 1998 (approx. 3 wk to 3 mo after they were captured and before hydrocarbon administration had begun); and late-stage, from Jan. 18 to Feb. 7, 1999 (2 mo after hydrocarbon administration had ceased and rehabilitation was complete; Ben-David et al. 2002). Individuals were uniquely marked with small clippings of fur. Observations were made from a room adjacent to the otter enclosure between 0800–1100 and 1600–1700 h in association with feeding to avoid potential bias that could have been caused by inactivity of several individuals. While all individuals were active during feeding time most, but not all, were inactive during the rest of the day.

Each day a list of focal animals was randomly drawn. Each focal animal was observed for 30 min (for more details see Rostain et al. 2004). In 284 h of monitoring (204 in the early-stage, and 80 in the late-stage period), we observed each focal animal for an average of 38 (SE = 2.7, range 33–46), 30-minute periods. A total of 3181 behavioral interactions were recorded. For each interaction, we recorded the direction of the interaction (i.e., whether the interaction was initiated by the focal animal or its companion). We also noted whether the interaction was mutual or not. Negative

Table 1: Description of 14 social behavioral interactions for river otters captured in PWS in spring 1998 and held in captivity at ASLC in Seward between May 1998 and Mar. 1999

Behavior	Type of interaction	Description
Grooming	Positive	Two animals are gently gnawing each other's head and shoulders
Multi-otter grooming	Positive	More than two animals are grooming each other
Touching noses	Positive	Two or more animals are touching noses together
Rubbing bodies	Positive	Two or more animals are in full body contact and are moving and rubbing on each other. No biting or gnawing
General interaction	Positive	Two otters are running, eating, standing or lying together
Multi-otter general interaction	Positive	More than two animals are running, eating, or standing or lying together
Playing in the pool or tote	Positive	Two or more animals are chasing each other on land and in water. No body contact
Playing on structure	Positive	Two or more animals are chasing each other on a structure in the enclosure
Wrestling	Positive	Two or more animals are rolling together on land and in water. Full body contact but no aggression
Grooming attempt rejected	Negative	One animal tries to groom another and is rejected
Mounting	Negative	One animal mounts another
Fighting	Negative	Two or more animals are rolling together on land and in water, while biting each other and screeching. Can result in open wounds
Aggression rejected	Negative	One animal approaches another with aggression. The other backs off and rejects the aggression
Screaming	Negative	One animal screeches at another. No body contact

interactions (grooming attempt rejected, mounting, aggression rejected, fighting, and screaming) were rare among the captive otters (4.2% of 3181 observed interactions); therefore, we made little use of these data in subsequent analyses. Also, because patterns of all positive interactions (all behaviors excluding grooming attempt rejected, mounting, aggression rejected, fighting, and screaming) were similar across behaviors, they were pooled in the final analyses. We tallied behavioral interactions between dyads (pairs of individuals) for each individual otter in 15×15 matrices for positive interactions during both the early- and late-stages of captivity. The resulting matrices of interactions were asymmetric; the number of interactions initiated by animal X toward animal Y could differ from the number of interactions initiated by Y toward X.

Using the matrices for positive interactions (weighted for observation effort for each individual calculated based on the number of 30-minute observation periods), we constructed social network models for the early and late stages of captivity in the program UCINET™ (Borgatti et al. 2002). We analyzed the interaction-weighted networks with the Network > Cohesion > Distance > Cost algorithm in UCINET to compute a matrix of path lengths for travel among nodes (i.e., male river otters). Because the cost algorithm calculates increasing path lengths as the number of interactions increases, we inverted path lengths (i.e., 1 = 6, 2 = 5,…6 = 1) to depict dyads with high number of positive interactions closer in the network. We then summarized the matrix of path lengths by averaging the values (interactions initiated by animal X toward animal Y and vice versa) for each dyad.

We also used the program UCINET™ (Borgatti et al. 2002) to compute the network metric information centrality (Stephenson & Zelen 1989) for the early and late stage social networks. Information centrality is the weighted sum of the number of paths among members of the network that connect through any given individual. It is one of several metrics of node centrality (Wasserman & Faust 1994) and proved a useful predictor of status in a study of social organization in lek-mating long-tailed manakins (*Chiroxiphia linearis*; McDonald 2007). We visualized the late stage and early stage social networks using Netdraw 2.504 (Borgatti 2002), representing tie strength (or number of weighted interactions) by line thickness, animal age by the shape of the node symbol, and information centrality with node size.

Relatedness

To explore the effects of relatedness on behavioral interactions, we determined the relatedness among all 15 animals using DNA analysis of blood samples. For details on procedures for blood draw and genotyping protocols see Ben-David et al. (2000) and Blundell et al. (2002b, 2004). Once genotypes were established we calculated the coefficient of relatedness (r) using the program Kinship (Version 1.2; Goodnight et al. 1994; Queller & Goodnight 1989). This coefficient was calculated between dyads concurrently with 95 other individual otters captured in the same area (Blundell et al. 2002a,b) to avoid potential biases that may result from the small sample size of captive animals. Genetic distance for each dyad was calculated as $1 - r$ and used to create a 15×15 matrix for subsequent analyses.

Age

We estimated the age of each otter (young adult – coded 1, adult – coded 2, old adult – coded 3) using morphological measurements (body mass; body length, tail length, and total length; total skull length and width of zygomatic arch), and tooth wear and staining (Blundell et al. 2002a,b). This classification of age was correlated with age as determined from cementum annuli on the first upper premolar in 50 individual otters (Blundell et al. 2002b). We calculated the pairwise differences in age between all individuals by subtracting the estimated age class of one from the other in order to create a 15×15 matrix, with values ranging from 0 to 2.

Testosterone Levels and Testicular Width

Because the late-stage period of observations coincided with the onset of the breeding season for otters (Blundell et al. 2002b), we measured levels of plasma testosterone by radioimmunoassay using commercial coated tube kits (Diagnostic Products Corporation, Los Angeles, CA, USA). Analyses were conducted by Dr. J. E. Rowell, Institute of Arctic Biology, University of Alaska Fairbanks. The assay had a sensitivity of 0.04 ng/ml and a standard curve range of 0.2–16 ng/ml. The samples were run in duplicate assays. Intra-assay coefficient of variation (CV) for a low, medium and high reference sample averaged 22.2%, 6.6% and 10%, respectively. Inter-assay CVs averaged 1.6%, 13.2%, and 11.5%, respectively, for low, medium, and high reference controls. The assay was validated for river otters by spiking river otter plasma with standards and demonstrating parallel curve displacement. We also measured the combined width of right and left testes of each animal to the nearest 1 mm with digital calipers five times during captivity (Aug. 16, 1998; Oct. 19, 1998; Nov. 30, 1998; Jan. 11, 1999; Feb. 22, 1999).

Distance Among Dyads After Release

Otters were implanted with radio transmitters following the protocol described by Blundell et al. (2000) and Bowyer et al. (2003). The radio transmitters (IMP/400/L; Telonics®, Mesa, AZ, USA) had 21 mo of battery life and were equipped with a mortality sensor that indicated whether the otter was motionless for over 9 h (Ben-David et al. 2002). On Mar. 21, 1999, the otters were transported back to PWS. The four otters that were originally captured on Naked Island were released together at that site. Heavy iceberg accumulation prevented releasing the otters back into Unakwik Inlet and Wells Bay (Fig. 1). Therefore, those eight animals and the three otters previously captured at Esther Passage were released at that location. Each otter was followed via aerial tracking on a weekly basis until May 25, 1999. Thereafter, the otters were tracked every 2 wk through the life of the radio transmitter or the otter (Ben-David et al. 2002). Distances between every pair of otters were determined from GIS (ArcView 3.2; ESRI Redlands, CA, USA), for the first three tracking flights (Apr. 3, 18, 27 1999 for Naked Island; Apr. 3, 18 1999, May 3, 1999 for Esther Island), because several otters perished after this time, although post-release survival did not differ between animals that were released at site of capture and those that were translocated (Ben-David et al. 2002). To evaluate the relation between social distance at the late-stage period of captivity and distance post-release, we averaged the distances for the three tracking flights. Because the Naked Island release site consisted of a four-island archipelago where even short movements resulted in long shoreline distances, while the Esther Passage coast was continuous (Fig. 1), we divided the pairwise distance for each dyad by the average distance between all animals within that release site and constructed separate matrices for the two release locations.

Data Analysis

We used paired t-tests to explore changes in positive and negative behaviors of otters through their tenure at the ASLC (Zar 1999). The number of observations per individual was corrected for the total time of observation for that individual, thus representing a rate for each type of behavior. We used repeated-measures ANOVA to explore changes in testosterone levels and testicular width between the different sampling dates, which encompassed the early and late stages (Zar 1999).

To test whether behavioral interactions of the otters were influenced by kinship, familiarity, or age, we used the matrices of early- and late-stage social network distances and Mantel tests (Manly 1991) implemented with Mathematica™ to evaluate the relations between this social distance and the matrices of genetic distance (1 − r), and age difference. Similarly, we used Mantel tests to evaluate the relations between social distance during the late stage, genetic distance, and age difference, and post-release geographic distance (i.e., spatial proximity). A total of 5000 randomizations were conducted in each comparison.

Results

The captive river otters exhibited more positive than negative interactions (Table 2). Overall, the rate of positive interactions among the otters increased by a factor of 2.81 between the early-stage and the late-stage periods (Table 2; one-tailed paired t-test p = 0.0005). Only two individuals (WB02 and WB06) exhibited lower rates of positive interactions during the late-stage period than they did when first brought into captivity. The rate of negative interactions also increased between the early-stage and late-stage (1.74 times; Table 2; one-tailed paired t-test p = 0.035), but to a lesser extent than did positive interactions (one-tailed paired t-test p = 0.0004), and four individuals (EP07, UI05, WB02, WB06) exhibited lower rates of negative

Table 2: Total number and mean rate (± SE) of interactions (calculated as number per length of observation time) for 15 male river otters during the early and late stages of their captivity at the Alaska Sealife Center, in Seward, Alaska, 1998–1999. Otters were captured in four geographic locations in Prince William Sound, Alaska in April and May 1998. All positive interactions (Table 1) were pooled as were all negative interactions

	Early stage			Late stage		
	Total	Mean rate	SE	Total	Mean rate	SE
Positive	1451	0.474	0.046	1597	1.331	0.277
Negative	79	0.026	0.004	54	0.045	0.010

interactions after several months in captivity. During both sampling periods, the rate of positive interactions was much higher than the rate of negative interactions (18.4 and 29.6 times, respectively; Table 2).

The social network changed configuration during the captive period. The early-stage network had more links among individuals and more animals exhibited higher information centrality (Fig. 2a). The change in information centrality between the early and late stages was driven mainly by younger animals (age class 1) becoming more interactive (average increase of +5.0 ± 2.05 units; Fig. 2b; ANOVA, $p = 0.06$), while older animals (age class 3) became less interactive (average increase of −4.4 ± 2.62; Fig. 2b). Animals of age class 2 showed a slight decrease in levels of interactions (average increase of −1.6 ± 2.97; Fig. 2b). In the early stage, three animals (UI02, UI05, WB07) were weakly connected to the network and could be considered solitary. Similarly, three animals (UI05, WB02, WB06) were weakly linked to the network during the late-stage period. Only UI05, however, exhibited low levels of interaction during both sampling periods (Fig. 2).

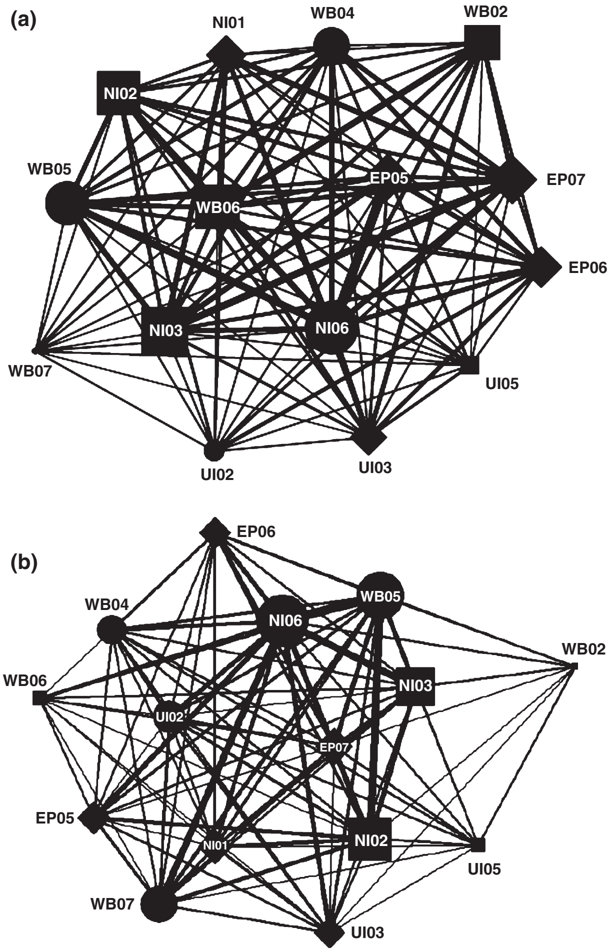

Fig. 2: Social network diagram for 15 male river otters held in captivity at Alaska Sealife Center, Seward, Alaska, between May 1998 and Mar. 1999. (a) Early-stage period; density 0.97 (102 of 105 possible links). (b) Late stage; density 0.90 (95 of 105 possible links). Thickness of lines represents interaction intensity. Node size depicts the network metric information centrality, a weighted sum of the number of paths among members of the network that connect through any given individual. Circles: young adults; diamonds: adults; squares: older adults. Note that several of the adults and older adults (EP05, EP06, WB02, WB06) have lower information centrality in the late-stage network, because of increasing asociality likely as a result of increasing levels of testosterone.

Testosterone levels were relatively low (Fig. 3), with relatively high CV in all our assays, probably due to the long time intervals between sampling occasions. Nonetheless, more samples during the late stage (Jan. 11, 1999 and Feb. 22, 1999) had detectable testosterone values than in earlier sampling occasions, and there was a significant increase in both testosterone values and testicular width during the late stage (repeated-measures ANOVA: $F_{5,89} = 11.540$, $p < 0.0001$, and $F_{4,56} = 332.48$, $p < 0.0001$, respectively; Fig. 3). Although mean testosterone values were correlated with mean testicular width for the five sampling occasions ($r = 0.54$, $p < 0.001$), no such correlation occurred at the individual level ($r = 0.04$, $p = 0.88$), probably because testosterone excretion is pulsed. Both testosterone levels and testicular width at the last sampling occasion were higher in older than younger otters (Fig. 3; $p = 0.06$ for testosterone, $p = 0.058$ for testicle width). Although change in information centrality was uncorrelated with testosterone ($r = -0.08$, $p = 0.77$) and only marginally so with testicular width ($r = -0.45$, $p = 0.09$), the mean values of these parameters for the three different age classes were correlated ($r = -0.99$, $p < 0.001$ for testosterone, $r = -0.93$, $p < 0.001$ for testicular width).

The relatedness coefficients between dyads of the 15 captive otters ranged from −0.031 to 0.75 (average 0.2). This was comparable to the range of relatedness coefficients seen in wild otter groups in PWS (range −0.63 to 0.89, range of averages within groups 0.05–0.17; Blundell et al. 2004). Social distance was not correlated with genetic distance in either the early-stage (Mantel test, $p = 0.46$) or the late-stage periods of captivity (Mantel test, $p = 0.27$).

Similarly, age difference was not correlated with social network distance in either the early stage (Mantel test, $p = 0.27$) or the late stage (Mantel test, $p = 0.09$) of captivity. Nonetheless, post-release

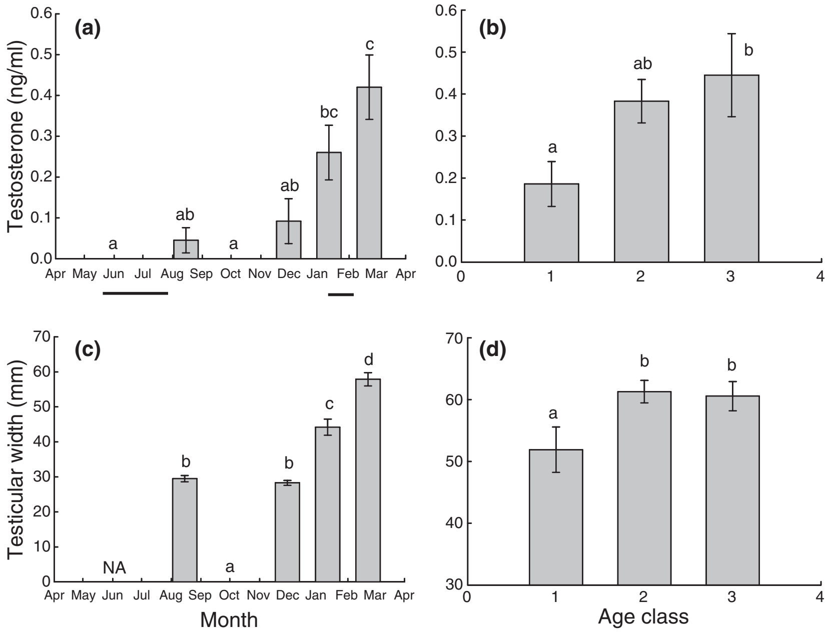

Fig. 3: Mean ± SE of testosterone levels (ng/ml; a) and testicular width (mm; b) for 15 wild-caught male river otters were held in captivity at the Alaska Sealife Center, Seward, Alaska, between May 1998 and Mar. 1999. Data on testicular width were not available for the Jun. 29, 1998 sampling session. Testosterone levels (c) and testicular width (d) during the February sampling occasion were lower in younger animals (age class 1). Significant differences are denoted by different letters. Horizontal lines represent the observation periods.

geographic distance (i.e., spatial proximity) among individuals did correlate with age differences (Fig. 4a; Mantel test, p = 0.02), as well as with social distances among individuals prior to release (Fig. 4b; Mantel test, p = 0.015), but not with genetic distance among them (Fig. 4c; Mantel test, p = 0.46).

Discussion

Our results suggest that familiarity and past experience largely determine the formation of male groups in coastal river otters, as demonstrated by the positive correlation between network connectivity in captivity and geographic proximity after release. In contrast, we found no relation between social and genetic distances, indicating that group formation and maintenance in coastal river otters is not driven by kinship. The maintenance of groups, especially during the mating season, is a function of reproductive status and age. Older reproductive males become solitary, while younger males maintain male–male cohesion. Nonetheless, because coastal river otters exhibit isolation by distance (Blundell et al. 2002b), geographic proximity and relatedness do correlate at larger scales. Indeed, of the 15 captive males, seven (EP05, EP06, UI02, NI01, NI06, WB06, WB07) were on average more related to conspecifics captured within the same area than they were to animals captured in areas 28–42 km apart across large bodies of open water (minimum of 9 km; Fig. 1). In addition, three otters (UI03, WB04, WB05) had relatedness values that were similar for within-capture-area and outside-capture-area comparisons, while only five (EP07, NI02, NI03, UI05, WB02) were less related to animals captured within their area. Interestingly, of the latter, four individuals were older animals (age class 3), consistent with the hypothesis that older, reproductively active males traverse greater distances as they search for mates.

In many species, cooperation occurs more often among individuals of the sex that is less likely to disperse (Wrangham & Rubenstein 1986). While male river otters in PWS are more likely to disperse than are females, male otters disperse shorter distances (16–30 km) than do those females that disperse (60–90 km; Blundell et al. 2002b). In addition, newly dispersed males often join established male groups that forage cooperatively on schooling pelagic fishes (Blundell et al. 2002b), whereas females establish exclusive home ranges where they forage on intertidal/demersal fishes (Blundell et al. 2002b; Ben-David et al. 2005). Thus, the likelihood of interacting with close relatives in male river otters should be high. Nevertheless, Blundell et al. (2004) found that social groups showed no evidence for either kin attraction or avoidance. In a companion study investigating scent-marking behavior in the same 15 captive otters, Rostain et al. (2004) established that these individuals exhibited no preference for the scent of close kin. These observations, together with our data, suggest that, similar to slender mongooses

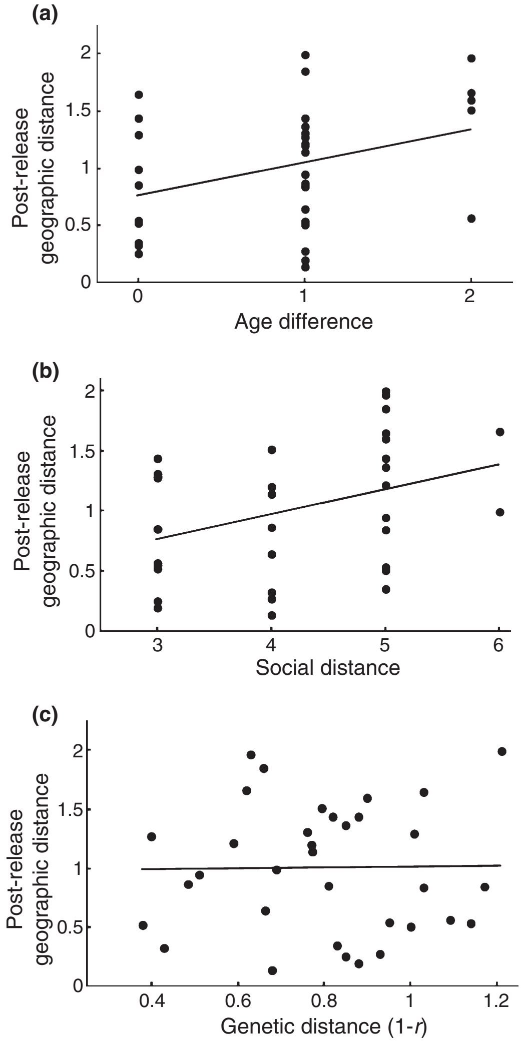

Fig. 4: Post-release geographic distance was positively related to age difference (a) and late-stage social distance (b), but not to genetic distance (c) for 34 otter dyads (pairwise combinations). These results suggest that social familiarity is an important factor in group formation in male river otters, whereas age in important for group maintenance during the breeding season when older males withdraw from the social network. Eleven otters were released in Esther Passage and four in the Naked Island complex (see Fig. 1).

and smaller male coalitions in lions (Packer et al. 1991; Waser et al. 1994), kinship in coastal river otters plays little role in the formation or maintenance of male groups, but rather that limited male dispersal produces increased familiarity among individuals.

Despite the lack of relation between age and social distance, age plays a role in the maintenance of otter groups, especially during the breeding season. We found that during the late-stage period, which coincided with the onset of the mating season, older animals had higher testosterone levels and larger testicles. These same older individuals reduced their level of interaction, changing the configuration of the social network, and causing increased post-release geographic distances between older and other animals. During the mating season, therefore, younger, non-reproductive individuals maintain group cohesion.

During the mating season, age may also influence local relatedness among male otters. Blundell et al. (2002b) found that reproductively active males engage in long breeding migrations. In several cases, these males later returned to their original home ranges and social groups (Blundell et al. 2002b). In our study, the five males with lowest relatedness to conspecifics in their capture locations were older individuals. We captured these otters in April and May at the height of the breeding season. Thus, it is likely that these older animals were breeding individuals caught outside of their usual home ranges. It is possible that age plays a lesser role in maintaining otter groups outside of the breeding season, because (1) Blundell et al. (2002b) found no difference in the average age of social and nonsocial male otters in PWS, suggesting that otter groups consist of mixed aged animals, and (2) younger and older individuals in our study had similar social distance and information centrality outside of the mating season.

It is interesting that the increase in testosterone levels during the late-stage period did not correlate with a large increase in aggressive behavior among the captive otters, but rather a reduction in positive interactions and withdrawal from the social network. Several researchers have described a positive relation between testosterone and increased aggression among males in elk (Peek 1982) dwarf mongooses (*Helogale parvula*; Creel et al. 1992; Creel 1996), lemurs (*Lemur catta*), and other primates (Mazur 1985; Cavigellis & Pereira 2000). It is possible that males were not exhibiting peak reproductive testosterone values, based on the relatively low levels of testosterone we recorded in late February. Because river otters mate between April and May in PWS (Blundell et al. 2002b), it is likely that testosterone levels would have been higher later in the season. Nonetheless, the values we observed in late February were higher than earlier sampling periods and are within the range of values described for other adult male mustelids, such as black-footed ferrets (*Mustela nigripes*; Wolf et al. 2000) and mink (*Mustela vison*; Boisson-Agasse et al. 1981). It is possible that otters within a group use the indirect method of scent-marking to maintain dominance relationships, which reduce injury and energy expenditure. Indeed, Rostain et al. (2004) determined that dominant male river otters spent more time investigating familiar and unfamiliar male scent than did subordinate males. Similarly, field studies of carnivores have demonstrated that dominant animals mark more, and often over-mark subordinate scent (Erlinge et al. 1982; Gosling 1982; Kruuk et al. 1984; Gorman 1990; Sliwa & Richardson 1998; Begg et al. 2003). Therefore, during the period of intense competition for mates, reproductively active, older otters may avoid group members and reduce the potential for conflicts. Reduced aggression may be important, because these individuals are likely to rejoin their groups after the mating season to cooperatively forage for high-quality schooling pelagic fishes in the nearshore environment (Blundell et al. 2002a).

Neither familiarity nor increased reproductive activity could fully explain the consistently low level of social interactions for UI05. This individual remained peripherally connected to the social network during both sampling periods. Similarly, Blundell et al. (2002a,b, 2004) identified solitary males in the wild, concurrent with the existence of large male groups. Nevertheless, Blundell et al. (2004) found no evidence that the fitness of these solitary animals differed from that of more gregarious ones. It is possible that these two social strategies survive in the population because fluctuations in the availability of schooling pelagic fishes average the reproductive success of social and solitary individuals over time (Blundell et al. 2004; Sih et al. 2004; Bell 2007). Whether the tendency to remain solitary is genetically based merits further investigation.

Where observations in the field are difficult, data on social behaviors in captive conditions can provide useful information (Stoinski et al. 2004; Colmenares 2006; Romero & Aureli 2007), despite the caveat that captive animals cannot completely avoid conspecifics. In our study, several individuals interacted little with others even while restricted to a 90-m^2 enclosure, and similar to anecdotal observations in freshwater systems (Beckel 1991; Crait et al. 2006) interactions were predominantly positive and changed through the course of the study. Also, that the behaviors of these otters were not affected by captivity-induced stress is evident from observations by Ben-David et al. (2001) that stress indicators (such as aspartate aminotransferase, blood urea nitrogen, and glucose), which were high during capture, declined after 2 wk in captivity. Together these suggest that the captive otters behaved similar to their wild conspecifics. Our conclusions would have had additional support if we could replicate across multiple networks. Unfortunately, the logistical constraints of maintaining river otters in captivity precluded that option.

Despite the potential aforementioned limitations, this study highlights the distinction between factors determining formation vs. maintenance of male social groups. On the one hand, as in red howler monkeys, meerkats, slender mongoose, and in small coalitions of male lions (Wrangham & Rubenstein 1986; Packer et al. 1991; Waser et al. 1994; Clutton-Brock 2002; Spong et al. 2002), social groups of male river otters form because cooperation among familiar individuals provides benefits, regardless of kinship or relative age. On the other hand, the maintenance of these social groups is driven by assortative interactions among younger individuals during the mating season, a time when older individuals withdraw from the social network. Thus, unlike ungulates (Geist & Petocz 1977; Lawson & Johnson 1982; Peek 1982; Ruckstuhl & Festa-Bianchet 2001) and squirrel monkeys (Boinski et al. 2005), the maintenance of group cohesion by younger river otters is restricted to the mating season. Nonetheless, it appears that additional factors that we did not measure may influence the formation and maintenance of otter groups. Although all 15 males were kept in one large enclosure, network links were sometimes sparse and variable, even among individuals of similar age. Thus, although all individuals had the opportunity to become familiar and gain mutual experience, interactions among specific individuals were limited. Several recent studies suggest that behavioral stages (McDonald 2007) or phenotypes (such as boldness; Sih et al. 2004; Pike et al. 2008) may influence the interactions of individuals with conspecifics. What additional factors, related to the behavioral phenotype of an otter, affect its interactions with others, regardless of familiarity or age and reproductive status, await future exploration.

Acknowledgements

We thank G. M. Blundell, J. B. Faro, L. Faro, H. Golden, H. Kruuk, O. A. Ormseth, and C. Taylor for assistance in live trapping of otters in the field. O. A. Ormseth was the lead project technician from the capture of otters to their final release. Without his enthusiasm, responsibility, and active participation in all facets of the experiment, this work would have been much more difficult to complete. We thank all ASLC employees, volunteers, and interns for their support of the project. A. K. Norin, C. Smith, M. Thompson, and S. Trillhose assisted in the care and husbandry of the captive otters. They also participated in the handling of otters and assisted in data collection. E. Maldonado, N. Levanon, and M. Brijbasi from NSF-Teachers Experiencing the Arctic and Antarctic (TEA) program assisted in collection of data on social interactions. We thank D. Ziel for assistance with laboratory analysis of DNA. N. P. Nibbelink and H. Maier assisted with GIS analyses. We thank Dr. J. E. Rowell for testosterone assay analyses and input on earlier versions of the manuscript. S. Horn, L. Ebensperger, and three anonymous reviewers provided helpful comments on earlier versions of this manuscript. This project was supported by *Exxon Valdez Oil Spill* Trustees Council (project/348), NSF-TEA program, the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the University of California, Davis (UOA991239-09), and the Prince William Sound Oil Spill Recovery Institute Grant 99-10-12 to M.B.D. and the Prince William Sound Oil Spill Recovery Institute Graduate Fellowship to H.H.

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