Animal Behaviour 120 (2016) 103–114

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Adi Barocas [a, b, *], Howard N. Golden [c], Michael W. Harrington [c], David B. McDonald [a, b], Merav Ben-David [a, b]

[a] *Department of Zoology and Physiology, University of Wyoming, Laramie, WY, U.S.A.*
[b] *Program in Ecology, University of Wyoming, Laramie, WY, U.S.A.*
[c] *Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, AK, U.S.A.*

ARTICLE INFO

Article history:
Received 23 February 2016
Initial acceptance 4 April 2016
Final acceptance 24 May 2016

MS. number: A16-00150R

Keywords:
carnivore
fission–fusion
proximity system
river otter
social information
sociality

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, &

---

* Correspondence: A. Barocas, Department of Zoology and Physiology, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, U.S.A.
E-mail address: abarocas@uwyo.edu (A. Barocas).

http://dx.doi.org/10.1016/j.anbehav.2016.07.016

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