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Coastal latrine sites as social information hubs and drivers of river otter fission–fusion dynamics

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Fission–fusion dynamics, consisting of regular shifts in the size and composition of social groups, are prevalent in animal societies and have implications for foraging success, disease and information transfer, and the fitness of individuals. Thus, the individual and environmental factors that drive social dynamics have become a focus of recent investigations. River otters, *Lontra canadensis*, in coastal Alaska have a plastic social system, influenced by forage fish availability. These carnivores also regularly frequent terrestrial latrine sites, where they associate and communicate through deposition of odorous substances. To investigate fission–fusion dynamics in this system we (1) deployed camera traps to record social behaviours at latrine sites and (2) attached proximity tags to quantify encounter rates among individuals. Camera detections demonstrated that most latrine visits were of single otters and small groups (2–8 individuals). Fusion events into large groups (up to 18 individuals) were infrequent. Larger groups were recorded at crossover latrines, where trails connected bodies of water, whereas social behaviour was more frequent at spatially central latrines. Visiting otters performed signalling behaviours more frequently than social behaviours, especially at crossover sites. Proximity tag data revealed that the timing of fission and fusion events coincided with latrine visits and that spatial overlap was a good predictor of social interaction. Thus, the structural and spatial features of latrines influence their function as centres of information exchange, social activity hubs and meeting places among small social units, with implications for river otter group dynamics. We conclude that shifting social and environmental conditions may lead to high communication complexity. This unique social system provides novel evidence of the role of olfactory communication in mediating social decisions.

Animal social structure has implications for the foraging success (Aplin, Farine, Morand-Ferron, & Sheldon, 2012), disease transmission (Kappeler, Cremer, & Nunn, 2015), information transfer (Sueur et al., 2011) and fitness of individuals (McDonald, 2007; Silk, 2007). Recent studies indicate that the flexibility of several animal social systems had previously been underestimated. These dynamic assemblages, described as fission–fusion societies (Aureli et al., 2008), exhibit continuous spatial and temporal shifts in group size and composition. Diverse female-driven or mixed-sex mammalian societies show fission–fusion dynamics, including primates (Asensio, Korstjens, & Aureli, 2009), carnivores (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008), bats (Fleischmann et al., 2013) and ungulates (Merkle, Sigaud, & Fortin, 2015). Social dynamics are influenced by several factors, among which the importance of environmental resource availability and predictability has recently been highlighted (Asensio et al., 2009; Smith et al., 2008; Sueur et al., 2011). Because animals vary in the degree of information they possess on resource availability during group movement, diverging motivations can emerge among individuals. This conflict of interests can result in shifting social configurations, where key individuals, as well as movement initiators, play an important role (Fleischmann et al., 2013; Merkle et al., 2015; Smith et al., 2015; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015).

Repeated visits by animals to specific locations promote social interactions and enable observation of the behaviour of other individuals (i.e. public information; Danchin, Giraldeau, Valone, &

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Wagner, 2004). In addition, in several mammal species, exchange of information on presence of conspecifics often occurs at specific scent-marking locations (latrines). Latrine behaviour is particularly common in small and medium-sized carnivores such as the honey badger, *Mellivora capensis* (Begg, Begg, Toit, & Mills, 2003) and the meerkat, *Suricata suricatta* (Jordan, Cherry, & Manser, 2007). In territorial species, marking locations can be concentrated along territory borders to deter entrance of individuals from other groups (Gorman & Mills, 1984; Kilshaw, Newman, Buesching, Bunyan, & Macdonald, 2009). Alternatively, scent stations can be more abundant in a group's core area to reduce marking efforts and maximize the probability of encounter by intruders (Darden, Steffensen, & Dabelsteen, 2008; Eppley, Ganzhorn, & Donati, 2016; Jordan et al., 2007). In addition, evidence suggests that marking locations are selected such that signal detection by receivers is maximized (Roberts & Gosling, 2001). Landscape features selected for by scent-marking animals include trail crossroads (Barja, de Miguel, & Bárcena, 2004), visually conspicuous sites (Begg et al., 2003; Eppley et al., 2016) and the vicinity of dens (Bohm, Palphramand, Newton-Cross, Hutchings, & White, 2008). When rates of fission–fusion are high and group composition changes constantly, the exchange of information at latrines can be used by individuals to inform adaptive grouping and foraging decisions (Aureli et al., 2008).

In addition to social and environmental information, space use can influence the tendency of animals to form social groups. Animals may preferentially associate with individuals that share a portion of their home range. For example, in the multilevel fission–fusion society of reticulated giraffes, *Giraffa camelopardalis*, social structure is correlated with space use of females (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; VanderWaal, Wang, McCowan, Fushing, & Isbell, 2013). Male alliances and spatial overlap are important for female defence in the open social networks of bottlenose dolphins (*Tursiops* sp.; Randic, Connor, Sherwin, & Krützen, 2012). Similarly, the multilevel societies of Guinea baboons, *Papio papio*, are characterized by low levels of aggression and high tolerance among unrelated males that belong to groups (or gangs) with substantial spatial overlap (Patzelt et al., 2014).

Coastal river otters, *Lontra canadensis*, in Alaska have a flexible social system, where males spend approximately 50% of their time in groups of up to 18 individuals but females are mostly solitary (Blundell, Ben-David, & Bowyer, 2002). Individual otters vary in several measures of sociality including spatial interactions, frequency of association and home range overlap (Blundell, Ben-David, Groves, Bowyer, & Geffen, 2004; Bowyer, Testa, & Faro, 1995). The main driver of otter associations is cooperative foraging for pelagic schooling fish, which provide substantial energy benefits (Ben-David et al., 2005; Blundell, Ben-David, & Bowyer, 2002; Kruuk, 2006). Tactile (allogrooming, co-rubbing, playing and wrestling) and acoustic interactions result in the formation of social networks, which are seasonally variable. In the wild, river otter groups are composed of relatives as well as nonkin (Blundell et al., 2004) and are largely form based on familiarity (Hansen, McDonald, Groves, Maier, & Ben-David, 2009). Group foraging promotes male affiliation and reduces aggression. During the limited mating season in Alaska (~1 month), older males travel long distances (Blundell, Ben-David, Groves, Bowyer, & Geffen, 2002), which may reduce competition for mating opportunities. Overall, the nutritional benefits that male river otters accrue from joint foraging overcome male–male competition, which is ubiquitous in other mating systems (Emlen & Oring, 1977).

The unique social system of coastal river otters is mediated by olfactory communication at latrine sites (Ben-David, Bowyer, Duffy, Roby, & Schell, 1998). From a landscape perspective, the sites selected for social behaviour and scent marking are characterized by high shoreline convexity and increased proximity to suitable fish habitat compared with random sites (Albeke, Nibbelink, Mu, & Ellsworth, 2010; Crowley, Johnson, & Hodder, 2012). In addition, latrine sites vary in size and shape and can be broadly separated into crossover sites (where long, overland trails connect two bodies of water) and piazza-style sites (where all trails from the water lead into one large open space). Some latrines also harbour dens and fresh water pools (Bowyer et al. 2003). Previous studies, based on radiotelemetry, suggest that social otters use a small number of available latrines with high intensity and that these communication hotspots change on the landscape seasonally and annually, suggesting that scent marking functions to convey messages within and between male social units (Ben-David et al., 2005). Behavioural evidence from captive otters indicates that male scent marking communicates individual identity, sex and dominance status (Rostain, Ben-David, Groves, & Randall, 2004). This information is likely encoded in a substance excreted from the anal gland. A chemical analysis of anal gland excretions collected at latrine sites revealed that they are composed of at least 31 volatile compounds; the proportions of these compounds vary among individual otters (Barocas, n.d.). Thus, river otters convey complex, individual information to conspecifics through olfactory pathways, using several chemical compounds. Based on large-scale movement data, Ben-David et al. (2005) hypothesized that olfactory communication at latrines could mediate group fission and fusion events on a finer temporal scale.

Here, we used advanced proximity tracking technology and sensor-activated camera traps to obtain fine-scale behavioural data and evaluate the influence of spatial structure and space use on river otter sociality. Based on previous research on river otter sociality, we formulated the following hypotheses.

(1) Although the spatial configuration of latrines influences selection for these sites (Albeke et al., 2010; Crowley et al., 2012), the effect of latrine structure on behaviours and social interactions of visiting animals is poorly understood. We hypothesized that in crossover latrines, river otters would perform behaviours associated with signalling to maximize the exchange of public information, whereas social behaviours would be more likely to occur at piazza-style latrines. We additionally predicted that because of the high content of social information (in the form of urine, faeces and anal gland secretions), trail-dominated latrines would receive more visits by larger groups compared with piazza-style latrines.
(2) Several species of carnivores show nonrandom patterns in the spatial configuration of communication sites, with concentrations of latrines in core areas (Darden et al., 2008; Jordan et al., 2007). Because river otters are socially flexible and have overlapping home ranges (Blundell, Ben-David, & Bowyer, 2002), we hypothesized that the spatial centrality of latrines would positively influence the number of river otter visits. Additionally, because central locations often serve as aggregation and information exchange hubs for social animals (Ward & Zahavi, 1973), we predicted that group size and social behaviour would be positively influenced by the spatial centrality of latrines.
(3) In addition to their importance as social hubs, coastal latrines have a role in information transfer among river otters (Ben-David et al., 2005). We hypothesized that otters would use this social communication to inform decisions about joining or leaving a group, and predicted that latrine visits and fission–fusion events would coincide temporally.
(4) Recent evidence suggests that social associations are spatially embedded and that individual fission and fusion decisions can be influenced by the spatial locations of conspecifics (Aureli

et al., 2008; VanderWaal et al., 2013). Thus, we predicted that the tendency of rivers otters to associate would be positively correlated with their spatial overlap.

METHODS

Study Area

We conducted field work in two maritime-montane coastal areas of southcentral Alaska (see Bowyer et al. 2003 for details; Fig. 1): (1) Kenai Fjords National Park (KEFJ), a protected natural area situated on the Kenai Peninsula, (59°92′N, 149°65′W) during summer 2012; and (2) an archipelago (including Knight and neighbouring islands) located in western Prince William Sound (PWS; 60°23′N, 147°40′W) during summer 2014. We selected 55 km of coastline in the eastern portion of Aialik Bay (KEFJ; 59°49′N, 149°40′W) and delineated our PWS study area, spanning 118 km of coastline, based on past surveys (Seymour et al., 2012; Fig. 1).

Camera Traps

During the field season of 2014 in PWS, we deployed 36 camera traps (30 Bushnell Trophy® video cameras, 3 Bushnell Sentry® still cameras, Bushnell, Overland Park, KS, U.S.A.; and 3 still Reconyx hc500®, Reconyx, Holme, WI, U.S.A.) at river otter latrines deemed active following a coastal survey of 122 previously known sites. We positioned cameras on trees approximately 25 cm above the ground, with the lens facing the main latrine entrance or a narrow passage on an otter trail. We configured Bushnell Trophy models to Normal sensitivity and Video mode (video length 30 s, reset time 1 s) and configured Bushnell Sentry and Reconyx models to Picture mode (5 captures per detection). We left the cameras secured to trees and operating for a total of 3 months (26 May – 20 August).

Camera Data Analysis

We used time stamps to determine the number of visit events at each latrine. For each video or picture in which we detected river otters, we counted the maximum number of animals observed simultaneously (group size). To analyse behavioural bouts, we defined social behaviour according to positive interactions previously observed for river otters in captivity (Hansen et al., 2009). We considered social behaviour as occurrences of grooming, touching noses, rubbing bodies, playing and wrestling in which more than one individual was involved (Supplementary Table S1). Following behaviours observed in captivity by Rostain et al. (2004), we also quantified behavioural bouts where otters were sniffing the air or

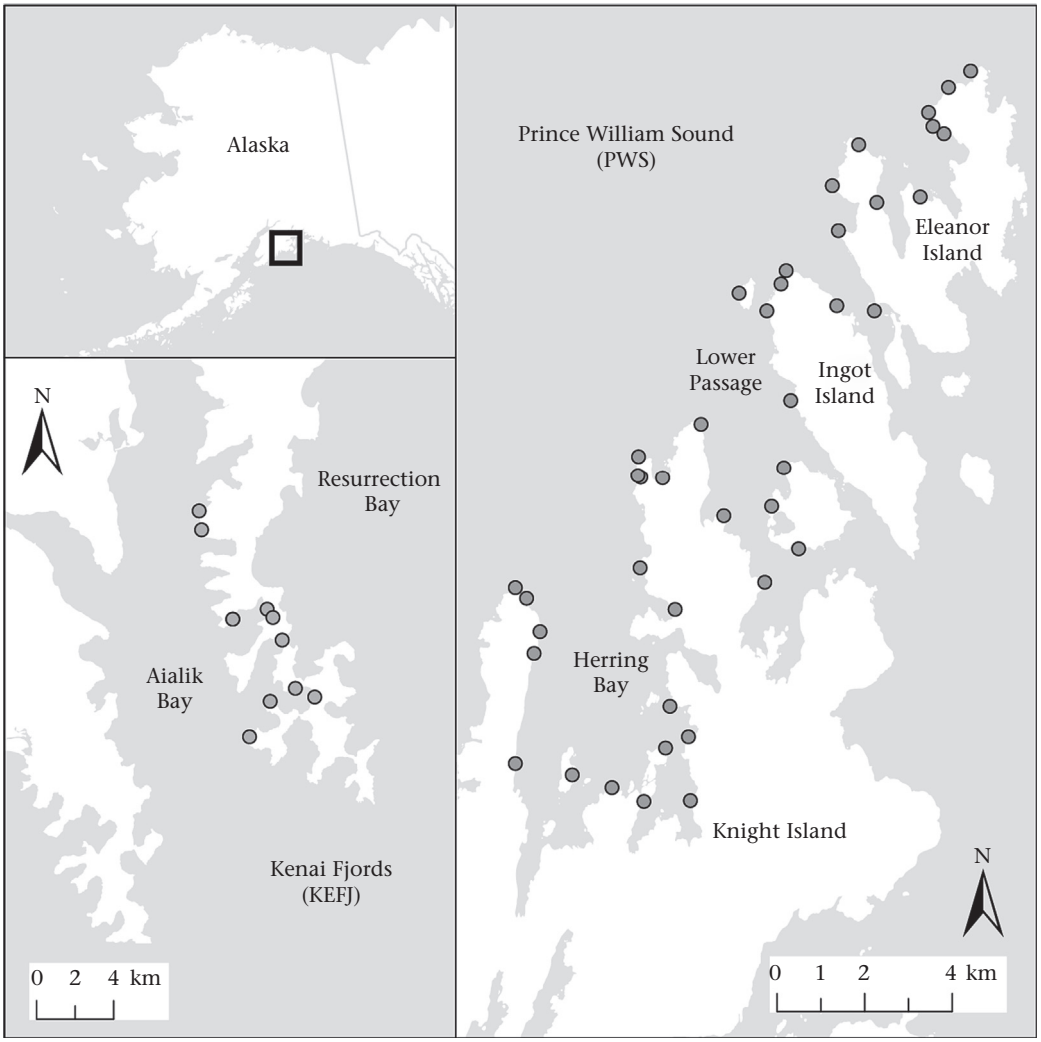

Figure 1. River otter research areas in coastal Alaska. Latrines where cameras or Encounternet base units were deployed are denoted with grey circles. Sampling was conducted during summer 2012 in Kenai Fjords National Park and during summer 2014 in Prince William Sound.

ground intensively, or were displaying before scent marking (Greene, Monick, Manjerovich, Novakofski, & Matheus-Pinilla, 2015) and signalling through defecation and urination. Finally, to assess the potential for interaction during river otter association events, we selected 20 videos in which river otters were observed interacting socially and estimated maximum distances between individuals (see Supplementary Material, Euclidean Distance between Interacting Individuals).

We used generalized linear mixed models (GLMM; Bolker et al., 2008) to examine effects of several factors (see below) on the number of visits, group sizes and the likelihood of river otters to perform social behaviour (Table 1). We fitted models with a Poisson distribution to the count data for total visits and group size. Similarly, because social behaviour, measured for each latrine visit, was a binary variable, models were developed with a binomial distribution following recommendations in Pinheiro and Bates (2006). The social behaviour data set included only visits in which more than one animal was observed. We ran GLMMs using package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014) in the R environment (R Development Core Team, 2007). We selected models based on Akaike's Information Criterion (AIC; Burnham & Anderson, 2002; see Supplementary Material, Model Selection).

We developed four predictor variables for river otter social behaviour, describing latrine structure (Supplementary Fig. S1), latrine spatial centrality (Supplementary Fig. S2), temporal variation in interactions and group size (Table 1). We based spatial centrality on the spatial network developed by Albeke, Nibbelink, and Ben-David (2015). We calculated least-cost distances among 310 sampled locations along the Knight Island Archipelago, PWS coastline (Supplementary Fig. S2) using the package 'igraph' (Csardi & Nepusz, 2006). We parameterized these distances as edges in a fully connected spatial network (Dale & Fortin, 2010). Based on this network, we calculated for each of our sampled latrines the node metric 'strength centrality' (i.e. the sum of all least-cost distance-weighted connections among nodes; Everett & Borgatti, 2005). We hypothesized that group size would positively influence river otter tendency to engage in social behaviour (Table 1). We included subarea or bay (Herring Bay, Lower Passage and Eleanor Island; Fig. 1) and camera type as random effects in the visits models. We examined correlations among predictor variables to avoid collinearity. To account for spatial autocorrelation among latrine locations, we performed Moran's I tests (Li, Calder, & Cressie, 2007) for total visits, mean group size and proportion of visits where social behaviour was observed.

Proximity Tag Testing

To quantify latrine visits and associations among river otters, we used an automated proximity tracking system (Krause et al., 2013) by Encounternet® (Encounternet LLC, University of Washington, WA, U.S.A.), consisting of tag units, base units and a master node (Rutz et al., 2015; Supplementary Fig. S3). Proximity tags use wireless technology to record date- and time-stamped presence of other tags in their proximity. Static base units, placed at locations frequently visited by animals, detect electronic signals from tag units and download the stored encounter records. The master node unit controls the system by setting unit configurations and downloading data from base units (Supplementary Fig. S3). Further technical information on the Encounternet system is available elsewhere (Mennill et al., 2012; Rutz et al., 2015). Tag units (mean ± SE weight: 29.9 ± 1 g, length: 5.3 cm, height: 2.3 cm, width: 3.5 cm; Supplementary Fig. S3) were adapted to the semi-aquatic lifestyle of river otters. Tags were composed of an outer layer of toughened epoxy, a middle layer of fibreglass and a core of lightweight epoxy and glass microsphere mix. The inner core layer was necessary to prevent the tag antenna from de-tuning. We conducted two types of performance tests on Encounternet tags prior to deployment in PWS (see Supplementary Material, Variability in Signal Reception and Transmission of Encounternet Tags). We used test results to apply a correction factor, which accounted for variability in reception range and signal strength among tags (Boyland, James, Mlynski, Madden, & Croft, 2013).

Proximity Tag Field Methods

We surveyed the coastline of KEFJ and PWS for active river otter latrine sites. From these, we selected sites for trapping using two criteria: (1) activity as revealed by fresh scats found within each site; and (2) suitability for trapping, based on the site layout and the safety of trapped animals. We set 31 Sleepy Creek® foot-hold traps (no. 11, Sterling Fur and Tool Co., Sterling, OH, U.S.A.) at 18 sites in KEFJ and at 30 sites in PWS, following procedures described by Blundell, Kern, Bowyer, and Duffy (1999). We equipped traps with transmitters for remote and continuous monitoring, and visually inspected them every 24 h. We anaesthetized captured animals using pneumatically projected darts with Telazol® (Zoetis, Madison, NJ, U.S.A.), at a dose of 9 mg/kg body mass (Bowyer et al., 2003). We glued an Encounternet tag unit to the hair on the otter's back approximately 10 cm behind the scapulae using a 5 min epoxy (Supplementary Fig. S3). We expected that this procedure would

Table 1
Description and justification of four explanatory variables and the corresponding variables for GLMMs used to explore river otter sociality

Variable	Abbreviation	Description	Justification	Response variable		
				Visit number	Group size	Social behaviour
Latrine identity	Latrine ID		Latrine ID examined as a random factor		+	+
Latrine structure	Structure	Crossover or piazza-style latrine	Latrine structure can determine whether it is a meeting point between individuals and influence the type of behaviour performed (e.g. otters are more likely to signal along trails)	+	+	+
Spatial network centrality	Centrality	Strength centrality metric calculated for the focal latrine based on the weighted spatial network	Central locations could be meeting places among small social units and promote social behaviour (Ben-David et al., 2005)	+	+	+
Temporal variation	Time	The number of days elapsed from sampling start date	Group size and social behaviour of otters can vary seasonally with resource availability (Ben-David et al., 2005) and breeding season (Blundell, Ben-David, & Bowyer, 2002; Blundell, Ben-David, Groves, et al., 2002)		+	+
Group size	Gsize	The total number of animals observed during a latrine visit	Animals in larger groups have more individuals to interact with			+

allow the tags to fall off the otters within 2–3 months, during or before their autumn moult. All animal capture and handling procedures complied with Institutional Animal Care and Use Committee permit A-3261-01 of the University of Wyoming and permits 2012-029 and 2014-08 of the Alaska Department of Fish and Game.

We deployed base units at 10 latrine sites in KEFJ and 41 sites in PWS. We selected latrine sites based on river otter activity inferred from scat surveys, while striving for a fairly uniform distribution along the coastline (Fig. 1). We wired base units to trees approximately 2 m above the ground (Supplementary Fig. S3) to achieve maximal reception range. During the collection period, data were downloaded weekly. We collected all base units within 30 and 69 days from deployment in KEFJ and PWS, respectively. Because we were unable to recapture river otters and retrieve mobile units, all encounters were subsequently inferred from data downloaded at base units.

Proximity Analysis

We programmed Encounternet tag units in KEFJ to work continuously and record every detection following deployment. Because test results revealed limited battery duration of these tags, we subsequently used 'sample' mode in PWS. Deployed tags were programmed to sample simultaneously for 2 of every 10 min, which extended the tracking period and increased the accuracy of measurement of encounter durations, eliminating confusion caused by multiple records of short contacts (Drewe et al., 2012). We subsequently corrected the KEFJ data to fit similar time intervals, ensuring consistency in analyses among study areas.

We determined fission and fusion events using the following steps: (1) we divided reciprocal tag detections into 8 min intervals, analogous to scan sampling (Altmann, 1974); (2) we plotted all 8 min detections over time (Supplementary Fig. S6); (3) we pooled events where individuals were found together in adjacent time steps to consolidate encounters; (4) we considered records of animals joining a group as fusion events and animals leaving a group as fission events (Supplementary Fig. S6; Psorakis et al., 2015). This procedure provided a conservative threshold for group formation and separation that was not dependent on a fixed time window but contingent on the distribution of detections from the data. An additional advantage of this method was that it filled gaps formed by imperfect detection (e.g. tag download malfunction) and inherent technical problems in the tracking system.

To examine temporal adjacency between latrine visits and fission–fusion events, we calculated the time elapsed between each latrine visit by a focal individual and the closest fission or fusion event in which it engaged. We removed all instances where these intervals were longer than 72 h because we considered this an upper limit for the relevance and persistence of olfactory information transferred by scats and anal gland secretions. This threshold was based on prior knowledge of the decay of chemical signals in this highly humid coastal environment and the chemical analysis of anal gland volatile substances, in which the majority of compounds evaporated after 3 days (Barocas, n.d.). We compared the observed values to the ones obtained from a random latrine visit model. In the random model, latrine visits for each individual were simulated during the time period in which it was available for detection (Supplementary Fig. S7). We constrained the random model to maintain the total number of visits per individual and the otter IDs at latrine visits, which included more than one individual from the observed data, and randomized them in time (Supplementary Fig. S7). The distribution of time intervals between latrine visits and fission–fusion events was compared using the Kruskal–Wallis test. For both the observed data and the random model, we also calculated the proportion of latrine visits in which individuals were found with a group. We compared these proportions using Fisher's exact test (Zar, 1999).

We used detections registered at base units (reflecting latrine visits) to determine a coastline use area for each individual. We subsequently calculated the proportion of overlap in coastline use for each pair of individuals in each area. In addition, we calculated the dyadic association rate for each pair of individuals by dividing the total number of 8 min scans in which animals were detected together by the total number of scans in which both animals were known to be carrying tags. We used a quadratic assignment procedure (QAP; Smouse, Long, & Sokal, 1986) with 10 000 permutations to examine the relationship between the space use and association matrices. We performed this analysis separately for each study area using program UCINET (Borgatti, Everett, & Freeman, 2002).

RESULTS

Camera Traps

In total, cameras were operational for 29–81 days (mean ± SE = 67.3 ± 3.4). Camera trap sampling effort totalled 2354 camera days, during which we obtained 264 videos and 307 pictures of 194 river otter latrine visits. Rates of otter visits varied among latrines (mean ± SE = 5.66 ± 1.11 visits; range 0–23). Otter group size ranged from 1 to 18 (mean group size ± SE = 3.20 ± 0.2; median = 2.0). Group size distribution was left-skewed (36% of detections included solitary individuals), indicating a rarity of large-group latrine visits (4% >10; Fig. 2a). In five visits, individuals observed in latrines included adults accompanied by one to three pups. During latrine visits, solitary and social river otters performed signalling behaviour (53%) more often than social behaviour (26%). Signalling behaviour was especially predominant at crossover latrines (65% of visits in crossovers, 48% in other latrines), whereas at piazza-style sites, river otters had a higher likelihood of performing social behaviour (32% versus 12% at crossovers; Fig. 3). The mean ± SE of maximum distances among interacting individuals was 6.9 ± 1.2 m. In 25% of instances, individuals interacted socially after separating 8 m or more from each other.

Camera Data Analysis

We did not detect significant spatial autocorrelation for any of the response variables (latrine visits: Moran's $I = 0.03$, $P = 0.69$; group size: Moran's $I = 0.06$, $P = 0.53$; social behaviour: Moran's $I = -0.28$, $P = 0.23$). GLMM results for latrine visits supported a model where visit rate was influenced by latrine crossover structure (in interaction with the centrality of a latrine; positive coefficient, meaning more visits to centralized crossover sites; Table 2). This model was significantly better supported than the null model (Model 1: $\chi^2_3 = 47.8$, $P < 0.001$) and achieved the highest relative support (ΔAICc = 14.3, weight = 100%; conditional $R^2 = 0.87$; Supplementary Table S2).

Several GLMMs explaining group size had similar support (ΔAICc <2; Supplementary Table S3, Fig. 2b). Among the models with the lowest AIC scores, model 3, which included additive effects of crossover structure, time and latrine centrality, had the highest explanatory power (conditional $R^2 = 0.39$). Results from the best supported models suggested that group sizes were larger at crossover latrines and became smaller as time progressed from the initiation of the study (Table 3). There was partial support for latrine spatial centrality as a predictor of group size (cumulative weight = 35%; Supplementary Table S3). Likelihood ratio tests indicated that all five top-ranked models were significantly

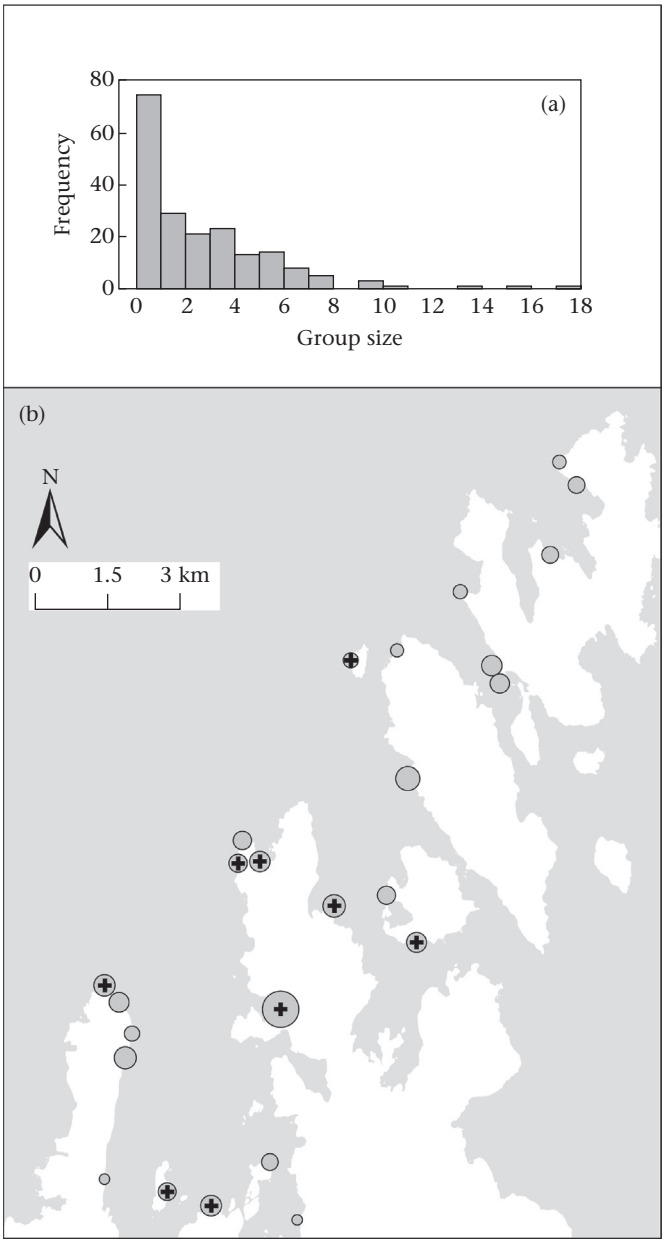

Figure 2. Camera trap results showing (a) the frequencies of river otter group sizes detected at latrines and (b) the spatial distribution of latrines where social otters were detected. In (b), circles are scaled by mean group size and crossover latrines are marked with a cross. Data were collected from 36 camera traps deployed during 3 months in summer 2014 in Prince William Sound, Alaska.

supported compared to the null model (Model 1: $\chi^2_2 = 8.2$, $P = 0.02$; Model 2: $\chi^2_2 = 5.89$, $P = 0.01$; Model 3: $\chi^2_3 = 9.4$, $P = 0.02$; Model 4: $\chi^2_{10} = 24.5$, $P = 0.006$; Model 5: $\chi^2_2 = 6.73$, $P = 0.03$). Models including only the restricted Video data set showed similar support for latrine structure and time compared to the null model (Model 1: $\Delta AICc = 3.8$, $\chi^2_2 = 6.07$, $P = 0.01$; Model 2: $\Delta AICc = 4.1$, $\chi^2_3 = 6.13$, $P = 0.01$; Model 3: $\Delta AICc = 2.0$, $\chi^2_2 = 6.07$, $P = 0.01$; Model 4: $\Delta AICc = 4.3$, $\chi^2_8 = 21.56$, $P = 0.006$; Model 5: $\Delta AICc = 2.1$, $\chi^2_2 = 6.29$, $P = 0.04$).

Several competing GLMMs for the likelihood to perform social behaviour had similar support ($\Delta AICc < 2$; Supplementary Table S4). Of those, the two best supported models (total 48% AICc weight) had a crossover * group size interaction term, and the two following models (total 32% AICc weight) had additive effects of group size and crossover. Thus, group size was a significant positive predictor of social behaviour (Table 4, Fig. 3). In addition, latrine spatial network centrality (positive effect; total 55% AICc weight) was included in the top models (Supplementary Table S4), suggesting that social behaviours occurred largely at centralized latrines. Likelihood ratio tests indicated that all four top models were significantly different than the null model (Model 1: $\chi^2_4 = 24.6$, $P < 0.001$; Model 2: $\chi^2_3 = 21.9$, $P < 0.001$; Model 3: $\chi^2_3 = 21.8$, $P < 0.001$; Model 4: $\chi^2_2 = 18.6$, $P < 0.001$). All four top-ranked models had conditional R^2 values ranging from 0.44 to 0.48 (Supplementary Table S4). Models including only the restricted video data set showed similar support for time and group size interacting with latrine structure compared to the null model (Model 1: $\Delta AICc = 14.0$, $\chi^2_4 = 22.62$, $P < 0.001$; Model 2: $\Delta AICc = 15.12$, $\chi^2_3 = 21.57$, $P < 0.001$; Model 3: $\Delta AICc = 13.5$, $\chi^2_3 = 19.92$, $P < 0.001$; Model 4: $\Delta AICc = 14.5$, $\chi^2_2 = 18.74$, $P < 0.001$). Group size was not a good predictor of per-capita social behaviour in the data set including only occurrences of social interactions ($\beta \pm SE = -0.06 \pm 0.04$, $P = 0.17$; see Supplementary Material, Model Selection).

Proximity Analysis

Our trapping efforts lasted for 11 days in KEFJ (effort = 222 trap-days) and 16 days in PWS (effort = 327 trap-days). Overall, we captured 21 adult otters (14 males and 7 females; Table 5), resulting in a capture success rate of 0.04 otters/trap-day. All were instrumented with proximity tags. Encounternet base units registered 5370 detections among 11 males tracked over 144 days. These detections were collapsed into 56 encounters, with a mean ± SE duration of 8.5 ± 1.2 h (Fig. 4). We registered 140 fission and fusion events, the majority in PWS. None of the seven tracked females was detected associating with any other individual. The proportion of time that tagged males were detected associating with other marked conspecifics ranged from 1% to 59%, suggesting that some of them were predominantly solitary. We additionally recorded 12 564 logs of river otter presence at latrines, which constituted 215 latrine visits, 205 by males and 10 by females (Table 5).

Our data set for the analysis of temporal proximity between latrine visits and grouping events included 163 cases. Mean ± SE time periods between latrine visits and fission or fusion events was 10.0 ± 0.9 h (Fig. 5a). Observed interval length was significantly shorter compared to the random model (random mean interval ± SE = 16.07 ± 1.1 h; Kruskal–Wallis test: $P < 0.001$). In addition, the proportion of latrine visits during encounters between individuals was similar in the observed and randomly generated data (observed = 0.41, random = 0.33 visits; Fisher's exact test: $P = 0.15$; Fig. 5b). QAP results indicated that spatial overlap was significantly related to association indices for PWS (QAP: $R^2 = 0.56$, $P = 0.02$; Fig. 6), but not for KEFJ (QAP: $R^2 = 0.58$, $P = 0.11$; Fig. 6).

DISCUSSION

River Otter Sociality

Our results show that the social system of river otters is mostly male-driven, although similar to females, some males may be solitary. We also observed that when socializing, otters usually aggregated in small and medium-sized groups (2–8 individuals) and were rarely (4% of visits) observed with 10 or more individuals. Animals in flexible social systems are faced with a trade-off between (1) joining larger groups, which may be more advantageous for foraging but entail substantial travel costs (Wrangham, Gittleman, & Chapman, 1993), and (2) staying in smaller social units with reduced conflict and increased cohesiveness (Avilés,

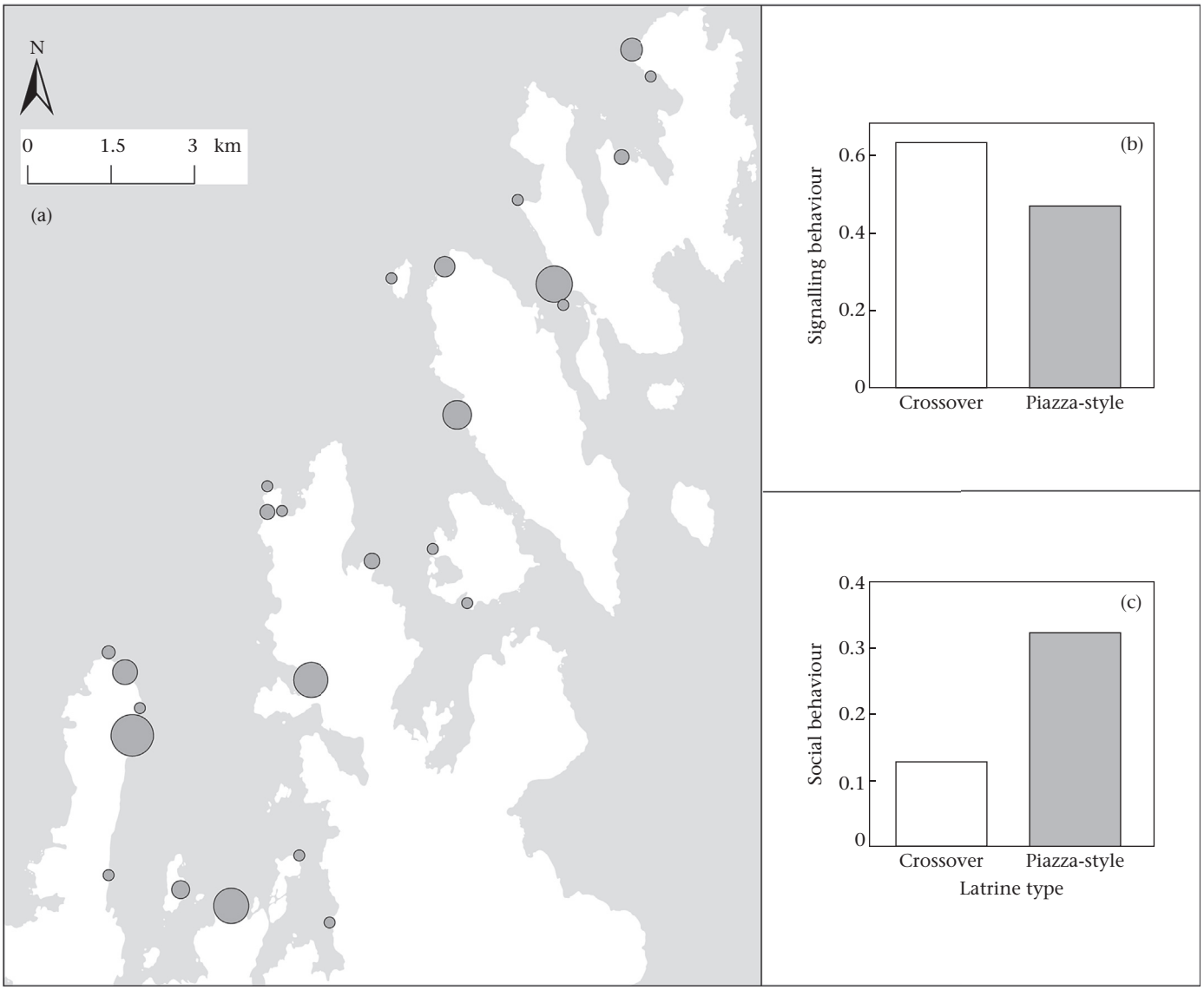

Figure 3. (a) Map of the spatial distribution of latrines where river otter behaviour was sampled; circles are scaled according to the proportion of detections in which river otters performed social behaviour. Proportion of (b) signalling behaviour and (c) social behaviour observations according to latrine type. Data were collected from 36 camera traps deployed during 3 months in summer 2014, in Prince William Sound, Alaska.

Table 2
Parameter estimates and significance of fixed explanatory variables in the best supported GLMM, for river otter latrine visits

Parameter	β	SE	*z*	*P*
Visits ~ structure * centrality				
Intercept	−0.9	1.17	−0.769	0.44
Structure	**2.74**	**0.65**	**4.20**	**<0.001**
Centrality	**27.5**	**8.36**	**3.29**	**<0.001**
Structure * centrality[a]	**−60.88**	**15.03**	**−4.05**	**<0.001**

Variables are described in Table 1. Random factors included subarea and camera type. Significant predictors are shown in bold. Data were collected from 36 latrines during 80 days in summer 2014, in the Knight Island Archipelago, Prince William Sound, Alaska.
[a] Interaction term.

Table 3
Parameter estimates and significance of fixed explanatory variables in the best supported GLMM, for river otter group size during latrine visits

Parameter	β	SE	*z*	*P*
Group size ~ structure + time				
Intercept	1.07	0.13	7.7	<0.001
Structure	**0.45**	**0.18**	**2.58**	**0.001**
Time	−0.03	0.02	−1.56	0.11

Variables are described in Table 1. The random factor was latrine ID. Data were collected from 36 latrines during 80 days in summer 2014, in the Knight Island Archipelago, Prince William Sound, Alaska.
Bold indicates significance at alpha ¼ 0.05.

Fletcher, & Cutter, 2004). Our results suggest that river otters solve this trade-off by predominantly travelling in groups of intermediate size, consistent with evidence on the advantages of optimal group sizes (Markham, Gesquiere, Alberts, & Altmann, 2015). Nevertheless, the high degree of fission–fusion events (140 in 144 tracking days of 11 males), the length of encounters (mean of 8.5 h) and the frequent changes in group size over time suggest complex social dynamics. The temporal adjacency of fission–fusion events and latrine visits by river otters, and the observation that visiting otters performed signalling behaviours more frequently than social behaviours, suggest that sensory cues are largely delivered and obtained through scent marking. Because shifting resource conditions

Table 4
Parameter estimates and significance of fixed explanatory variables in the best supported GLMM for river otter likelihood of performing social behaviour

Parameter	β	SE	*z*	*P*
Social behaviour ~ gsize * structure[a] + centrality				
Intercept	−5.33	1.54	2.08	<0.001
Gsize	**0.64**	**0.19**	**3.22**	**0.01**
Structure	−0.63	1.38	−0.46	0.65
Centrality	47.99	27.94	1.71	0.08
Gsize * structure[a]	−0.37	0.22	1.61	0.11

Variables are described in Table 1. The random factor was latrine ID. Data were collected from 36 camera traps deployed on latrines, during 80 days in summer 2014, in the Knight Island Archipelago, Prince William Sound, Alaska.
Bold indicates significance at alpha ¼ 0.05.
[a] Interaction term.

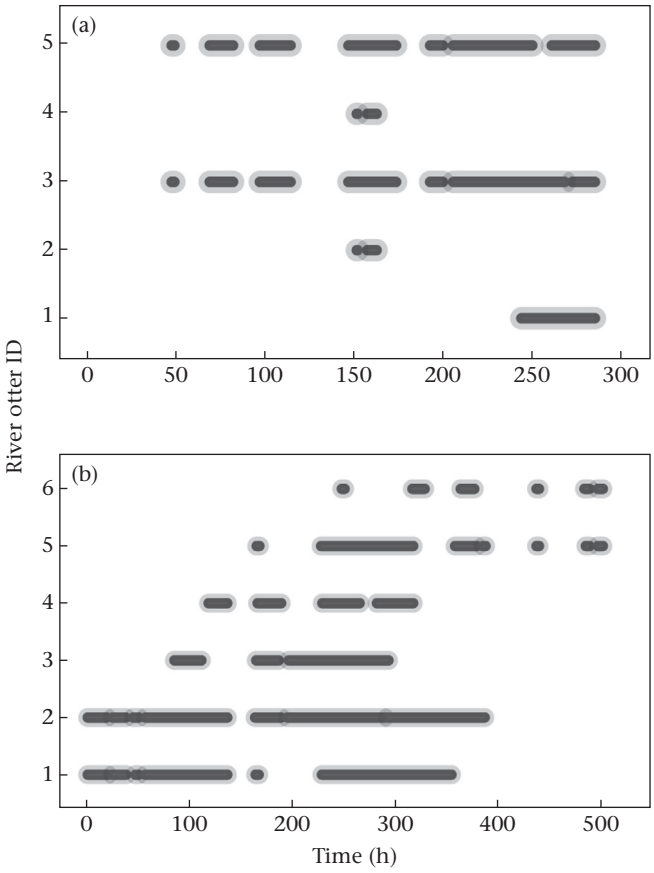

Figure 4. Representation of associations and fission–fusion events among coastal river otters in (a) Kenai Fjords National Park (KEFJ) and (b) Prince William Sound (PWS), spanning the entire periods when all animals were deployed with tags in both areas. Horizontal grey ellipses represent detection data streams of individuals in spatial proximity, pooled within 1 h time scans for clarity. Lighter shading shows encounter limits used for determination of fission–fusion events. Data include 11 males tracked over 144 days during summers 2012 (KEFJ) and 2014 (PWS).

may require frequent changes to group dynamics (Sueur et al., 2011), the maintenance of this highly flexible society is likely mediated through olfactory communication at information hubs.

Our proximity data is derived from a relatively small number of individuals, largely because none of the seven tagged females associated with any other otter. In addition, because river otters often swim and dive in tight groups (Blundell, Ben-David, & Bowyer, 2002), some of our fission–fusion events could reflect attenuation of the signal when animals were under water. In addition, proximity tags reliably recorded the presence of other tagged otters only at distances up to 8 m, whereas in our video footage we observed interactions at distances of up to 16 m. Although we corrected for some of these occurrences by pooling proximity records (see Supplementary Fig. S6), this correction may not have completely accounted for these issues. Furthermore, because we did not capture all individuals in the population, we were unable to quantify the full structure of the otters' social networks. However, by tagging 22% of the estimated population in PWS and 40% in KEFJ (Barocas et al., n.d.) and by uniquely combining proximity and camera trap records, we produced a high-quality data set on fine-scale dynamics of river otter sociality, which is in agreement with results from previous broad-scale studies (Blundell, Ben-David, & Bowyer, 2002).

The lack of associations and minimal latrine visits by tracked females is consistent with previous findings of high sociality among males and spatial segregation between the sexes (Blundell, Ben-David, & Bowyer, 2002). Sex-biased sociality has also been documented in the fossa, *Cryptoprocta ferox*, where sociality confers nutritional and reproductive benefits to males (Lührs, Dammhahn, & Kappeler, 2013). Evidence from both these systems suggests that, under certain ecological conditions, the benefits of securing resources may outweigh male–male competition as presented by sexual selection theory (Emlen & Oring, 1977). However, the rarity of similar social configurations among mammalian taxa indicates that these circumstances are uncommon and that in most cases social organization is driven by the need of females to secure resources, protect young and avoid predation (Silk, 2007).

Latrine Characteristics and Sociality

Our camera trap results revealed that signalling behaviour at latrines was more common than social behaviour, suggesting that these sites function as centres for information exchange. This pattern was especially evident at crossover sites (Fig. 3). Furthermore, river otters more frequently visited crossover latrines and latrines that had higher spatial centrality. Theory predicts that the spatial arrangement of signalling locations is adjusted for its particular social function so as to minimize energy costs to animals (Alberts, 1992). Similar to river otters, grey wolves, *Canis lupus*, show preference for crossroads when establishing and visiting scent stations within territories (Barja et al., 2004), and in southern bamboo lemurs, *Hapalemur meridionalis*, and swift foxes, *Vulpes velox*, latrines, which serve for communication between groups or pairs, are positioned centrally within core home range areas to maximize the probability of encounter by other individuals (Darden et al., 2008; Eppley et al., 2016). Because coastal river otters cooperatively hunt on schools of forage fish (Ben-David et al. 2005), preference for central latrines may maximize information exchange regarding food availability and individual identity. Previous studies

Table 5
Summary results of capture and deployment of the Encounternet tracking system in two areas in coastal Alaska (Kenai Fjords National Park, KEFJ; Prince William Sound, PWS)

Area	Year	Males	Females	Days tracked	Tag detections	Encounters	Fission–fusion events	Base detections	Latrine visits
KEFJ	2012	5	3	61	1338	10	32	12 279	157
PWS	2014	9	4	83	4032	46	108	596	58

Data were collected in summers 2012 and 2014.

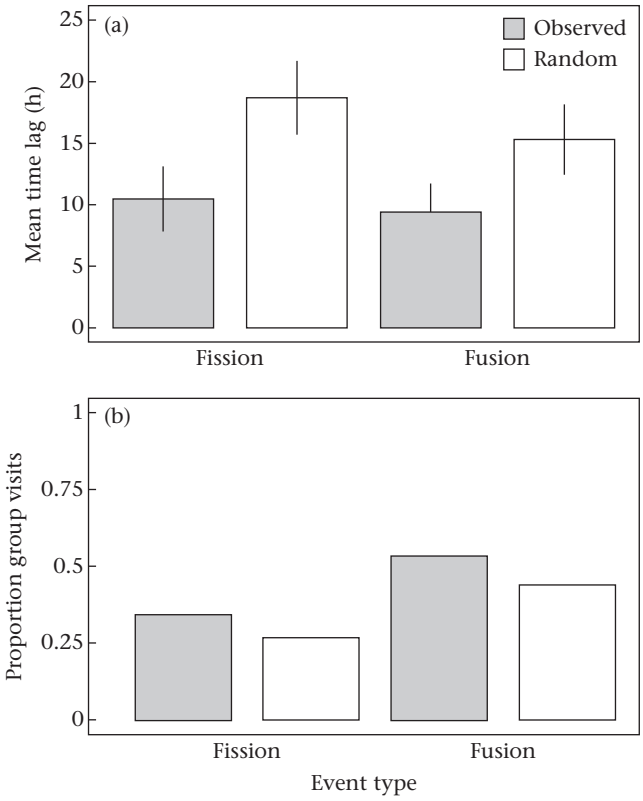

Figure 5. (a) Comparison of observed results to a simulated random model of time periods between river otter latrine visits and fission–fusion events (error bars represent 95% confidence intervals). (b) Proportion of visits when animals were in groups. Data were collected with an Encounternet proximity system during summers 2012 (Kenai Fjords National Park) and 2014 (Prince William Sound) in coastal Alaska.

in this system demonstrated that landscape variables are important in explaining river otter habitat selection (Albeke et al., 2010; Ben-David, Bowyer, & Faro, 1996, 2005; Bowyer et al., 1995). These variables were identified from comparisons of river otter latrines with random coastal sites. Our results, exploring the variation among active latrines, highlight the importance of structure and spatial centrality for selection of social information exchange sites.

Larger river otter groups tended to be found at crossovers, suggesting that these latrines may serve as meeting places among smaller social units. Conversely, at crossovers, river otters were less likely to perform social behaviour. This may be explained by the trail-dominated structure of crossovers, which entails lower spatial cohesion among visiting individuals compared to piazza-style latrines, where animals associate in a central area, promoting social interactions. Piazza-style latrines may therefore function as hubs of social activity. Latrine spatial centrality was additionally supported from model results as a predictor of group size (partial support) and social behaviour (marginal significance). Because of their higher accessibility on the landscape, central places may serve for associations and social interactions among smaller social units that are segregated in space. Evidence from various bird and mammal systems suggests that individuals aggregate at specific locations for sleeping and foraging purposes and that these aggregations promote information exchange (Brown, 1986; Kerth & Reckardt, 2003; Marzluff, Heinrich, & Marzluff, 1996). However, none of these studies explored the effects of spatial centrality of meeting places on group size or social behaviour. In human cities, central locations are more accessible and receive more pedestrian traffic and are therefore hubs for various economic and social activities (Porta & Latora, 2007). Our results indicate that accounting for spatial

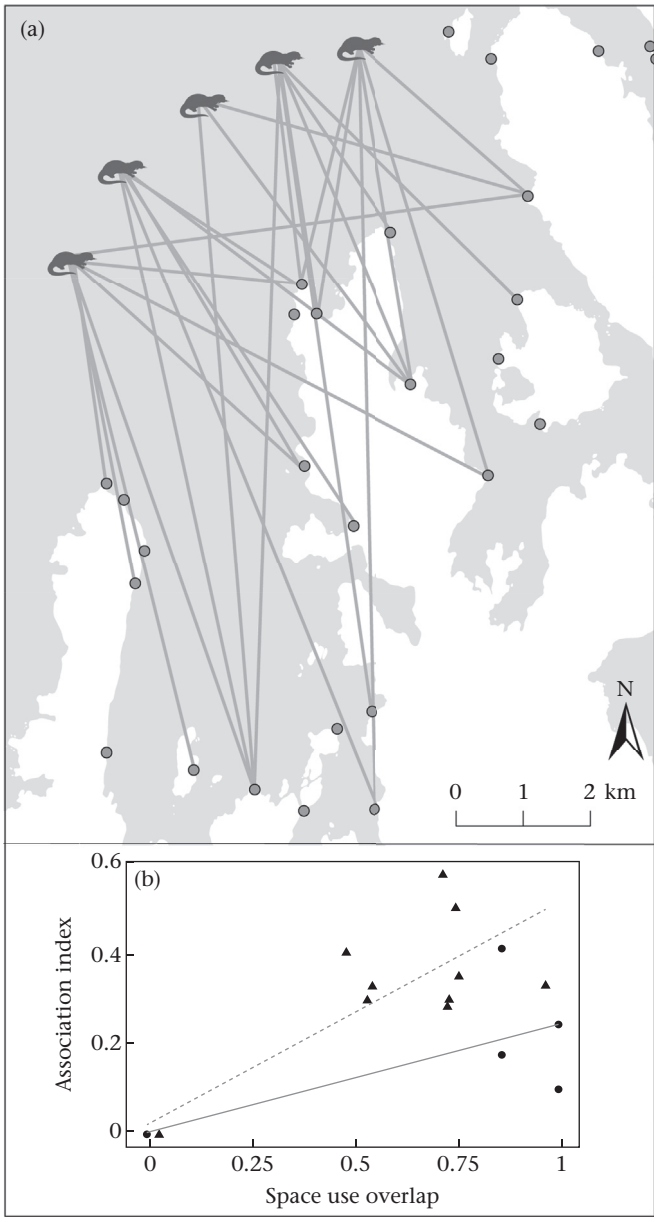

Figure 6. (a) Latrine use showing coastal overlap of five tagged river otters in Prince William Sound (PWS), with connecting lines representing latrine visits by individuals. (b) Relationship between association indices and space use in river otters. The dotted trend line represents a linear fit to dyad values in PWS (triangles) and the solid line represents dyads in Kenai Fjords National Park (KEFJ) (circles). River otters were tracked during summers 2012 (KEFJ) and 2014 (PWS) in coastal Alaska using the Encounternet proximity system.

centrality can be useful in determining the factors that drive animal social structure.

Seasonality and Social Behaviour

Similar to previous observations (Blundell, Ben-David, & Bowyer, 2002), our results revealed a decline in otter group size over the three summer months. The start of our sampling period coincided with the end of the mating season, when male river otters return from long-distance forays and social groups are re-established (Blundell, Ben-David, Groves, et al., 2002). Similarly, changes in interaction rates related to the mating season were observed among captive males (Hansen et al., 2009). Thus, larger

groups at the start of the study may reflect postbreeding behaviour. Alternatively, larger group sizes in June and July may reflect periods when schooling fish are more abundant in PWS (Suryan et al., 2002). Past results (Ben-David et al., 2005; Blundell, Ben-David, & Bowyer, 2002) and individual-based modelling (Albeke et al., 2015) indicate that forage fish availability is an important driver of river otter grouping behaviour. The observed adjustments in group size are consistent with theoretical predictions (Chapman, Wrangham, & Chapman, 1995; Sueur et al., 2011) and observations from several mammal taxa, where fission–fusion rates varied seasonally and larger subgroups formed during periods of high resource availability (Asensio et al., 2009; Smith et al., 2008). Compared to males, seasonality may affect female latrine visits differently. Our data indicate rare latrine visits of tagged females and observations of individuals with pups during the study period. Females accompanied by young pups may avoid visiting male group latrines. In addition, previous results suggest that females generally use distinct latrines and that female latrines may function for communicating intrasexual territoriality (Ben-David et al., 2005). To determine whether female use of latrines changes temporally, as a result of their breeding status, year-round data will be needed.

Spatial and Temporal Association Between Latrine Use and Sociality

Proximity tracking indicated consistent temporal adjacency between latrine visits and fission–fusion events. Solitary individuals or smaller social units may gather information on the presence of nearby individuals and decide to fuse into larger groups. Alternatively, detection of other individuals may drive fission to reduce travel costs to new foraging areas or associate with other highly connected or familiar individuals. Although we were unable to explore the occurrence of such scenarios with our data, the pattern of significant temporal clustering of latrine visits and fission–fusion events suggested an intriguing feedback between olfactory communication and social decisions, consistent with the social complexity hypothesis (Freeberg, Dunbar, & Ord, 2012). In concert, our results suggest that in the river otter social system, latrines have several functions: (1) general exchange of information on presence of conspecifics and resource availability; (2) exchange of fine-scale spatial and temporal individual information, possibly to inform fission–fusion decisions; (3) meeting places among smaller social units; (4) hubs of social activity. These functions differ to some extent from previous findings on systems where animals are predominantly solitary (Dröscher & Kappeler, 2014). Aureli et al. (2008) postulated that in high fission–fusion species, individuals are faced with increased demands on their ability to collect subtle social cues, which lead to the formation of a 'social picture' (Flack, 2012). Our results suggest that in river otters, olfactory communication at latrines significantly contributes to this process and may inform grouping decisions.

The positive relationship between male river otter spatial overlap and social associations (significant in PWS and marginal in KEFJ because of sample size) suggests a link between social decisions and space use. In reticulated giraffe societies, spatial cliques based on home range overlap and association networks are highly similar for females but not for males, suggesting that males actively avoid conspecifics sharing their home range (VanderWaal et al., 2013). In plains bison, *Bison bison,* individuals associate with others that differ in their spatial knowledge and use familiarity and recent knowledge of resource quality to decide which individuals to follow (Merkle et al., 2015). It is difficult to infer cause and effect from our analysis, because space use by individuals that follow or lead conspecifics could be a driver or a result of their social connections. However, it is evident that in river otters, similarly to other flexible animal social systems (Patzelt et al., 2014; Randic et al., 2012; VanderWaal et al., 2013), space use and sociality are interwoven.

Conclusions

One of the evolutionary routes to high fission–fusion social systems derives from a solitary ancestral state, when random or opportunistic associations became increasingly valuable and ecological conditions permitted the formation and maintenance of more cohesive social units (Aureli et al., 2008). Evidence from inland riverine systems, where river otters form smaller groups and show lower spatial overlap (Gorman, Erb, McMillan, & Martin, 2006; Reid, Code, Reid, & Herrero, 1994), suggest that this could be a plausible scenario for this species. Our high-resolution association and space use data, combined with evidence on the effects of latrine structure and temporal variation on several metrics of social behaviour, revealed a highly flexible society. Thus, constant fluctuations in resource availability, sex-specific difference in sociality and multiple contexts for interaction may create selective pressures on coastal river otter fission and fusion decisions. The heterogeneous social information landscape that these carnivores face as a consequence of communication at latrines makes this system suitable for exploring the relationship between sociality and chemical communication and the factors that drive animal social complexity.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.07.016.

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