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Impacts of Pollutants on Beavers and Otters with Implications for Ecosystem Ramifications

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Abstract: Anthropogenic pollution has impacted ecosystems and organisms globally. Aquatic freshwater systems are of particular concern because of their importance to human health and livelihoods. Sentinel species can serve as indicators for both individual and population-level health risks to both wildlife and humans, and therefore facilitate the mitigation and prevention of such contamination. When such species are also keystone species and/or ecological engineers in aquatic ecosystems, understanding the influence of pollutants on their physiology and behavior acquires added importance. Given that river otters (*Lontra canadensis* and *Lutra lutra*) and beavers (*Castor canadensis* and *C. fiber*) serve such roles and are susceptible to a wide-range of anthropogenic pollution, this makes them prime candidates as indicators or sentinels of aquatic ecosystem health. We review published evidence on the toxicological impacts of pollutants in beavers and river otters and discuss the implications of exposure to their behavioral systems, conservation, and surrounding ecosystem.

Keywords: *bioindicator, keystone species, ecosystem engineers, sentinel species, toxicity*

Ecotoxicologists take an integrative approach to understanding the effects of contaminants in the biosphere at the individual, population, species, and community levels in both terrestrial and aquatic ecosystems (Rattner 2009; Relyea and Hoverman 2006). A particularly strong body of research exists that examines the vulnerability of aquatic ecosystems to pollutants ranging from trace to high concentrations (Carpenter et al. 2011; Douglas et al. 2012; Houde et al. 2011; Rosi-Marshall and Royer 2012; Woodward et al. 2012). Direct toxic exposure in an aquatic ecosystem can result in lethal or sublethal health effects on aquatic wildlife (Fleeger et al. 2003). Even natural chemical signals, such as kairomones, can have cascading ecological effects (Marino et al. 2015), revealing the sensitivity of these systems to chemical inputs. The presence of water-borne pollutants is particularly likely to initiate a trophic cascade if pollutants exert either lethal or sublethal effects on foundation species (e.g., primary producers or species that affect ecosystem structure, such as hard corals [see Angelini et al. 2012]), ecosystem engineers (e.g., in some cases herbivores that modify habitat like beavers or elephants [Jones et al. 1994]), or keystone species (such as terminal or near terminal trophic predators [Fleeger et al. 2003]). For this paper, we focus on the sublethal effects of water-borne pollutants and the roles of an ecosystem engineer, the beaver, and a keystone species, the otter, in freshwater habitats. Our tenet is that the interactions between two such ecosystem forces can potentially have profound impacts on the ecosystem that might not be predicted by considering only one.

Ecosystem engineers are those species that "directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials" (Jones et al. 1994, 373). Eurasian and North American beavers (*Castor fiber* and *C. canadensis*, respectively) are notable ecosystem engineers because they create wetlands, affecting sediments, organic matter, nutrient cycling, decomposition, water flow and temperature, and plant and animal communities (Naiman and Melillo 1984; Naiman et al. 1986; Naiman et al. 1988; Naiman et al. 1994; Wright et al. 2002; Rosell et al. 2005). Similar to keystone species, ecological engineers can vary in their extent of impact based on location and habitat (Rosell et al. 2005; Moore 2006; Brzyski and Schulte 2009), requiring an understanding of abiotic, biotic, and anthropogenic inputs that affect ecosystem engineering. Beavers make their most profound impact on water flow and aquatic patch creation in their first two decades following colonization (Johnston and Naiman 1990). Thus, the flow of nutrients and pollutants within and through the system is dependent in part on the duration and extent of beaver-created wetlands and whether such systems go through their natural process of succession (Correll et al. 2000). While beavers themselves may be affected by pollutants, the ramifications of toxins on altering beaver activity as ecosystem engineers has the potential for much more profound ecological impacts.

As a top predator in this system, and one that interacts with beavers in various ways, river otters (*Lutra lutra* and *Lontra canadesis*) serve as a keystone species (Estes and Duggins 1995; Roemer et al. 2009) and a sentinel species for freshwater health. The keystone species concept was introduced by Paine (1969) to describe the critical importance of a top predator (a starfish) in an intertidal habitat. The term lost some value because it became increasingly used for a variety of other species and ecosystem effects. Davic (2003) attempted to rectify the issue by maintaining the top-down ecological role of keystone species and adding a delimiter that the effects of a keystone species are large relative to its occurrence within its functional group (e.g., suite of prey species). The scale of impact necessary to be labeled keystone has not been firmly established, but modeling trophic webs using a mixed trophic matrix can help to identify the level of 'keystoneness' for a species or group of species (Libralato et al. 2005). A particular species may not always be keystone, but the species plus the particular ecosystem interactions determine the extent to which a particular species plays a keystone role (Libralato et al. 2005; Menge et al. 1994). The use of keystone has even been extended further to natural, defensive compounds, such as guanidine alkaloid neurotoxins, that affect community structure (Zimmer and Ferrer 2007). Thus, species and chemicals may exert a stronger effect on community structure, typically through trophic dynamics, than would be expected by their abundance, indicating a keystone role in the ecosystem.

Humans have long used other species as indicators of potential toxin threats to humans; these species are termed sentinel species (van der Schalie et al. 1999). Sentinel species may react to these toxins before major environmental problems ensue (Pritchard et al. 1997; Milne and Guillette 2008). In addition, they may be more sensitive than humans to exposure and/or respond in a similar fashion as humans (Pritchard et al. 1997; Milnes and Guillette 2008). In aquatic environments, widespread apex predators, such as bald eagles (*Haliaeetus leucocephalus*) and osprey (*Pandion haliaetus*) (Grove et al. 2009), marine mammals (Bossart 2011), and mustelids (Basu and Head 2008) serve well as sentinel species. A number of studies have examined the exposure of mustelids to a variety of contaminants including pesticides, heavy metals, cesium 137, polychlorinated biphenyls (PCBs), and crude oil (see Table 1 in Bowyer et al. 2003), providing a strong foundation for examining environmental impacts.

Species may be considered keystone, ecosystem engineers, sentinels or some combination of these three classifications. The commonality among species in these classifications is that such species exhibit strong interactions with the biotic and often abiotic components of their habitat (Soulé et al. 2005). The benefit of interactivity as a concept is akin to that of keystoneness (see above) – it suggests a continuum and not a duality in relative importance of species to ecosystem function. Clearly, all species have the potential to be detrimentally affected by contaminants, yet not all species can be effectively examined. Thus, those species with greater connectedness and impact on ecosystem operation provide a focus. When these species also are appealing to humans and parallel aspects of human physiology and behavior, they can be especially operative bellwethers of impending ecological damage.

In this paper, we examine beavers as ecosystem engineers and river otters as keystone species. We suggest that they might serve together as a sentinel species unit in light of aquatic contamination. Considering the two species is interesting because of their shared habitat yet different trophic levels. River otters are common in and around beaver ponds (LeBlanc et al. 2007) and have been considered competitors with beavers and sometimes predators on young beavers (Saunders 1988; Reid et al. 1994, 1998). In northern winters, otters will travel from one beaver pond to another, creating holes in dams for passage. This lowers the water level in a pond until the beavers can repair the dam. This periodic change in water flow even during winter could affect the movement of contaminants. In addition, the differences in trophic level (herbivorous beavers and carnivorous otters) and mobility (high site fidelity by beavers compared to otters) can influence the degree of biomagnification (Kidd et al. 2012) that may occur in these species and the environment. Together, these factors warrant considering the two species as a meaningful bioindicator unit and thus motivate their combined conservation (Kushlan 1993). We discuss the behavioral and toxicological impacts of anthropogenic pollutants on the conservation of beavers and river otters. To accomplish this, we first present the natural history of these species as a conservation concern. Second, we review the published evidence on the toxicological impacts of anthropogenic pollutants on these species and suggest potential behavioral abnormalities that may result as a consequence of exposure to anthropogenic pollution. Finally, we highlight the potential ecological implications of such exposure and behavioral abnormalities.

Natural History and Historical Conservation of Beavers and River Otters

The two extant beaver species are semi-aquatic rodents that belong to the order Rodentia and family Castoridae (Müller-Schwarze 2011). Prior to the nineteenth century, both species resided in a wide range of ecoregions, ranging from subtropical to subarctic throughout the globe, including the American, European, and Asian continents (Rosell et al. 2005). Due to overhunting for castoreum and fur, as well as agricultural expansion, beavers on a large portion of the North American continent were nearly extirpated by the end of the 20th century (Macdonald et al. 1995; Schulte and Müller-Schwarze 1999). Similarly, Eurasian beavers were over-hunted until there were approximately 1200 left in only a few isolated regions (Nolet and Rosell 1998). Since then, government-mandated artificial and natural recolonization of beavers have aided in the re-expansion of beavers on both continents. Beavers have been used to restore wetlands, improve stream dynamics, and reduce flooding (Müller-Schwarze 2011; Gibson and Olden 2014). The most recent estimate on the population size of the North American beaver is 6-12 million (Naiman et al. 1988) and the Eurasian beaver is estimated at 639,000 (Halley and Rosell 2003).

Similar to the beaver, river otters were once abundant throughout the waterways of Canada, the United States (Lariviere and Walton 1998), and Europe (MacDonald and Mason 1994). Drastic population declines of river otters (*Lontra canadensis*) in North America have been attributed to hunting for pelts, urbanization, changes in the availability of food sources, and pollution (Latch et al. 2008; Serfass et al. 1993). In the United Kingdom, reductions in the Eurasian otter (*Lutra lutra*) populations occurred starting in the 18th century, initially because of perceived competition with humans for fish and for sport, and later from pollution, persecution, habitat loss, and prey reduction (Jeffries 1989; Kruuk and Conroy 1991; Kruuk 1995). A similar pattern occurred for populations in mainland Europe (MacDonald and Mason 1994). Protection and recovery came slowly as by the early 1980s river otters were still rare in many locales west of the Mississippi (Jenkins 1983), while populations in Europe remained sparse or absent in many historic locations (MacDonald and Mason 1994). Over the next twenty years, reintroductions and improved habitats led to an expansion of river otters to much of their former range in North America (Raesly 2001), and in some places in Europe (Robataille and Laurence 2002). At least in coastal areas, natural range expansion can be relatively slow such that translocations may still be important for restoring populations (Blundell et al. 2002b).

Exposure to Anthropogenic Pollutants

Anthropogenic contamination has been considered to be one of the factors responsible for decreasing population sizes in otters in Europe (Chanin and Jefferies 1978; Gutleb 2000; Mason et al. 1986) and North America (Wren 1991), but the role of pollution in declining beaver populations on both continents is unknown. Exposure to PCBs and other organochlorides may be responsible for later twentieth century population declines in both American (Wren 1991) and Eurasian otters (Mason et al. 1986). River otters have been of particular interest to wildlife toxicologists due to their potential as biomonitors of environmental contaminants for humans, water quality, and riparian habitat conservation (Anderson-Bledsoe and Scanlon 1983; Basu et al. 2005a; Basu et al. 2005b; Kannan et al. 2002). On the other hand, there is little primary literature showing the effects of environmental contaminants in beavers for either *C. canadensis* or *C. fiber* (Fimreite et al. 2001; Giżejewska et al. 2014; Giżejewska et al. 2015; Hillis and Parker 1993; Nolet et al. 1994; Wren 1984; Zalewski et al. 2012).

Deaths resulting from direct poisoning are rare, potentially due to sampling limitations in the field. However, sublethal effects (low-level to high-level not fatal exposure) could cause organ failure and disease, as well as impact life history and behavioral systems responsible for successful reproduction and population dynamics. Furthermore, the widespread distribution of multiple pollutants at once increases the likelihood of synergistic effects. Together, these factors can result in population declines and prevent impacted populations from rebounding.

Both species accumulate various metals and organochlorine chemicals. In both otters and beavers, the focus of research has been on tissue and body burdens as a result of mercury exposure in river otters and cadmium exposure in beavers due to their food preferences. Accumulation of metals (arsenic, cadmium, lead, mercury, selenium, copper, manganese, and zinc) and PCBs in both species can be age-specific (Fimreite et al. 2001; Giżejewska et al. 2015; Hillis and Parker 1993), sex-specific (Walker et al. 2011), and tissue-dependent (Chadwick 2007; Kang et al. 2015; Wren 1991; Zalewski et al. 2012).

Beavers

For beavers, the focus has been on the accumulation of cadmium in tissues due to their herbivorous nature and consumption of plant material exposed to hazardous concentrations of this and other metals (Nolet et al. 1994). For example, mercury accumulates in both beavers (Giżejewska et al. 2014; Sheffy and Amant 1982; Wren 1984) and beaver wetlands (Driscoll et al. 1998; Painter et al. 2015). Beavers prefer an herbaceous and woody diet for both consumption and engineering of dams and dens (Bryzski and Schulte 2009), leaving them susceptible to pollution in the aquatic ecosystem and plant material.

Elevated levels of cadmium in tissues have been reported in multiple studies in both polluted areas and areas considered "ecologically clean" (Fimreite et al. 2001; Giżejewska et al. 2014; Giżejewska et al. 2015; Nolet et al. 1994; Zalewski et al. 2012). Fimreite et al. (2001) found that beavers' preferred plant species (aspen [*Populus* spp.], birch [*Betula* spp.], and rowan [*Sorbus* spp.]) were the highest accumulators of cadmium and that this likely induced the high cadmium concentrations found in beaver tissues in their study. Levels of cadmium in both the kidney and hair are correlated with concentrations of cadmium in both the bark and leaves of willow (*Salix* spp.) and poplar (*Populus* spp.) trees (Nolet et al. 1994). In the only known study of relocation of beavers into a contaminated area (Nolet et al. 1994), accumulation of cadmium in the kidney significantly increased in relation to the residential time, i.e. the length of presence in the contaminated ecosystem. In less than six months, there was a threefold increase in cadmium concentration in the hair (Nolet et al. 1994).

In addition, there is a relationship between fat content (an indicator of condition) and cadmium concentration in the kidneys; higher than normal cadmium concentrations may therefore reduce fat content in beavers (Fimreite et al. 2001). They store fat in their tails in an effort to decrease potential starvation during harsh winter conditions (Aleksiuk 1970). Therefore, cadmium exposure may increase their susceptibility to not only disease but also over-wintering starvation.

Otters

While otters consume a large number of species, they feed mostly on fish and shellfish (90% of their diet), and less so on other invertebrates, amphibians, birds, and mammals (Anderson-Bledsoe and Scanlon 1983; Carss 1995; Cote et al. 2008; Evans et al. 2000; Fretueg et al. 2015; Kean et al. 2013; Mason et al. 1986; Reid et al. 1994). This is of prominent conservation concern because the position of river otters at the top of the food chain increases their susceptibility to bioaccumulation of a wide-range of contaminants (Anderson-Bledsoe and Scanlon 1983; Evans et al. 2000; Kean et al. 2013; Mason et al. 1986).

Accumulation of mercury is well documented in mustelid tissues, particularly otters. Mercury poisoning is considered a risk factor for river otter survival because it is a ubiquitous neurotoxin that readily bioaccumulates in the food chain (Basu et al. 2005a; Basu et al. 2005b; Dornbos et al. 2013). Concentrations of mercury have been observed in various tissues in otters (Evans et al. 2000; Dornbos et al. 2013; Sleeman et al. 2010; Wren 1984; Wren et al. 1986; Giżejewska et al. 2014). Several authors have found quantifiable mercury levels in the brain (Dornbos et al. 2013: Evans et al. 2000), with significant mercury-associated neurochemical changes (Basu et al. 2005a; Basu et al. 2005b; Basu et al. 2007a; Basu et al. 2007b; see Basu and Head 2008 for a complete review; Dorbos et al. 2013). Thus, mercury exposure can have severe effects on the nervous system of river otters.

During and post oil spills, both river and sea otters are at risk of sublethal exposure to pollutant petroleum products in coastal marine regions via consumption of prey and during grooming. Run-off from engine oil discharges contributes to widespread contamination of hydrocarbons in freshwater ecosystems; this leads to chronic exposure to a host of chemical compounds that comprise gasoline (Mason 1989). Sublethal exposure induces many resultant health deficits in river otters, including increased haptoglobin (an indicator of tissue damage), decreased body mass, chronic inflammation, liver injury (Duffy et al. 1993; Kimber and Kollias 2000), and malnutrition (Kimber and Kollias 2000). Acute exposure reduces waterproofing of their fur, resulting in heat loss and hypothermia (Mason 1989; Stoskopf et al. 1997).

Oil spills in coastal regions can lead to changes in the diet of river otters (Bowyer et al. 1994) by reducing the variety of prey (Kimber and Kollias 2000). In a study by Ben-David et al. (2000), river otters experimentally exposed to oil from an oil spill were anemic relative to control otters; the oiled otters had higher oxygen consumption when foraging and dove for food less. In addition, exposure to petroleum products reduces buoyancy (Mason 1989) and increases the number of abandoned latrine sites (Kimber and Kollias 2000), which are important in social recognition and spacing (Oldham and Black 2009).

Potential Behavioral and Ecological Ramifications

Individual-level effects on behavior (such as movement and spatial use, foraging, social organization, and reproductive behavior) can impact biodiversity (Berger-Tal et al. 2011), particularly in this system due to the status of both the otter and beaver individually, and synergistically. Therefore, considering behavioral ramifications will be important in promoting conservation efforts for both species and the aquatic ecosystem at large.

Behavioral Ramifications

Toxicants can have a variety of physiological effects that can alter or eliminate behaviors important for survival and reproduction in the exposed generation (Clotfelter et al. 2004; Scott and Sloman 2004; Weis et al. 2001). As a result of low-level exposure to endocrine-disrupting chemicals (EDCs), a range of behaviors important for fitness and effective social organization of populations can be altered (including but not limited to: mating, aggression, territoriality, parental care, coordination and balance, memory, chemosensory communication, and motivation and activity; see Zala and Penn 2004 for a complete review). EDCs that adversely affect predatory behavior, parental care, and sociality, in particular, could potentially alter species interaction with the ecosystem and change the ecosystem dynamics via predator-prey interactions and use of latrine sites. In addition, remediation of EDCs from the environment does not eliminate resulting behavioral modifications, as shown in studies testing transgenerational exposure (meaning that the parental generation is exposed and three subsequent generations are unexposed, see Anway and Skinner 2006 for a complete review; Crews et al. 2007). This means that even low-level exposure to EDCs can have long-lasting effects on conservation efforts, well past environmental remediation.

In otters, decreased appetite, decreased pup survival, and reproductive failure are a common response to a host of pollutants (Kean et al. 2013; Wren 1991 for a complete review). Kean et al. (2013) found a reduction in baculum weight and increases in reproductive abnormalities (such as cryptorchidism and cysts on the vas deferens), attributed to high levels of persistent organic pollutants. Reductions in male reproductive organs can potentially feminize males, inducing changes in cognitive processing, stress responses, sexual behaviors, and territorial behaviors, as shown in research in mammalian model systems (von Saal et al. 1995; Zuloaga et al. 2008). In response to cadmium toxicity, beavers exhibited a similar response in reproduction: decrease in reproductive fertility via abnormal sperm counts (Zalewski et al. 2012). Changes in reproductive viability are likely to have a cascading effect on continued conservation of these species and maintenance of their status as sentinels, keystone, and ecosystem engineers.

Ecological Ramifications and Synergistic Effects

The presence of otters often correlates with that of beavers (DePue and Ben-David 2010; Dubuc et al. 1990; Gallant et al. 2009; Newman and Griffin 1994; Swimley et al. 1999). Thus, the protection and reintroduction of beavers can be a positive contributing factor to the recovery and maintenance of river otter populations, at least in North America (Collen and Gibson 2001; LeBlanc et al. 2007). However, this also indicates that each species could not only be exposed to similar contaminants, but their individual and interactive action could affect the storage or flow of said contaminants.

The predatory behavior and the creation of latrines by river otters influence the dynamics of both their aquatic and terrestrial habitats. Piscivory by river otters facilitates the movement of nutrients, notably nitrogen and phosphorus between sea or freshwater systems and land, enhancing productivity of terrestrial vegetation (Ben-David et al. 1998; Lilleskov et al. 2001; Roe et al. 2010). The social nature of river otters also relates to the species of fishes caught, and the availability of particular fish species may affect the distribution of social otters. Male river otters are found in social groups more often than females who care for the young (Blundell et al. 2002a).

In coastal Alaskan waters, social otters cooperatively hunt on fast swimming pelagic fish, but sociality is not kin based (Blundell et al. 2004). Although typically having a diverse diet, river otters may be more restricted in some systems, such as their dependency on cutthroat trout in Yellowstone Lake (Crait and Ben-David 2006). In such situations, factors, including toxins, which adversely affect one or a few prey species, could have more immediate and dire consequences than for otters with a more diverse diet.

Latrine sites are areas that are scent-marked with feces, urine or anal gland secretions for either intra-group communication (marked more heavily in social groups) or mutual avoidance in nonsocial groups (Ben-David et al. 2005). Although otter diet improves the movement of nutrients and subsequently the productivity of vegetation (Roe et al. 2010) through increases in fish density at latrine sites (Ben-David et al. 2005), the physical activity of creating latrines can damage smaller plants (Roe et al. 2010). The influx of nutrients released at river otter latrine sites varies with respect to the social nature of the otters (Ben-David et al. 2005); less social otters use a relatively large number of different latrine sites with infrequent revisits, whereas more social otters visit fewer latrines frequently. Kimber and Kollias (2000) found increased abandonment of latrine sites post-petroleum exposure; higher levels of abandonment of latrines may indicate changes in sociality in otters but would subsequently decrease damage to smaller plants. However, abandonment would also result in decreased piscivory at latrine sites, causing a decrease in the productivity of the local terrestrial vegetation.

Contaminants can be moved in a similar fashion as nutrients. While we could find no work directly on the potential nutrient flow related to scent mound construction by beavers, the physical modification of habitat exacted by beavers could clearly influence the location of pollutants in the water and sediment. Destruction of dams by the U.S. Department of Agriculture Forest Service in Lake Tahoe occurs annually in the early fall in an effort to provide kokanee salmon (*Onchorynchus nerka*) spawning grounds (Muskopf 2007). The creation of beaver ponds reduced the total phosphorus concentration in the environment, potentially improving the water quality via nutrient retention. Roy et al. (2009) found that downstream aquatic communities with beaver ponds less than ten years old contained the greatest methylation efficiencies and methyl mercury concentrations, incurring high heterotrophic activity as a result. Painter et al. (2015) also found increased levels of methylmercury, periphyton, and invertebrates in the water downstream of beaver ponds. The conflicting nature of the phosphorous and mercury results indicates the potential impact of beaver on either the remediation or worsening of pollution. Because beaver ponds serve as habitat for salmonid fishes (Colleen and Gibson 2001), toxins may pass from these fish to higher predators such as otters or humans. Thus, further research is needed to determine the influence of beaver activity on environmental contaminants.

The environmental context can influence the ecological impact of a toxicant (Liess and Beketov 2008). For example, beavers and otters may show few effects under good conditions, but during times of stress (e.g., extended severe weather), contaminants could have a more pronounced impact. Thus, direct effects on a species can be modulated by conditions, but there also can be important indirect effects (see review by Fleeger et al. 2003). In some cases, the effects on a predator and a prey may offset, such that no net impact can be attributed to the toxicant (Bridges 1999). Yet, when the health and behavior of keystone species or ecological engineers are altered by contaminants, the trophic cascades and competitive releases have the potential to be dramatic, potentially reducing the quality of ecosystem functions and services (Cairns and Niederlehner 1994; Peters et al. 2013) that such species provide.

Conclusion

Given the importance of both beavers and river otters in the productivity and health of the freshwater aquatic ecosystems, it is important to understand the implications of the vast number of potential contaminants that pose both sublethal and lethal risks. Understanding resulting behavioral modifications due to exposure to sublethal levels still needs to be explored in more detail. Further wildlife studies are needed, particularly with a focus on behavior conservation to determine behavioral indicators and species management (see Berger-Tal et al. 2011 for the behavioral conservation framework). In particular, potential research avenues could include studies that focus on: 1) behaviors that relate to fitness and reproductive success, 2) impact of behavioral changes on ecosystem biodiversity and function, and 3) the interaction of otters and beavers as a unit to determine their impact as a synergistic unit on ecosystem toxicity or remediation. This will lend insight into how changes in the behavior of these keystone and engineer species will in turn modify the individual, population, and community-level responses.

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