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REVIEW

# Conservation of the Eurasian beaver *Castor fiber*: an olfactory perspective

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## ABSTRACT

**1.** Chemical communication in mammals includes an array of specific behaviours that are often ignored in terms of their potential relevance to conservation. Often used during territorial or social interactions between animals, chemical communication can also be used as a tool in reintroduction programmes. Reintroductions still exhibit high failure rates and methods to improve success should be investigated. The Eurasian beaver *Castor fiber* has been widely reintroduced across Europe after its near extinction in the 19th century.

**2.** Using olfactory studies in the beaver, we aim to demonstrate how scent transfers a range of information about the sender which can be used to monitor social and territorial behaviour along with general well-being. Scent manipulation can be used to reduce human–beaver conflicts, and aid reintroduction success through reducing stress and territorial conflicts, and by influencing dispersal and settlement.

**3.** Two species of beavers, the Eurasian beaver and the North American beaver *Castor canadensis*, occupy freshwater habitats throughout North America and in parts of South America, most of Europe and parts of Asia. Most of the reviewed literature concerns the wild Eurasian beaver, its chemical communication and conservation; however, captive studies and those addressing North American beavers are also included.

**4.** Chemical communication is advanced and has been well documented in this highly territorial species. However, few studies directly link olfaction with conservation practices.

**5.** Olfactory studies in beavers can provide non-invasive methods to monitor translocated animals and indicators of health. We conclude that chemical analysis, olfactory studies and behavioural manipulations involving semiochemicals have important impacts on conservation and can generate practical solutions to conservation problems including aiding animal capture, captive stress reduction, breeding pair formation and release site fidelity.

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## INTRODUCTION

Studies in behavioural ecology have much to offer to conservation biology and can provide important information to inform conservation decisions (e.g. Caro 1998, Gosling & Sutherland 2000). Detailed knowledge of animal behaviour enables theories and methodology to be developed that can aid both *in situ* and *ex situ* conservation, e.g. captive welfare, population monitoring, dispersal, habitat selection, human–wildlife conflicts and translocation programmes. Conservation biology is increasingly concerned with population monitoring, particularly when population growth comes into conflict with human land use. Conservation efforts need to consider animal well-being whether animals are from wild, captive or newly reintroduced populations, and should employ the minimum possible intervention.

Chemical communication in mammals includes an array of specific behaviours that are often ignored in terms of their potential relevance to conservation. Swaisgood (2007) calls for greater investigation into the role of olfaction in animal dispersal, territorial conflict and predator recognition, to aid conservation. Work with giant pandas *Ailuropoda melanoleuca* by Swaisgood et al. (1999, 2000, 2001) reveals how vital olfactory cues are to the conservation of this species by using conspecific scent to encourage mating, reduce aggressive interactions, and possibly pre-establish home ranges for reintroduced and translocated individuals. Decoding the information transmitted by these cues enables their manipulation, to encourage breeding and increase welfare in captivity. Roberts and Gosling (2004) and Roberts (2007) highlight how the regulatory role that scent marking has on social behaviour offers practical solutions for animal welfare and conservation concerns. Preliminary scent broadcasting experiments in the black rhinoceros *Diceros bicornis*, with individual scent, display the potential to manipulate post-release movement distances in translocated animals (Linklater et al. 2006). More generally, and as stated by Linklater (2004), the manipulation of scent is an 'underused part of the conservation biologist's toolbox'.

Olfactory studies, especially in nocturnal or secretive species, offer non-invasive means to monitor animals. Sutherland (1998) highlights numerous areas in which animal behavioural research could aid conservation. Within conservation biology, reintroduction programmes are often criticized for their lack of associated focused monitoring programmes (Armstrong & Seddon 2008), while Sutherland (1998) cites behavioural reasons for the failure of so many release programmes. Olfactory studies could make vital contributions to these areas and should be incorporated into studies suggested by Sutherland (1998), including studies of species isolation; dispersal in fragmented populations; predation reduction; behavioural manipulation; release schemes; captive breeding and population census.

In species which use olfactory communication, chemical marking can be employed to manipulate, monitor and control populations. Beavers *Castor* sp. represent such a species as they are highly territorial and regulate most of their social interactions through chemical signalling (Sun & Müller-Schwarze 1997). The Eurasian beaver *C. fiber* was once widespread in Europe and Asia, but was reduced to approximately 1200 individuals by the beginning of the 20th century (Nolet &

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Rosell 1998). The present growth of beaver populations throughout Europe is largely facilitating by natural spread, however, some areas are unlikely to be naturally repopulated (e.g. Britain, Po basin and lower Danube), therefore reintroductions and translocations have played an important role in beaver population recovery (Nolet & Rosell 1998, Halley & Rosell 2002, 2003). Out of 87 reviewed beaver reintroductions, 53% resulted in reproducing pairs and were therefore deemed successful (Macdonald et al. 1995).

In this paper we review how olfaction studies, chemical analysis and behavioural manipulations involving semiochemicals have important impacts on conservation and can generate practical solutions.

## METHODS

We reviewed the available literature using the keywords beaver, *Castor fiber*, *Castor canadensis* with chemical communication, chemical ecology, conservation, health, olfaction/olfactory, reintroduction and semiochemicals, in the following search engines: ISI Web of Science, ScienceDirect, SpringerLink and Wiley InterScience. This literature includes published book chapters, journal articles, scientific reports, seminar proceedings and PhD theses. We use the wild Eurasian beaver as our main model, but also include information from captive studies and those addressing the North American beaver. Beavers currently occupy freshwater habitats throughout North America, and in parts of South America, most of Europe and parts of Asia. The majority of the text addressing the Eurasian beaver refers specifically to studies on wild, Norwegian populations from the Telemark region.

## RESULTS

### Past and present demography of the Eurasian beaver

During the 19th century the Eurasian beaver almost became extinct through overhunting (Nolet 1996, Nolet & Rosell 1998). The current population recovered from approximately 1200 individuals in eight isolated populations (Nolet & Rosell 1998). Translocation and reintroduction programmes were widely used, so that today the beaver occupies much of its former range (Halley & Rosell 2002, 2003). Over 158 translocations have been recorded, in 25 European countries (Halley & Rosell 2002). The current estimated population of the Eurasian beaver in Europe is 639000 (Halley & Rosell 2003).

Beavers are part of the native fauna of Europe and, as their demise was caused directly by human actions, many argue that we have an ethical responsibility to conserve this species and restore it to its natural range. The Eurasian beaver appears on the International Union for Conservation of Nature Red List of threatened species. It is now categorised as ‘Least Concern’, but conservation efforts are recommended to ensure this species does not become threatened again (Batbold et al. 2008). At the landscape scale, beaver habitats and foraging behaviours increase the biodiversity of both plant and animal species (Rosell et al. 2005). Beaver activity can stabilise water flow, which in turn increases the resistance of an ecosystem (Rosell et al. 2005). Beaver dams act to filter water and retain sediment so water quality is improved, and erosion and flooding rates are reduced (Bergstrom 1985, Parker 1986, Harthun 2000, Rosell et al. 2005). The two species of beavers represent a distinct branch of evolution which displays a unique foraging behaviour that has conservation value in itself (Rosell et al. 2005). The socio-economic benefits of beavers arise from hunting, trapping and wildlife tourism (Rosell & Pedersen 1999, Campbell et al. 2007). The latter may be particularly lucrative in countries where beavers have been absent for centuries, for example in Britain.

Although beaver populations in Europe are expanding, populations in Asia are small and under threat (Durka et al. 2005). Asian populations consist of three subspecies (*C. f. tuvinicus*, *C. f. pohlei* and *C. f. birulai*; Durka et al. 2005). It is estimated that <700 individuals of *C. f. birulai* exist (Chu & Jiang 2009) and hence this subspecies is classified as 'Endangered' in the Chinese Red List (Batbold et al. 2008). Current population size and geographical separation of these Asian subspecies have led to calls for them to be managed as evolutionary significant units (ESUs), thus requiring special conservation efforts to stabilize numbers and protection from expanding European populations (Stubbe et al. 1991, Durka et al. 2005).

**Impact of over-hunting**

The history of beavers in Europe is an example of how one species can be over-hunted. Where hunting of beavers is permitted, it is generally restricted to particular seasons, e.g. October to early May in Norway (Parker & Rosell 2003). Adult beavers, particularly pregnant females, are more prone to being shot than any other demographic group (Parker et al. 2002). In general, pregnant mammals have between 17% and 32% greater food intake requirements than non-pregnant females (Robbins 1993), and gravid female beavers spend 52% of their active time feeding (May–June), compared with 29% for adult males (Buech 1995). Pregnant females are therefore highly susceptible to hunting. The removal of pregnant females can have a significant effect, by reducing the population's productivity (Parker et al. 2002). Adult males are also highly susceptible to removal as they scent mark more frequently than any other family members (Rosell & Thomsen 2006) and tend therefore to be more visible. Removal of adult males can delay breeding of adult females: although adult males are quickly replaced, females may be reluctant to breed with new dispersers which tend to be younger (Parker et al. 2007). Breeding later in the season can also lead to reduced offspring survival (Parker et al. 2007). Parker et al. (2002) found that harvesting 25% of the autumn population of Eurasian beavers led to an overall decline in occupied colonies of 46% in only 3 years. Hence, beaver populations can be easily over-hunted unless harvest programmes are carefully devised (Nolet & Rosell 1998).

Beavers significantly alter ecosystems and in doing so can come into conflict with human activities (Müller-Schwarze & Sun 2003, Rosell et al. 2005). In several countries beaver populations have recovered enough to enable harvesting to occur, and hunting and trapping are permitted (e.g. Finland, Norway and Sweden; Nolet & Rosell 1998, Parker & Rosell 2003). In countries where trapping and hunting are presently controversial or not permitted, non-lethal control methods may be devised and could include olfactory deterrents. The most considerable beaver damage occurs when beavers forage on plants of economic importance and build dams (Richard 1986, Rosell et al. 2005). Plants may be protected through fencing or by wrapping wire netting around individual trees (Richard 1986), and floods may be prevented by destroying dams or by using overflow pipes (Schneider 2001). Beavers are now generally culled as a means of damage control rather than for sport or pelts (Nolet & Rosell 1998), but hunting for beaver meat is popular in Norway and Sweden (Hartman & Georèn 1987, Parker & Rosell 2003). The use of olfactory-related deterrents has received increasing investigation and may offer an alternative to lethal controls.

**Chemical communication and scent marking behaviour in the beaver**

Beavers live in family groups, are highly territorial and all individuals over 5 months old defend their territory mainly through scent marking (Wilsson 1971, Nolet & Rosell 1994, Rosell 2002, Herr & Rosell 2004, Campbell et al. 2005, Rosell & Thomsen 2006). The two main sources of scent are castoreum and anal gland secretions (AGS), from two primary scent structures, castor sacs and anal glands (Svendsen 1978, Walro & Svendsen 1982). These are located in two cavities found between the pelvis and the base of the tail (Walro & Svendsen 1982, Valeur 1988). The anal gland is a holocrine secretory gland, while the castor sac is a pocket lined with non-secretory epithelium (Svendsen 1978, Walro & Svendsen 1982). Both open into the cloaca (Svendsen 1978).

Scents are largely deposited on specially constructed piles of mud and vegetation formed along territory boundaries, near feeding and resting sites throughout the year (Aleksiuk 1968, Rosell & Nolet 1997, Rosell et al. 1998). Castoreum is more frequently deposited on these scent mounds and acts as the main scent used in territorial defence (Rosell & Sundsdal 2001). Castoreum is mainly composed of dietary derivatives and does not show differences between the sexes (Müller-Schwarze 1992, Sun & Müller-Schwarze 1999). Families counter-mark and act aggressively towards conspecific scents (Rosell & Bjørkøyli 2002, Rosell & Steifetten 2004, Rosell & Sanda 2006). The Eurasian beaver exhibits sexual dimorphism in the development of scent structures; this difference is presumed to arise through variations in territorial behaviours (Rosell & Schulte 2004). The smaller castor sacs found in males are associated with high flushing rates, while their larger anal glands represent their greater use of both glands in territorial defence (Rosell & Schulte 2004). Beavers often fight with intruders, which may result in death (Piechocki 1977, Campbell et al. 2005).

Chemical profiles of AGS in the North American beaver reveal that related individuals possess more similar profiles (Sun & Müller-Schwarze 1998a) than unrelated individuals. Numerous scent discrimination experiments have revealed that AGS contains information relating to individuality, kinship and family membership (Sun & Müller-Schwarze 1999). North American beavers can discriminate between unfamiliar related and unrelated individuals through AGS, but not through castoreum (Sun & Müller-Schwarze 1997). AGS also displays sexual dimorphism in both species (Grønneberg 1978, Grønneberg & Lie 1984, Rosell & Sun 1999, Sun & Müller-Schwarze 1999, Rosell & Sundsdal 2001).

Male Eurasian beavers spend significantly more time in territorial defence at territory borders, and deposit more scent marks during the summer than females (Rosell & Thomsen 2006). Adults of both sexes display similar use of space within their territories (Herr & Rosell 2004). Scent marking is significantly higher from April to June, when dispersal of subadults occurs (Rosell & Nolet 1997, Rosell et al. 1998). This represents the time of greatest threat to territory holders, as dispersers seek feeding resources and mating opportunities. However, during the mating season (January–March), scent marking peaks around February when females are in oestrous (Rosell & Bergan 2000). Studies reveal that the Eurasian beaver provides evidence to support the scent-matching hypothesis (Rosell 2002, Rosell & Bjørkøyli 2002, Rosell & Steifetten 2004, Rosell & Sanda 2006). This proposes that scent marks provide an olfactory link between resident animals and their territory, which enables intruders to recognize the probability of conflict escalation (Gosling 1982, Gosling & Roberts 2001). Only with knowledge of beaver chemical communication will meaningful manipulations with scent result in practical applications.

**Use of scent in species and subspecies discrimination**

The North American and Eurasian beaver are morphologically, behaviourally and ecologically very similar (e.g. Wilsson 1971, Novak 1987, Schulte & Rosell 2003). They were established as two distinct species through differences in diploid chromosome counts (Lavrov & Orlov 1973, Lavrov 1983), and to date only these two species are recognized. The North American beaver was introduced to Europe in Finland, Poland, France, Austria and parts of Russia, before the two distinct species were recognized (Nolet & Rosell 1998). Currently, populations of North American beaver in France, Poland and Austria are thought to be extinct. However, recent evidence suggests that North American beavers are present in Luxembourg and in the German county of Rhineland-Palatinate (Schley et al. 2009). Where they coexist, the North American beaver is thought to outcompete and displace the Eurasian beaver (Lahti & Helminen 1974, Ermala et al. 1989). North American beavers have been discovered on the Finnish-Swedish border, not far from the Norwegian border. At present, the very north of Norway is free of any beavers, though the eventual spread of North American beavers into this region seems likely (Parker 2005). In simulated intruder scent experiments, it was found that the Eurasian beaver perceives conspecifics, rather than North American beavers, to be a greater threat to its territory (Rosell 2002). This lack of interest and aggressive response towards the North American beaver may facilitate its spread in Europe. Population control of the North American beaver is becoming a major task for wildlife managers, especially in Finland (Nummi 1996). In the Eurasian beaver, female AGSs tend to be thicker and greyer, while male AGSs are more fluid and have a yellow tinge. In the North American beaver, males have brown and viscous AGSs, while in females AGSs tend to be runny and whitish or light yellow in colour (Schulte et al. 1995, Rosell & Sun 1999). Colour and viscosity of AGS, collected from live or dead animals, provides a cheap, reliable and easy method to distinguish these two species and enable trapping for population control (Rosell & Sun 1999).

Within the Eurasian beaver, eight subspecies have been named, which reflect the eight isolated populations that survived the near extinction of the species in the 19th–20th century. These eight populations were defined as subspecies due to differences in cranial morphology (Heidecke 1986). Recent mDNA analysis suggests that these eight stock populations are not genetically divergent enough to be described as separate subspecies (Durka et al. 2005). Instead the Eurasian beaver can be described as being composed of two lineages (eastern and western) that separated in the last ice age, and so should be treated as two ESUs (Durka et al. 2005). Genetic studies have revealed phylogeographical differences between western and eastern European lineages that are great enough to warrant that the western populations (*C. f. gallicus*, *C. f. albicus* and *C. f. fiber*) be managed as a separate ESU (Durka et al. 2005). Conservation measures should therefore ensure hybridization between eastern and western ESUs is discouraged until planned, future genetic work clarifies the situation.

Evidence of behavioural isolating mechanisms within the western ESU suggests that subspecies may be in the process of speciation. Rosell and Steifetten (2004) found that individuals of *C. f. fiber* displayed more interest and aggression towards scent from their own subspecies in stimulated territorial intrusions, than towards scent from *C. f. albicus*, indicating that they did not treat the latter as a strong threat to their territories. This provides evidence that olfactory cues exist and are recognized between these subspecies. As well as identifying differences between subspecific populations, diverging olfactory cues also encourage speciation (Müller-Schwarze 2006) through variation in mate recognition signals (Wyatt 2003). This raises issues of subspecies status, protection and conservation priorities, and has implications for reintroduction and translocation programmes. These conservation strategies have been a vital part in the recovery of the Eurasian beaver, though little attention was given to subspecies origin of the founders, and many resulting populations are a mixture of different geographical forms (Nolet & Rosell 1998). As a result of genetic studies, it has been recommended that reintroductions to western Europe should only involve western subspecies, whereas reintroductions of beavers east of the Oder and Vistula rivers should only involve eastern subspecies (Durka et al. 2005). As olfaction is the beaver's main communication system, further research into the existence of behavioural isolating mechanisms should be incorporated with genetic studies when planning future conservation strategies.

**Predator recognition through olfactory cues**

Predators of beavers in Europe include wolves *Canis lupus*, bears *Ursus arctos*, wolverines *Gulo gulo*, lynx *Lynx lynx*, red foxes *Vulpes vulpes* and dogs *Canis familaris* (Rosell et al. 2005). River otters *Lutra lutra* and pine martens *Martes martes* have also been suspected of predating on beaver kits in Europe but evidence remains inconclusive (Reid 1984, Tyurnin 1984, Rosell & Hovde 1998). Training captive animals to recognize and respond appropriately to predator odours has received scientific investigation in a range of species (e.g. Blumstein et al. 2002). The ability of captive beavers to respond to predator odours has not been tested; such research would be complicated by the fact that many beavers have bred for several generations in captivity. However, the removal and reduction of many former beaver predators across Europe provides a more realistic opportunity to test the recognition of predator odours by beavers. For example, the wolf and bear are now much reduced in numbers throughout Europe, and many beaver populations have existed for numerous generations without experiencing predation from these species. Will this result in behaviourally incompetent animals, which is often a criticism of captive breeding programmes? Also, if beavers are being translocated throughout Europe, what are the welfare implications of releasing animals with no former experience of predators into areas where predators exist? For example, beavers in Latvia are regularly predated on by wolves (Andersone 1998). Translocating beavers into areas with active predators of which they have little or no experience raises welfare issues. Reactions to wolf scent in naïve beavers may give some indication of whether these beavers will actively avoid or be indifferent to predator scent on release (see below).

**Control of foraging damage through non-lethal means**

Non-lethal methods to reduce damage are required, to minimize beaver conflicts with humans in order to discourage culling, in countries where shooting is not permitted, or to reduce damage outside the hunting season. The beaver is a highly olfactory-oriented species, so odours and semiochemicals that it shows natural aversion to offer a real means of reducing damage. Applying scent from conspecifics has been demonstrated to prevent colonization in the North American beaver, however, reapplication must occur regularly and the effect is reduced at high population density (Müller-Schwarze & Heckman 1980, Welsh & Müller-Schwarze 1989). The artificial distribution of dominant beaver scent may restrict movements, especially in newly reintroduced animals. Beavers that are moved into new areas presumably have no concept that they may be the only members of their species in that area. By creating false or artificially created territories (see Swaisgood 2007) with dominant scent in areas from which humans wish to exclude beavers, damage could be reduced.

A promising area of limiting damage through scent manipulation is through the application of predator odour (see Apfelbach et al. 2005 for a review). On presentation of predator odours, Eurasian beavers display reduced foraging (Rosell & Czech 2000) and territorial defence behaviours (Rosell & Sanda 2006). Clearly, beavers distinguish predator from non-predator odour, and adjust their behaviour to reduce their perceived risk of predation. Predator odours could therefore be used to reduce feeding damage to crops, fruit and forest tress, providing a humane and environmentally friendly option for the management of free ranging beavers (Engelhart & Müller-Schwarze 1995, Rosell & Czech 2000). Norwegian beavers still display strong behavioural reactions towards allopatric wolf scent (Rosell & Sanda 2006). This suggests that even predator odours beavers are not regularly exposed to, or have been exposed to historically, may be effective deterrents. Long-term effectiveness and possible habituation towards the repellent effects of predator odours on Eurasian beavers have yet to be fully investigated.

**Removal of ‘problematic’ beavers**

‘Problematic’ beavers include those that cause damage to crops or property, which cause a nuisance to humans and/or cause flooding of inappropriate areas. Conspecfics’ scent may be employed to attract animals to traps for the translocation of ‘problematic’ individuals. Territorial responses can be elicited, and the scent of the opposite sex may act as a lure for lone beavers, to encourage these animals into traps (Rosell & Kvinlaug 1998, Müller-Schwarze 2006). Presently most ‘problematic’ beavers in central Europe are trapped and relocated to establish new populations elsewhere (Schwab & Schmidbauer 2001, Halley & Rosell 2002).

A special case in which beaver removal is vital for conservation currently exists in South America. In 1946, 25 mating pairs of North American beavers were introduced by the Argentine government to Tierra del Fuego, to encourage the fur industry (Lizarralde 1993). Beaver foraging has greatly affected native vegetation structure and regeneration, which in turn has altered the unique, indigenous ecosystem and facilitated the invasion of exotic species (Anderson et al. 2009). Due to a lack of predators and potential competitors, beaver numbers have reached an estimated 100000 (Choi 2008). The Argentine and Chilean governments are now considering a total eradication programme (Choi 2008). The application of beaver scent to traps has been carried out by trappers for at least 250 years (Barrus et al. 1997). This method could be applied to modern beaver trapping, to ensure the majority of beavers are removed, in order to hinder repopulation.

**Using olfaction to aid reintroduction and translocation programmes**

*Capture, handling and transportation*

The capture, handling and translocation of wild animals are recognized as stressful procedures that are essential to the reintroduction process (Teixeira et al. 2007). First year mortality rates in translocated beavers have been reported as 14% in Poland (Zurowski & Kasperczyk 1988), 17% in Germany (Heidecke 1986) and 36% in Netherlands (Nolet et al. 1997). Infectious disease was the main cause of mortality, including yersiniosis, leptospirosis and avian tuberculosis in the Netherlands programme (Nolet et al. 1997). Nolet et al. (1997) implicate the stress involved in the translocation process as encouraging the onset of these diseases, by weakening the animals' immune systems. We believe the application of scents may serve to reduce stress in this highly olfactory dependent species. In captive husbandry it is generally recognized that retaining some odour cues (e.g. scent-marked substrate) when transporting beavers (Swallow et al. 2005) or cleaning their enclosures, reduces aggression, reduces the stress of the procedure and helps the animals settle more quickly (Jennings et al. 1998, Waiblinger 2002, Van Loo et al. 2003). Placement of scent in transport crates and in temporary holding enclosures (e.g. for quarantine) may serve to reduce the stress experienced by beavers during transportation and when entering novel environments. The application of a family's scent may also serve to encourage acceptance of any removed individual back into the group and discourage aggression.

*Influencing dispersal, habitat selection and pair bonding*

Release site fidelity may be important in reintroduction programmes, especially in trial situations or when the release area is restricted. Current interest in beaver reintroduction programmes provides the perfect model to test manipulations with scents and behavioural ecology theories. The application of a family's scent to artificial lodges prior to release may encourage them to use these facilities. The presence of an animal's own scent may also increase its confidence in a novel environment and encourage it to settle and remain within the release site (Swaisgood 2007). However, Linklater et al. (2006) found that translocated black rhinoceroses *Diceros bicornis* moved further away when their own scent was spread or 'broadcasted' at their release site. Faeces used to create the scent were collected during captive periods, suggesting that these animals may have formed negative associations with scents experienced during captivity, or have reacted to stress metabolites in their own faeces (Linklater et al. 2006). The animals did display an attraction to conspecific scent, which the authors postulate demonstrates the potential to manipulate post-release behaviour. Artificial lodges for beavers have been used in some translocation programmes, however, Nolet et al. (1997) determined that only 2 out of 11 released families used these post-release as their winter shelter. This suggests that the beavers may have negative associations with these artificial lodges or release sites. The deployment of their own scent within the lodges prior to release, with actual release occurring nearby, not within the lodges, may encourage the use of these artificial lodges. Consideration should also be given to the correct placement of artificial lodges.

Translocation or reintroduction programmes do not always involve the release of already formed pairs or family groups. To encourage lone adults or subadults to form pair bonds upon release, and potentially reduce the numbers of aggressive encounters, unmated individuals could be exposed to the scent of a potential mate, e.g. while in quarantine. Britain in particular has long statutory quarantine periods for mammals. Beaver deaths during quarantine may lead to the release of unpaired individuals. Exposing these individuals to scent from other unpaired beavers may reduce injury and aid pair bond formation when these animals are mixed. Exposure to the scent of potential mates in giant panda (Swaisgood et al. 2000, 2004) and harvest mice *Micromys minutus* (Roberts & Gosling 2004) has served to reduce aggression and encourage higher rates of natural matings.

*Kin recognition and translocation of family groups*

The information encoded in scent can also aid the selection of animals to be translocated. AGS of the North American beaver has been demonstrated to contain information on family membership and degree of relatedness (Sun & Müller-Schwarze 1998a, b), which are important when establishing which family groups to move. Post-translocation survival may be greatly affected by social relationships (Kleiman 1989). Degree of relatedness and familiarity may also affect territorial behaviours upon release. Will familiarity with the scents of other families kept in close proximity, in quarantine for example, lead to reduced aggression upon release, therefore lowering the chance of escalated conflicts and the risk of injury or death? Death, especially of a reproducing adult, could be significant when small numbers of animals are released. In this monogamous species, the loss of a reproducing adult may significantly affect population growth, and has welfare implications for the remaining family members as they may experience increased challenges to their territory. Black-tailed prairie dogs *Cynomys ludovicianus* translocated in related pairs (adult and juvenile from the same family) exhibit higher survival and reproductive success than non-related pairs (Shier 2006). Furthermore, predation was less for animals translocated as related pairs. Translocation success can be significantly increased through founder group familiarity (Shier 2006); this may also apply to beaver translocations.

*Reducing territorial conflicts*

Translocation of beavers to supplement existing populations, or to relocate 'problematic' beavers, could induce territorial conflicts. Eurasian beavers respond for significantly longer to, and display more aggression towards scent from strangers, than towards scents from animals in bordering colonies, their neighbours (Rosell & Bjørkøyli 2002). This is referred to as the 'dear enemy phenomenon' (DEP; Fisher 1954): territorial animals exhibit less aggression towards neighbours intruding into their territory than towards strangers intruding (Temeles 1994). Strangers pose greater threats to territory holders, as they generally represent animals that are searching for territories or mates. Aggressive responses towards neighbours could waste time and energy, and risk serious injury (Jaeger 1981, Temeles 1994). Beavers should learn the identity of their neighbours through repeated exposure to their scent marks along territorial borders (Rosell & Bergan 1998, Rosell et al. 1998). Therefore, the addition of previously unknown beavers through translocation could serve to escalate conflicts and may have severe welfare consequences. Releases should be encouraged in unoccupied territories and distances between colonies should contain enough suitable habitats to support the additional animals. Territorial conflicts may also be reduced by trapping and translocating neighbouring beaver families or subadults, then releasing them near each other. If beavers are held in captivity for any time prior to release, scent exposure may facilitate the retention of familiarity so that reduced aggression is displayed towards neighbours upon release. The effect of scent exposure in captivity upon behavioural reactions of released individuals has yet to be scientifically investigated.

The expression of the DEP may vary depending on various conditions including the degree of relatedness and familiarity between individuals (Rosell & Bjørkøyli 2002), and population density (Temeles 1994). Schulte (1993, 1998) found little support for the DEP in the North American beaver. However, in Schulte's study area the distance between neighbouring sites averaged (±SD) 0.95 ± 0.47km and there was always an unoccupied stretch of stream between territories. Therefore, encounters with the neighbours may be rare, and, in this context, there were no real neighbours, only strangers. However, beavers living in areas with adjacent territories showed a clear DEP (Rosell & Bjørkøyli 2002).

North American beaver male subadults tend to disperse shorter distances than females (Sun et al. 2000). This therefore raises the question: do these males settle and form territories between neighbours that they may be related to and/or familiar with? Sex differences in the display of DEP have been revealed in root vole *Microtus oeconomus* (Rosell et al. 2008). Intruder sex may also affect the level of threat to resident animals (Ferkin 1988). Recent simulated intruder experiments have determined that age and social status are coded for in male Eurasian beaver AGS (Tinnesand et al. 2009), and that resident adult beavers spent more time responding aggressively to AGS from a son (a non-territory holding 'floater') than to that from his father (a territory owner; Tinnesand et al. 2009). Resident adult beavers are threatened by 'floater' beavers that are dispersing and therefore trying to obtain new territories. AGSs from non-territory holders could be used to encourage other dispersers to move away from beaver colonies into unoccupied areas, which may reduce conflicts within family territories. AGS from territory holders could be used to create fake, 'virtual' territories, to encourage newly released families to stay within an area.

In translocation programmes, the creation of virtual territories may reduce conflict with resident animals that often attack and exclude newly released animals (Swaisgood 2007), as familiarity with odours can serve to reduce aggression (Jones & Nowell 1973). Artificially introducing the scent of individuals or family groups prior to their release may not only increase territorial confidence, but also encourage greater acceptance by resident animals (Swaisgood 2007). This concept requires further scientific investigation, for which current beaver release programmes could provide a good model.

### *Health and monitoring of translocated beavers*

Physiological assessment, of either translocated beavers or animals to be selected for release programmes, could be achieved through the non-invasive collection and analysis of scent samples. Collecting scent marks from snow is a perfect non-invasive method of obtaining samples that avoids capture and handling stress (see Rosell & Sundsdal 2001). Determining health and nutritional status should influence the selection of individuals to act as founder members of a population, and those being introduced to an established group. Heath monitoring is vital to determine the success of these conservation measures; it may also reveal information on habitat quality and the welfare of released animals. Nutritional status has been determined from urinalysis of urine marks left by free-ranging mammals (e.g. Delgiudice et al.

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1989). As castoreum is largely derived from dietary components (Müller-Schwarze 1992), it could provide a reliable indicator of habitat quality and therefore nutritional status. The use of health and dietary status indicators could greatly influence mate selection and habitat selection, and therefore settlement rates of newly released animals (see Stamps 2001). Rodents can evaluate the health status of conspecifics via olfactory cues (e.g. Kavaliers & Colwell 1995, Penn et al. 1998, Zala et al. 2004), and are able to identify food-deprived individuals (Pierce et al. 2007). Therefore the health and diet of resident conspecifics may encourage or discourage dispersal from the release site.

Reintroduced animals should be monitored so that the success of the programme can be assessed. Monitoring can also be used to identify problems, enable practical solutions to be sought and help inform future programmes. Olfactory studies offer non-invasive monitoring methods for numerous mammalian species, and are particularly useful for rare and evasive species such as carnivores (Long et al. 2008), or for nocturnal species like beavers. A greater understanding of scent marking sites and behaviours has and can provide important information on population dynamics (Rostain et al. 2004), ecology and social behaviours (Hutchings & White 2000). Signs of scent marking can be used to map territories (Nolet & Rosell 1994, Campbell et al. 2005), so that distribution can be assessed and areas protected if necessary.

### Reintroduction of beavers to Britain – an opportunity to bridge the gap between animal behaviour and conservation biology

The reasons for reintroducing beavers to Britain are similar to those stated for the rest of Europe. The Eurasian beaver appears on the Bern Convention and on the European Community (EC) 'Habitats and Species' Directive, 1992. As an EC member, Britain has a responsibility to investigate the reintroduction of extinct species (Macdonald et al. 1995, Gurnell et al. 2008). Geographical isolation makes it unlikely that the beaver will naturally repopulate Britain, so active reintroductions have been proposed. Beavers occurred widely throughout Britain (Coles 2006); the last extinctions occurred in Scotland in the 16th century (Kitchener & Conroy 1996). Extinction was largely because of over-hunting; habitat loss was a contributing factor (Macdonald et al. 1995, Nolet & Rosell 1998).

The first formal trial reintroduction of beavers to Britain took place in Scotland during May 2009. Preliminary assessments of this reintroduction suggest that survival and persistence are high (Parker et al. 2000, South et al. 2000). There is strong public support for the project, which is ecologically feasible, however, concerns raised by agriculture, forestry and fishery bodies have led to the agreement of a 5-year trial reintroduction (Gaywood 2001). Feasibility reports for the release of beavers in England and Wales have also been developed (Gurnell et al. 2008, Halley et al. 2009). These introductions provide a unique opportunity to test theories incorporating the role of chemical communication in aiding reintroduction success.

## DISSCUSSION

Olfaction in the Eurasian beaver has received much scientific attention and is the key form of communication in this species. However, literature specifically addressing the inclusion of olfaction in the generation of practical solutions for conservation issues is lacking. Experimental manipulation of chemical signalling systems could have significant impact on conservation dilemmas.

Beavers provide a mammalian model in which behavioural ecology theories, including olfactory mate recognition, territorial behaviours, dispersal and settlement can be explored. Conservation issues with beavers include: active reintroduction, translocation and removal programmes; reducing their behavioural impact on sensitive areas or vegetation; human–beaver conflicts, and species and subspecies genetic purity. Olfaction studies should be developed into practical solutions that address each of these issues (see Table 1). Chemical communication is vital in this species. However, it is often the area least incorporated into animal husbandry or conservation action plans, if it is considered at all. Recent studies of other mammals including giant pandas, black rhinoceroses and harvest mice demonstrate how scents can significantly influence behaviour, and enable it to be manipulated to achieve conservation outcomes. Olfaction is an important part of the behavioural repertoire of beavers, which is often ignored during current conservation practices.

Beaver population dynamics and behaviours exemplify how human activities such as hunting can significantly impact upon population size and distribution. Active conservation and animal management measures have ensured that the extinction of this species was averted, however, continued action is required to maintain this success. As obvious modifiers of ecosystems, beavers can come into conflict with human activities and land use. Methods that incorporate natural behavioural reactions towards scent provide more reliable, non-lethal or toxic means to reduce these conflicts.

Individual animal welfare is an increasingly important issue that should be considered in conservation actions, such as reintroductions and captive husbandry. Traditionally, the success of release programmes has often been assessed by measures of population viability. However, monitoring behaviour and health can provide information on individuals, so that implications for welfare can also be assessed. Non-invasive methods that enable demographic parameters to be monitored are vital to species conservation and can highlight the need for action, especially in predominantly nocturnal species like the beaver. Chemical analysis of semiochemicals and alterations in olfactory communications can provide important, non-invasive methods to inform future conservation measures. Chemical communication in mammals incorporates an interesting series of behaviours that have intrinsic conservation value in themselves and could be promoted to generate public interest in the conservation of such species. Ignoring or failing to provide opportunities for olfactory behaviours may actually cause stress and have detrimental effects on animal welfare.

This review demonstrates that beaver behaviour, ecology and chemical communication are well documented, but the potential of this knowledge to benefit conservation should be explored. It also highlights the current lack of literature that relates olfactory behaviours in species conservation. Further systematic research is needed to establish and evaluate how the mechanisms of chemical communication can be manipulated to aid both *in situ* and *ex situ* conservation practices in this, and other, mammalian species.

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**Table 1.** Potential uses of scent within conservation, as described in the literature

| Conservation practice | Potential use of scent | Beaver | General mammal |
|---|---|---|---|
| Identification | Relatedness/familiarity | Sun and Müller-Schwarze (1998a, b) | |
| | Sex identification | Schulte et al. (1995); Rosell and Sun (1999) | |
| | Species recognition | Rosell and Sun (1999) | |
| | Subspecies recognition | Rosell and Steifetten (2004) | |
| 'Problematic' animals | Trapping | Rosell and Kvinlaug (1998) | Müller-Schwarze (2006); Long et al. (2008) |
| | Deterrents | Rosell and Czech (2000); Rosell and Sanda (2006) | Apfelbach et al. 2005) |
| Captive husbandry | Predator training | | Blumstein et al. (2002) |
| | Reducing cleaning stress | | Jennings et al. (1998); Waiblinger (2002) |
| | Reducing transportation stress | | Swallow et al. (2005) |
| Reintroduction | Habitat selection | | Stamps (2001) |
| | Release site fidelity | | Linklater et al. (2006) |
| | Pair bonding | | Swaisgood et al. (2000, 2003, 2004); Roberts and Gosling (2004) |
| | Territory conflicts | Tinnesand et al. (2009) | Swaisgood (2007) |
| | Translocating family groups | | Shier (2006) |
| Monitoring | Health | | Delgiudice et al. (1989) |
| | Population dynamics | | Long et al. (2008) |
| | Territory mapping | Nolet and Rosell (1994); Campbell et al. (2005) | |

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