The Importance of Chemical Communication Studies to Mammalian Conservation Biology: a review

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Abstract

The relevance of chemical communication to mammalian conservation is not often the focus of scientific investigation. Our review identifies and discusses ten key areas in which the study of chemical communication aids conservation behaviour. Articles (n = 140) were revealed, most were concerned with population monitoring (22.50%), reducing human-wildlife conflicts (18.93), influencing habitat selection

(18.57%), increasing welfare of captive animals (12.86%), encouraging captive breeding (12.86%), reducing predation (5.71%), and increasing the success of release programmes (5.00%). Few articles (<4%) were found relating olfactory studies to health status of wild populations, reducing hybridization or as indication of pollution. A growing number of articles are addressing how olfactory studies may aid conservation, but more rigorous experimental testing and manipulations are required. The vast majority of studies linking olfaction with conservation involved the population monitoring of wild carnivores. We suggest that animal behavioural studies and manipulations of chemical communication can have significant impacts on conservation in these areas, which should be further developed to generate practical applications. Areas of future study include chemical communication of aquatic mammalian species, the transfer of olfactory cues under water, and the identification of genetic markers that may link ‘personality’ with olfactory responses. Linking olfactory studies to fitness, either on an individual or population scale, particularly in a wider ecological context is more likely to increase conservation value. Animal translocations and reintroduction programmes may offer a means to do this and could be an important area to direct future studies.

Keywords

Behavior; Conservation; Non-invasive; Olfaction; Scent; Welfare

1. Introduction

Conservation behaviour is the application of behavioural research as a tool to solve conservation problems (Blumstein and Fernández-Juricic, 2010). Chemical communication is one area of animal behaviour that is often ignored for its potential relevance to conservation. Fisher et al. (2003) highlight how few references are made to odour or scent related terminology in texts calling for greater integration between conservation and behaviour. Olfaction is the prominent sense in most mammalian species and plays a crucial role in spatial organisation, sexual and social behaviours (Brown and Macdonald, 1985; Stoddart, 1976). Detailed knowledge of animal behaviour enables theories and methodology to be developed so that successful solutions to conservation and wildlife management issues, such as captive breeding, reintroduction, translocation, social behaviour, predation and movement, may be found. For example, animal welfare is of increasing concern within conservation with more research now being directed towards identification of welfare parameters and consequences to individual fitness (Swaisgood, 2007).

Previous studies have provided a large amount of information on the behavioural reactions of mammals to various scents (e.g. Brown and Macdonald, 1985; Müller-Schwarze, 2006; Wyatt, 2003). However compared to the comprehensive body of knowledge gathered on invertebrates (e.g. Breithaupt and Thiel, 2011; Carde and Miller 2004) and other vertebrates (e.g. Waldman and Bishop, 2004; Wyatt, 2003), there is a lack of published research addressing mammals, specifically relating olfaction to evolutionary/individual fitness and conservation. A description of the mammalian olfactory system is beyond the scope of this study; for reviews see Brennan and Zufall, 2006; Firestein, 2001; Lledo et al., 2005. Sources of scent in mammals include urine, faeces and glandular secretions. All excretions and sources of body odour can be detected by other animals, however, signals are intentional forms of communications whilst cues are incidental and can unintentionally provide information (Steiger et al. 2010). Scent marking involves specific behaviours and occurs at selected locations (Kleiman, 1966). Research into scent and scent marking behaviours provides vital understanding of species ecology (Gorman, 1990) and socio-biology (Hurst and Beynon, 2008). Olfaction differs from other forms of communication as signals are still conveyed in the absence of the sender and can therefore persist in the environment after the signaller has dispersed (Bradbury and Vehrencamp, 1998) (see Table 1 for utility and limitations of chemical communication). While the practical application of semiochemicals has been widely discussed, these often relate to domestic mammals and pest control (Müller-Schwarze, 2006; Wyatt, 2003). Linklater (2004) and Swaisgood (2007) discuss scent manipulation and the need for greater investigation into the role of olfaction in animal dispersal, territorial conflict and predator recognition to aid conservation. Ignoring olfaction may be highly anthropomorphic and therefore have detrimental consequences on how we view and manage a species.

In this paper we review the degree of integration between mammalian olfactory studies and conservation in recent publications. We suggest that animal behavioural studies and manipulations of chemical communication in mammals can have significant impacts on conservation and generate practical applications.

2. Methods

We quantified the use of chemical communication studies in conservation by performing a keyword search in ISI Web of Science database. For the search one of the following conservation related keywords, "biodiversity"; "conservation"; "(animal/wildlife) management"; "reintroduction"; "captivity" were linked with one of the following olfactory related key words, "chemical communication"; "chemosignals"; "odour/odor"; "olfaction"; "olfactory"; "scent" and "semiochemicals", for all combinations. The pair of keywords must appear in the title, abstract and/or keyword listings of each article and refer to mammalian species. We included articles from 1995 to 2010. Articles were excluded if articles referred to humans, non-mammalian species or appeared in contexts other than the purpose of this review (e.g. water conservation).

3. Results

This search revealed articles (n=140, Appendix A.) which were categorised according to the main focus of the conservation application. Ten key topic areas were revealed which we discuss in descending order of literature volume. Figure 1 displays the number of articles revealed addressing each key conservation topic, with the main subject focus of the journal in which it was published. The vast majority of articles concerned wildlife population monitoring (22.50%), human-wildlife conflicts (18.93%), and habitat use by wildlife (18.57%). These were mainly published in wildlife, ecology and conservation journals. Papers relating olfactory research to improving the welfare of captive populations (12.86%) and increasing the success of captive breeding (12.86%) were mainly published in zoology and behaviour journals, rather than conservation journals. The majority (62.78%) of the articles involved research on free ranging animals in wild settings, compared to captive (29.56%) and laboratory studies (7.66%). Most studies focused on carnivore species (58.03%), with rodent (14.23%) and primate (8.76%) species also appearing frequently (Table 2). The majority of studies involved terrestrial mammals (89.78%), with otter (*Lutra lutra, Lontra canadensis*) and beavers (*Castor* spp.) being the main semi aquatic species studied. Two studies focused on bats (Bianconi et al., 2007; Ruczynski et al., 2009), while one investigated the use of scent dogs (*Canis familiaris*) to trace whale (*Eubalaena glacialis*) faeces (Rolland et al., 2006).

4. How studies in chemical communication can aid conservation

4.1 Population monitoring

Monitoring populations, assessment of demographic parameters and predicting trends are vital to species conservation. Scent has long been used as an attractant for target species to encourage animals to live-traps, for collection of biological samples, fitting monitoring devices or translocation (e.g. Schemnitz, 1996). Scent stations gather information concerning population size and densities (Long et al., 2008), species presence (Swiart et al., 2003), habitat selection and spatial distribution (Gehrt and Prange, 2007; Gehring and Swihart, 2003). Non-invasive sampling methods use scent lures to attract animals to track stations (to sample footprints) or hair collection points such as rub stations for DNA analysis (e.g. Kendall and McKelvey, 2008; Romain-Bondi et al., 2004). A greater understanding of scent marking sites (Rostain et al., 2004) and behaviours can provide important information on population dynamics and enable corresponding environmental samples to be collected (Long et al., 2008), particularly for secretive or rare species. For example scent mounds can be used to map Eurasian beaver (*C. fiber*) territories (Campbell et al., 2005; Nolet and Rosell, 1994).

A higher quality and greater scope of ecological data can be collected from animal populations when individual animals can be identified and numerous methods exist for marking and tagging animals (McGregor and Peake, 1998). This may be a stressful process and disrupt behaviours, especially in more sensitive species or at specific times (e.g. breeding season). Zhang et al. (2008) have identified individual "*odour fingerprints*" in the anal gland secretions of giant pandas (*Ailuropoda melanoleuca*) which have been used in wild census (Zhan et al., 2006). Recognition and monitoring of individual scents can provide accurate counts of endangered species (Kerley and Salkina, 2007). Overestimates of endangered populations can have significant negative impacts and effect conservation actions, for example overestimates in Siberian tigers (*Panthera tigris altaica*) were discovered by using sniffer dogs to identify individuals (Jones, 1997). Identifying individuals enables data on life history parameters to be gathered and predictive models developed (Sutherland, 1996) that aid conservation efforts and direct management decisions. Important information could be gathered from chemosignals (e.g. DNA from hyena, *Hyaena brunnea*, scent marks, Malherbe et al., 2009), without requiring the animal to be present and thus avoid any behaviour alteration or welfare issues involved in mark and recapture of endangered populations (McGregor and Peake, 1998).

4.2 Reducing human-wildlife conflicts

The lethal control of wildlife through the use of toxic chemicals is often controversial due to the death of non-target species and alternatives such as the deployment of natural compounds to deter pest species rather than toxic chemicals are receiving more attention. Odours may be used in control programmes to attract the target species to traps or discourage non-target species (Reynolds et al., 2004). Application of scent from one sex can attract significantly more conspecifics, thereby increasing the trap rate of a species (e.g. Northern pocket gophers, *Thomomys talpoides*, Proulx, 2004). Predator odours may have potential in controlling prey species distribution (e.g. Ramp et al., 2005) or reducing the impact of damaging behaviours (e.g. Rosell, 2001). Eurasian beavers, for example, are less likely to display scent marking or foraging behaviours when predator scent is presented (Rosell and Czech, 2000; Rosell and Sanda, 2006). The applications of predator odour as deterrents are likely to vary between species, predators, prey populations and their historic and geographical exposure.

Learned food aversions can be generated in wild mammals, by linking odour cues with chemical repellents then applying these odours to sensitive items such as human foodstuffs or vulnerable bird eggs (Baker et al., 2005, 2007). The use of an odour cue rather than just taste aversion means the animals avoid the protected item before having to taste and potentially inflict damage (Nicolaus and Nellis, 1987). Large carnivore species exist in low numbers and are often persecuted by humans, aversive odours may provide a means by which they can coexist. For example, essential oils from tea tree (*Melaleuca alternifolia*) and peppermint (*Mentha piperita*) result in feeding aversion in captive wolverines (*Gulo gulo*), which could be developed to reduce predation on sheep (Landa and Tømmeras, 1997).

The use of chemical communication to manipulate animal behaviour has also been demonstrated in wild elephants (*Elephas maximus* and *Loxodonta Africana*). Applying chemical cues found in musth with mechanical deterrent devices, to create a conditional aversion (Rasmussen and Riddle, 2004), acts on the avoidance tendencies of female elephants (Hollister-Smith, 2005). These chemicals can then be spread around fields providing a cheaper and easier method of deterring crop raiding than surrounding whole fields with mechanical devices (Schulte et al., 2007). The potential use of natural aversive chemical cues in modifying animal behaviours to aid conflicts may offer cheaper and more applicable options than culling or translocating problem animals, and prove more effective (Schulte et al., 2007).

4.3 Influencing habitat selection

Anthropomorphic activities are rapidly changing landscapes and impacting on species. Numerous cues influence colonisation of a habitat and even minor changes that do not affect habitat quality can deter animals from settling (Gilroy and Sutherland, 2007). This bias in dispersal can lead to conservation concerns including source-sink dynamics, local patch extinctions, colonisation rates of empty patches (Hanski and Singer, 2001), spread of invasive species and reintroduction success (Davis and Stamps, 2004). Recognition of the cues species use in habitat selection allows them to be manipulated for conservation objectives (Reed, 2004; Reed and Dobson, 1993).

Animals use cues such as the presence of conspecifics (Stamps, 1988) or heterospecifics with similar ecological requirements (Thomson et al., 2003), to assess habitat suitability (Stamps and Krishnan, 2005). Stamps and Swaisgood (2007) discuss how the natal habitat preference theory, in which dispersers select a habitat that contains cues they experienced in their natal environment (Davis and Stamps, 2004), could be used by conservation managers to encourage released animals to select suitable habitats and remain within the release site. Identifying these cues, of which odours are likely to be highly significant, and providing them to captive animals may help to retain them when released. Rapid departure from the release site can reduce fitness at a critical time, adding to animal translocation failure (Stamps and Swaisgood, 2007). Positive correlations have been made between mortality and post-release travel distances (Letty et al., 2000; Moehrenschlager and Macdonald, 2003). Greater training and manipulation with odours could be applied to encourage reintroduced mammals to select and settle in appropriate, available environments, such as nature reserves.

4.4 Increasing the welfare of captive animals

Captivity and its effect on animal behaviour has been the subject of numerous welfare texts (e.g. Appleby and Hughes, 1997; Hosey et al., 2009; Shepherdson et al., 1998; Young, 2003). Environmental enrichment aims to enhance the psychological and physiological well-being of captive animals (Shepherdson, 1998). In the last twenty years, environmental enrichment has received increased attention and its application is now generally accepted as an important tool in increasing the welfare standards of captive housed species in research (Olsson and Dahlborn, 2002), food production (Appleby and Hughes, 1997), and zoological settings (Shepherdson et al., 1998).

Olfactory stimulation in captive animals (see Wells, 2009 for review) has traditionally been a neglected area of enrichment studies (Clark and King, 2008) despite the importance of odours to wild mammals. Enrichment can greatly aid conservation of endangered species in captivity by producing animals more behaviourally capable for reintroduction programmes, through increasing their ability to cope with challenges, and promoting reproduction through increased health status, improved immune system and the expression of successful reproductive behaviours (Carlstead and Shepherdson, 1994; Young 2003). Neurological evidence shows that environmental enrichment increases the cognitive function of animals, which is critical for interaction and adaptation to an environment (Healy and Tovée, 1999).

Clark and King (2008) highlight the bias in zoo olfactory enrichment studies towards more charismatic species, such as large cats (46% of studies) and primates (16% of studies). Varying results exist between species and individuals; in some the presentation of odours increases behavioural diversity and activity levels (e.g. captive black-footed cats, *Felis nigripes*, Wells and Egli, 2004), whereas Wells et al. (2007) found olfactory enrichment had little effect on the behaviour of captive gorillas (*Gorilla gorilla gorilla*). Greater understanding and testing of the type of scent used and species specific reactions would be a useful area of future research with testing across zoological collections likely to generate results faster than wild studies.

Odours can also be chronic sources of stress in captivity (Morgan and Tromborg, 2007). Exposure to predator odour induces stress responses (Buchanan-Smith et al., 1993; Monclús et al., 2006) as does the detection of odour from distressed conspecifics (Vieuille-Thomas and Signoret, 1992). Therefore exposure of certain species to others (e.g. location in a zoological collection) and type of scent presented should be considered carefully as this may have welfare and reproductive consequences. However, not all exposures to acute stress are negative and can in fact be beneficial by increasing behavioural repertoires (Breazile, 1987; Moodie and Chamove, 1990) and aiding retention of behaviours key to reintroduction success.

4.5 Encouraging captive breeding

Captive breeding is an important ex-situ conservation strategy and applied behavioural research has greatly aided captive breeding success of endangered animals (Swaisgood, 2007). However, behavioural problems are the main cause of failure in captive breeding (Synder et al., 1996). Captive breeding via natural matings are notoriously low for certain species e.g. clouded leopards (*Neofelis nebulosa*) (Yamada and Durrant, 1989) and cheetahs (*Acinonyx jubats*) (Marker-Kraus and Grisham, 1993). Few studies have rigorously tested or incorporated the role of olfaction and mate selection in captive breeding programmes where animal pairings are often selected by humans.

Swaisgood et al. (2000) demonstrated the importance of social odours in their studies on chemical communication in giant pandas. This species exhibits low reproductive success in captivity due to excessive aggression and poor sexual motivation (He et al., 1994; Lindburg et al., 1997). Giant pandas rely heavily on chemical communication in the wild. Odours presented to potential breeding pairs prior to introduction could serve to reduce aggression, increase libido in males and receptivity in females (Swaisgood et al., 2000). This scent exposure study could serve as a template, particularly in carnivore captive breeding programmes. Chemosignals are regularly employed to stimulate breeding in agricultural mammals (Rekwot et al., 2001), and the potential implications for zoo husbandry are only beginning to be realised (Swaisgood and Schulte, 2010).

An increasing criticism of captive breeding programmes is the exclusion of mate choice, in a goal to maximize outbreeding and increase genetic variation. Selected pairs may be incompatible reducing breeding success (Sutherland and Gosling, 2000; Wielebnowski, 1998) and as females that can select their mates tend to produce more viable offspring (Drickamer et al., 2000). The major histocompatiblity complex (MHC) is one such mechanism of mate choice that may be ignored in captive breeding. In mammals the MHC is a highly variable region of the genome (Johnston, 2003) that codes for volatile constituents of urine and other body odours as demonstrated through behavioural experiments (Beauchamp and Yamazaki, 2003; Brennan and Zufall, 2006). Mammals tend to avoid mating with individuals of similar MHC genotype, suggesting an adaptive mechanism for preventing inbreeding (Eggert et al., 1999; Penn and Potts, 1998; Yamazaki et al., 1998). In sexual selection literature, few studies focus on the role of chemical communication in mate choice (Coleman, 2009). Although it may be highly difficult to achieve, particularly with larger mammals, provisioning for mate choice has the potential to greatly improve breeding success (Grahn et al., 1998). Providing potential breeders with olfactory access before actual introduction has been demonstrated to increase captive breeding of cheetahs at San Diego Zoo (Lindburg, 1999). Fisher et al. (2003) successfully used odour cues to experimentally modify mate choice in pygmy lorises (*Nycticebus pygmaeus*), a vulnerable species that can be difficult to bred in captivity. Scent marks appear to be an important form of communication in this primate and the authors determine that females use competitive counter marking to assess male quality. Through manipulation of exposure of male odours to females, the authors succeeded in creating a preference towards certain males regardless of actual qualities. Roberts and Gosling (2004) also demonstrated mate choice manipulation in harvest mice (*Micromys minutus*), where the behaviour of initially unpreferred males was altered using odours of preferred males, resulting in their increased attractiveness to females. As discussed by the authors, the use of scent transfer is a cheap and non-invasive tool for manipulating the environment of captive animals, and may serve to promote mating through familiarity of potential mates before physical exposure. It may also be used to encourage mating between human-selected, genetically unrepresented pairs, countering possible female perceptions of less desirable males. The use of conspecific scent could receive further investigation, however, the effects of any applications should be monitored carefully for negative effects, for example in prairie voles (*Microtus ochrogaster*), odours can act to suppress reproduction in subordinate individuals (Carter and Roberts, 1997).

4.6 Reducing predation

Predation is a significant cause of mortality in newly released animals, particularly naive captive bred individuals, and is therefore a limiting factor in reintroduction success (Banks et al., 2002; Beck et al., 1991; Fisher and Lindenmayer, 2000; Miller et al., 1994). Understanding the importance of olfaction in predator/prey relationships, especially between species that have not evolved together or are no longer sympatric is particularly relevant to conservation by producing behaviourally competent animals for reintroductions, especially as some studies indicate that the threat of predation from olfactory cues may have to be learned (Blumstein et al., 2002).

The majority of studies investigating the training of naive animals to recognise predation threat focus on the use of visual or acoustic predator cues by presenting predator models with conspecific alarm calls (e.g. Blumstein et al., 2008; McLean et al., 1994). Scent marking behaviours can have negative consequences as they enable predators to “*eavesdrop*” and thus advertise a prey’s location (e.g. Hughes et al., 2010). However, prey can also “*eavesdrop*” on predator odour before detection and increase predator avoidance behaviours such as vigilance. The few existing studies appear conflicting, strengthening the need for further experimental investigation. Some mammals do adjust their scent marking behaviours when they detect predator olfactory cues (Roberts et al., 2001; Rosell and Sanda, 2006). Orrock et al. (2004) tested the effect of predator scent on rodent foraging and concluded that rodents rely on indirect environmental cues to assess predation risk rather than predator scent, a direct cue. Wolff (2004) found no evidence that prairie voles alter their scent marking behaviours with detection of predator scent, concluding that the benefits of scent marking outweigh the costs of increasing predation risk. However, presentation of predator scent has been reported to produce stress responses in captive mammals (Buchanan-Smith et al., 1993), heighten vigilance and increase avoidance while feeding (Monclús et al., 2005). Although this predator recognition may be innate, learning and experience are important to ensure that an individual displays the appropriate behavioural response and decreases their predation risk (Griffin et al., 2000). The use of predator scent as a training tool to aid recognition and enable captive animals to assess predator risk has implications for species conservation and requires further investigation across a range of species.

Release site fidelity and the associated accumulation of odorous waste caused by the low mobility of reintroduced animals has been determined to increase mortality from scent-hunting predators shortly after release (e.g. voles, *M. rossiaemeridionalis*, Banks et al., 2002). Social interactions may also encourage predation of newly translocated animals as resident animals, with established territories, may experience greater fitness through dominance of best shelter, food resources, habitat knowledge and predator experience. For example, dominant bank voles (*Clethrionomys glareolus*) heavily scent mark around the nests of subordinates to display dominance (Rozenfeld et al., 1987). These nests may therefore be discovered by predators more easily (Banks et al., 2002).

4.7 Increasing the success of release programmes

Sutherland (1998) cited behavioural reasons for the failure of so many release programmes. Swaisgood et al. (2004) stated that "*efforts to reintroduce captive mammals to the wild may be seriously compromised by ignorance of the animal's use of scent for territory settlement, establishing social relationships, courting and mating*". The use of olfaction to improve success of release programmes has failed to receive much experimentation but has been proposed as a possible solution to some of the numerous issues involved in animal translocation (Campbell-Palmer & Rosell, 2010; Roberts and Gosling, 2004; Swaisgood, 2007). Scent broadcasting experiments on translocated black rhinoceros (*Diceros bicornis*) proved inconclusive but demonstrate the need for future studies to combine behavioural ecology with robust empirical testing (Linklater et al., 2006). Hutchings and White (2000) identified habitat preferences from scent mark patterns in otters (*L. lutra*). These can be used to determine the ecological requirements of a species and measure habitat quality. Such information could aid identification of suitable release sites for translocation programmes.

Trapping wild animals can be aided through the use of scent lures, by eliciting territorial and mate seeking behaviours (Long et al., 2008; Müller-Schwarze, 1996). In some instances it may be important that a whole family group is collected for translocation. Identifying family groups and degree of relatedness through anal gland secretion analysis has been demonstrated in the North American beaver (*C. canadensis*) (Sun and Müller-Schwarze, 1998). Collection of whole family groups maintains important social bonds, behaviours and can increases survival (Shier, 2006). Capture, handling and transportation can have negative physiological consequences to animal welfare, which in turn can affect the success of reintroductions (Moorhouse et al., 2007). The inclusion of an animal's scent in transport containers or living quarters can aid settlement, reduce stress, aggression and the display of over scent marking behaviours (Swallow et al., 2005; Veillette and Reebs, 2010).

Swaisgood (2007) hypothesises that the artificial creation of "*virtual territories*" prior to release could reduce conflict with resident conspecifics which often attack or exclude newly released individuals. Studies demonstrate familiarity with odours can reduce aggression (Jones and Nowell, 1973). The discriminatory ability of giant pandas to identify conspecific scent could be used to familiarise residents with newly released individuals, thus reduce aggression, encourage them to stay in the release site and reduce the stress of entering a new habitat (Swaisgood et al., 1999). Misidentifying population status and abundance of a species may lead to conflicts between residents and introduced individuals, with resulting animal welfare issues (Hutchings and White, 2000).

To aid success and inform future releases programmes, chemical communication studies could provide vital information on population health and dynamics. Conservation success is often determined in terms of survival, settlement and establishment of a viable population (Festa-Bianchet and Apollonio, 2003; Gosling and Sutherland, 2000). Changes in reproductive hormones and therefore reproductive state are coded for in odours across many mammalian species (Eisenberg and Kleiman, 1972). Monitoring semiochemicals or olfactory behaviour may provide a measure of reproductive fitness in a newly released population. For example, Khazanehdari et al. (1996) monitored the anal gland secretions of European mole (*Talpa europea*), whilst Palagi et al. (2003) studied olfactory investigations between ring-tailed lemurs (*Lemur catta*). Development of these studies could apply this data and draw inferences to population fitness. Nutritional status of some mammals can be determined from scent marks, such as urine, which can change with diet and particular odours may become associated with an ability to acquire food (Blaustein, 1981; Delgiudice et al., 1989). Castoreum is the main scent used by beavers in territorial defence and is mainly composed of dietary derivatives (Sun and Müller-Schwarze, 1999), thus could provide a reliable indicator of nutritional status. Identification of sex is vital for species monitoring, predicting population trends and selecting individuals for translocation. Both species of beaver show no external dimorphism except for prominent nipples in pregnant and lactating females (Wilsson, 1971). However, sex of all ages can be determined through differences in the colour, viscosity and odour of anal gland secretions (Grønneberg and Lie, 1984; Rosell and Sun, 1999; Schulte et al., 1995), providing a cheap method with instantaneous results in the field compared to molecular techniques (e.g. Crawford et al., 2008). However, with advances in genetic analysis and associated lowering of costs, these methods may provide more efficient means of determining sex and individual identification.

Scents may also have an application in fragmented populations and encourage movement of animals along corridors, thus promote genetic flow (Swaisgood et al., 1999). Mikich et al. (2003) used the essential oil of ripe fruits of *Piper gaudichaudianum* to attract a frugivorous bat (*Carollia perspicillata*) to mist nets. However, they suggest this scent could be used to promote tropical forest restoration in areas cleared by humans, as bats act as seed dispersers and aid forest recovery (Medellin and Gaona, 1999). Future studies may focus on the application of these behavioural traits and investigate if they could be manipulated to encourage movement, habitat use and settlement.

4.8 Health status of wild populations

Wildlife health, including reasons behind mass fatalities and loss of biodiversity, is often the focus of scientific attention. Human actions can place animal populations under stress, increasing their susceptibility to disease (Deem et al., 2001) and introducing novel diseases (Altizer et al., 2003; Daszak et al., 2000; Roelke-Parker et al., 1996). Understanding the role of olfactory communication and scent marking behaviours in disease transmission within and between species has important implications for conservation. Rushton et al. (2000) discussed this issue in their study of red squirrel (*Sciurus vulgaris*) decline in Great Britain which they link to the spread of introduced grey squirrels (*S. carolinensis*) and parapox virus. The two squirrel species rarely come into direct physical contact (Rushton et al., 2000) but scent mark throughout their home ranges through face wiping and anal dragging behaviours (Gurnell, 1987). Squirrels may become infected whilst displaying scent-marking behaviours through skin lesions in the facial and genital regions (Duff et al., 1996; Sainsbury and Gurnell, 1997; Sainsbury and Ward, 1996).

Odours and scent making behaviours provide honest signals of health to conspecifics in mammals (Brown and Macdonald, 1985; Gelperin, 2008; Gosling and Roberts, 2001; Penn and Potts, 1998). Scent can provide an indication of both infection and the activation of the immune system (Zala et al., 2004), therefore individuals may refuse to settle in areas where odours of conspecifics indicate poor health or a lack of resources. Meadow voles (*M. pennsylvanicus*) discriminate between food deprived conspecifics through odour cues (Pierce et al., 2007). Female rodents can discriminate between infected and non-infected males, finding infected male scent less attractive (e.g. *malaria*, Barthelemy et al., 2005; nematode infection, Kavaliers and Colwell, 1995; *Salmonella*, Zala et al., 2008). Greater understanding of the information encoded in odours and the behavioural effects these generate in conspecifics can be utilised to assess health in both wild and captive populations. Identifying low health status is vital when selecting individuals for release programmes. These selections can have lasting consequences on population fitness and animal welfare.

4.9 Reducing hybridisation

Hybridisation can lead to extinction and has implications for species evolution and is therefore a threat to biodiversity (Allendorf et al., 2001) and species recovery (e.g. red wolf, *Canis rufus,* Adams et al., 2003). The chemical signals of exotic species may interfere with native species' ability to recognise and respond appropriately to conspecific signals, decreasing fitness through wasted energy expenditure, failure to select highest quality mates or hybridisation (Angeloni et al., 2010). Olfactory cues have been demonstrated to act as behavioural isolating mechanisms in some mammals, e.g. bats (*Saccopteryx bilineata, S. leptura,* Caspers et al., 2009) and mice (*Mus musculus,* Cox 1984). Many small mammals lack elaborate courtship displays or conspicuous secondary sexual characteristics; instead odour is the dominant pre-mating isolating mechanism (e.g. Blaustein, 1981; Nevo, 1976). In the Eurasian beaver, subspecies display behavioural differences in their response to odours from the same and other subspecies (Rosell and Steifetten, 2004). Subspecies identification and the mechanisms by which they are maintained are of significant interest to biodiversity and evolution. This raises issues of subspecies protection and conservation priorities, and has implications for reintroduction and translocation programmes (e.g. Campbell-Palmer and Rosell, 2010).

4.10 Indication of pollution

Human population expansion with associated resource consumption, development and resultant pollution pose significant conservation threats (Hambler, 2004). Anthropogenic chemicals or alterations to natural chemical levels interfere with and have damaging effects on chemical communication in a range of animals (Lürling and Scheffer, 2007). Mammalian examples are lacking, implying the need for further investigation. However, vertebrate examples include impaired mate and species recognition in fish (*Xiphophorus* spp., Fisher et al., 2006); mating success in amphibians (*Notophthalmus viridescens*, Park et al., 2001) and predator avoidance in fish (*Oncorhynchys mykiss*, Scott et al., 2003) and amphibians (*Rana luteiventris*, Lefcort et al., 1998).

Endocrine-disrupting chemicals can affect hormones, development and expression of scent producing glands and olfaction (Zala et al., 2004) with measurable behavioural effects (Clotfelter et al., 2004). These behavioural changes may be used as bio-indicators, presenting an opportunity to apply behavioural research to a conservation problem (Clotfelter et al., 2004). Zala et al. (2004) and Zala and Penn (2004) demonstrate how abnormal behaviours in vertebrates are induced by chemical pollution and that behavioural effects can be more apparent than developmental and physiological parameters, enabling potential impacts to be identified that may not otherwise become apparent (Peterle, 1991). Their review gives few mammalian examples of effects on chemical communication except results from laboratory rodents, but calls for increased research into the effects of pollutants in wild populations. Laboratory experiments demonstrate that even low doses of pesticides alter scent marking behaviour in mice (*M. musculus*) (vom Saal et al., 1995). Using the mouse as a model it is likely other mammalian species could be affected and therefore scent marking behaviour may be used to detect pollutants within a habitat.

6. Directions for future research

Senders of olfactory signals improve their fitness (reproduction and survival) through manipulating or influencing the behaviour of the receiver (Müller-Schwarze, 1999). The importance of olfaction to neonate survival and normal social development has been demonstrated in mammals (Mermet et al., 2007). Exposure and experience of odours results in learning, defined as an "*enduring change in the mechanisms of behaviour that results from experience with environmental events*" (Domjan and Burkhard, 1986). Even innate behavioural responses to olfactory signals are not revealed unless 'normal' development and exposure occur (Wyatt, 2010). This exposure to scents, which incorporates novelty, can affect an animal's capability for behavioural change (Ellis and Wells, 2010) and therefore adaptive response to environmental variation.

Understanding the role of olfaction can play in sexual selection and mate choice can have direct links to fitness, as by permitting female choice can result in greater number of offspring or increased offspring viability (e.g. Jennions & Petrie, 2000). The tendency for mammals to select mates with differing MHC genotypes, encouraging heterozygosity, may produce offspring with resistance to various pathogens (e.g. Penn and Potts, 1998). There are strong theoretical arguments for the importance of mate choice to conservation but current research lacks empirical studies which address the manipulation of the proximate mechanisms (Roberts and Gosling, 2004). Many studies on mammalian chemical communication are species-specific, often concerning laboratory rodents, of known sex, age, genotype, health and reproductive state. Differences across a range of mammalian species may be recognised through the integration of chemical and behavioural studies involving both captive and wild animals. As suggested by Penn (2006) comprehensive knowledge of chemical communication requires an understanding of a species ecology and evolution. Species in which such knowledge is most developed make good models for future research. For example, extinction of the Eurasian beaver was prevented through a series of reintroduction and translocation processes. The chemical ecology of this keystone species is well studied and as such provides a model for integrating chemical communication and conservation dilemmas including increasing success of reintroduction, site fidelity and human-wildlife conflicts (Campbell-Palmer and Rosell, 2010). Although conservation acts across ecosystems, limited resources demand strategic conservation planning and by directing attention to selected or "surrogate" species that can "*represent other species or aspects of the environment to attain a conservation objective*" (Caro, 2010).

An individual’s “personality” represents a consistent individual difference over time (Rèale et al., 2007), and has implications to conservation as it relate to how an individual interacts with their environment, e.g. sociality, shyness/boldness (Blumstein and Fernández-Juricic, 2010). Various personalities may exhibit differing behavioural responses to chemical signals. These personalities may have fitness consequences (Rèale et al., 2007), knowledge of which could be applied to increase captive breeding and post-release survival through the selection of specific traits (Blumstein and Fernández-Juricic, 2010). Molecular genetics is revealing that olfactory receptor genes exhibit homology across a range of insect species (Jacquin and Merlin, 2004; Robertson et al., 2003; Vosshall 2003), comparison studies across vertebrates could provide a focus for future work. Understanding the genetic regulation of chemical communication will further our understanding of ecological interactions (Takken and Dickie, 2006) and also enable the marking and testing of specific olfactory traits, which may reflect “personality” and potential suitability of individuals for conservation programmes such as reintroductions. All of these will require a more empirical approach, thorough experimental design, implementation and evaluation.

The impact of pollution and other anthropogenic environmental changes on olfactory behaviours requires further investigation particularly in relation to fitness and population demography (Angeloni et al., 2010). The effects of chemical pollutants require assessment at ecologically relevant levels across a range of species and it is recommended that behavioural effects are incorporated in toxiciology testing (Zala et. al., 2004). For example, the effects of endocrine-disrupting chemicals on wildlife is still a controversial area of research as these have more subtle effects on endocrine, neural, immune and behavioural responses (Penn, 2006). The ability of species to modify their signalling behaviour, particularly if masked by anthropogenic changes such as pollution, e.g. through frequency shifting or microhabitat selection (Blumstein and Fernández-Juricic, 2010), could be an important measure of a species ability for long term survival.

The role of olfaction in mate choice, mate quality and sexual selection could be further developed (see Roberts and Gosling, 2004). The function of MHC on both mammalian behaviours (e.g. mother-infant recognition, mate attraction) and physiology has yet to be fully determined, in addition the production and expression of these chemosignals are also affected by genetic and environmental variations (Kwak et al., 2010). Genetic variations between individuals and interactions across populations and within ecosystems, all influence physiology and the expression of behaviours. As highlighted by Coleman (2009), research bias exists concerning visual and acoustic sexual communications. This human sensory bias may also be limiting the diversity of stimulus provided to captive animals, particularly to those species with perceived low reliance on olfaction (Somerville and Broom, 1998). More expansive scientific investigations into the role of scent to captive animals may encourage the application of more sensitive husbandry techniques (e.g. cleaning techniques, transportation) and reintroduction tools (e.g. scent broadcasting, predator recognition training) which promote beneficial behaviours, increase welfare and ultimately improve conservation (Clark and King, 2008).

Although laboratory and captive studies reveal vital information on scent function for example these studies also aim to reduce variables in testing conditions. Olfactory studies undertaken in the wild, under real ecological contexts will increase our understanding of populations and community interactions across species and within varying environmental conditions (Angeloni et al., 2010; Müller-Schwarze, 2006). For example many olfactory studies focus on chemosignals that are transmitted on land. Very little research has investigated scent marking in water or olfaction within aquatic mammals. Catania (2006) is one of the few studies that describe a possible mechanism for underwater olfaction in mammals. To develop such work, rigorous testing and extrapolation across aquatic mammalian species could be an important way forward. Numerous authors have called for a greater integration of behaviour and conservation research to generate practical solutions for conservation problems (e.g. Caro, 1998; Clemmons and Buchholz, 1997). However, aside from single species conservation problems such as captive breeding, conservation biology is often concerned with ecosystem level concepts and only a few studies have successfully applied behavioural knowledge to conserve a species (Angeloni et al., 2008; Caro, 2007). As suggested by Bunting et al. (2011) behavioural studies would prove more valuable in determining conservation solutions if knowledge operated at a community and ecosystem level, and/or saved time and resources.

8. Conclusion

Chemical communication in mammals is receiving increasing scientific interest. However, a limited number of articles specifically address the relevance of olfactory behaviours to conservation and wildlife management. Few studies incorporate experimental manipulation of chemical signalling systems to test behavioural theories, such as mate choice or habitat selection, which could have significant impact on conservation dilemmas. As stated by Linklater (2004) "*new understanding and manipulation of behavioural mechanisms, development and evolution may provide novel solutions to conservation problems*". In many articles revealed by this search, olfaction or conservation is briefly mentioned as a direction for further investigation. In order to generate applications with conservation benefits, olfactory behavioural traits could be quantified in terms of consequences to fitness and demography (Angeloni et al., 2010).

Olfaction is the main sensory perception in many mammals and regulates numerous behavioural mechanisms; generally this information is not always available for endangered species. Captive breeding and reintroduction are vital tools in single species conservation. However, captive conditions, the associated handling stress and monitoring of released individuals can have negative physiological effects and thereby affect reintroduction success (Moorhouse et al., 2007). Detailed understanding of the use and behavioural effects of chemical signals could serve to increase welfare and health status of captive animals as well as encourage settlement of newly released or translocated animals into suitable habitats. Ignoring its importance may significantly hinder development and reproduction in captive animals. This will affect the production of animals behaviourally competent for survival in the wild and hence population growth and species evolution. Welfare of captive animals may be compromised by excluding the incorporation of this sense into animal husbandry practices. Reintroduced individuals may experience improved welfare through recognition of self or conspecific scent within a novel environment. Which in turn may reduce stress and enhance "*territorial confidence*" (Mykytowycz et al., 1976), encourage settlement, reduce dispersal and the associated costs to fitness (Swaisgood et al., 1999). Manipulations with scent may also serve to retain animal movements within a designated area, such as protected reserves, thus reducing human conflicts. Substantial contribution to conservation does not only have to involve studies with endangered species. Scientists could choose to work with closely related species or species that are numerous globally but rare in specific areas (Sutherland, 1998). Conservation attention may have to focus on "surrogate species or taxa" to identify areas of conservation interest and/or anthropogenic disturbance or to promote public support and education of conservation issues (Caro, 2010).

The use of natural cues, such as scents, may provide more reliable, species specific methods of reducing conflicts between humans and wildlife in a world where less and less natural range exists for wildlife. Human induced environmental changes are affecting animal behaviour, some of which may not be immediately apparent and are yet to be fully identified. Identifying cues that influence animal distribution and habitat selection enable decisions to be made on area protection, encouraging population, community and landscape conservation. Although this review addressed mammals a growing body of evidence indicates that birds not only possess but utilise a functional, and in some cases highly developed olfactory system (see Caro and Balthazart, 2010 for review). A sensory bias into chemical communication within birds has traditionally existed which is only now beginning to be addressed. Future studies are likely to use mammalian templates. We suggest that animal behavioural studies coupled with manipulations of chemical communication can have significant impacts on conservation. Therefore the olfactory component of behaviours should not be ignored. It is recommended that future scientific attention aims to generate practical solutions and applications beyond the single species level.

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Table 1

Utility and limitations of chemical communication from an animal perspective and in the use of olfaction research in the application of conservation behaviour.

	Utility	Example	Limitation	Example
Animal	Persists in the environment, both time and space	*Müller-Schwarze, 2006*	Decays over time, original signals may be misinterpreted	*Ginzel, 2010*
	Energetically efficient to produce	*Ginzel, 2010*	Production can be energetically expensive	*Gosling et al., 2000,* life history trade offs in mice
	Enable information gathering and territorial defense, no physical contact	*Müller-Schwarze, 2006*	Rapid changes in physiological and emotional state cannot be advertised quickly	*Müller-Schwarze, 1999*
	Rate of decay can provide temporal information	*Cavaggioni et al., 2008*	Modification of frequency/ amplitude when released	*Ginzel, 2010*
	Independent of light, crepuscular	*Fisher et al., 2003*	Application can be time and	*Roberts and Gosling,*

	and nocturnal species	prosimian primates	energy consuming	*2001*
	Often honest signals	*Schulte et al., 2007* musth in elephants	Unintentional receivers, e.g. predators	*Roberts et al., 2001* scent marking in mice in presence of predator odour
	Can travel around obstructions	*Fisher et al., 2003* dense vegetation, prosimians		
	Allows individual identification	*Swaisgood et al., 1999* discrimination giant pandas		
	Environmental odours can be used for communication	*Drea et al., 2002* scent rolling in spotted hyenas		
Research sensory	Non-invasive collection possible	*Fisher et al., 2003* pygmy lorises	Anthropomorphic detection bias	*Coleman, 2009*
	Manipulation of behaviours	*Swaisgood et al., 2004*	Habituation	*Müller-Schwarze and*

	captive breeding giant panda		*Heckman, 1980* beaver re-colonisation
Ease of storage and transport	*Roberts and Gosling, 2004*	Difficult to observe and measure	*Penn, 2006*
Cheap	*Roberts and Gosling, 2004*	Repeated application	*Müller-Schwarze and Heckman, 1980*
Familiarity can influence behaviour	*Roberts and Gosling, 2004*	Familiarity can influence behaviour	*Roberts and Gosling, 2004*
Generate innate reactions	*Sullivan, 1986* red fox urine inhibits herbivore feeding		
Stimulate physiological processes	*Rewort et al., 2001* stimulate ovulation and sperm transportation in female tract		

Table 2

Results of literature search according to order of main species investigated (n=137; 3 theoretical articles were excluded as they did not discuss specific species).

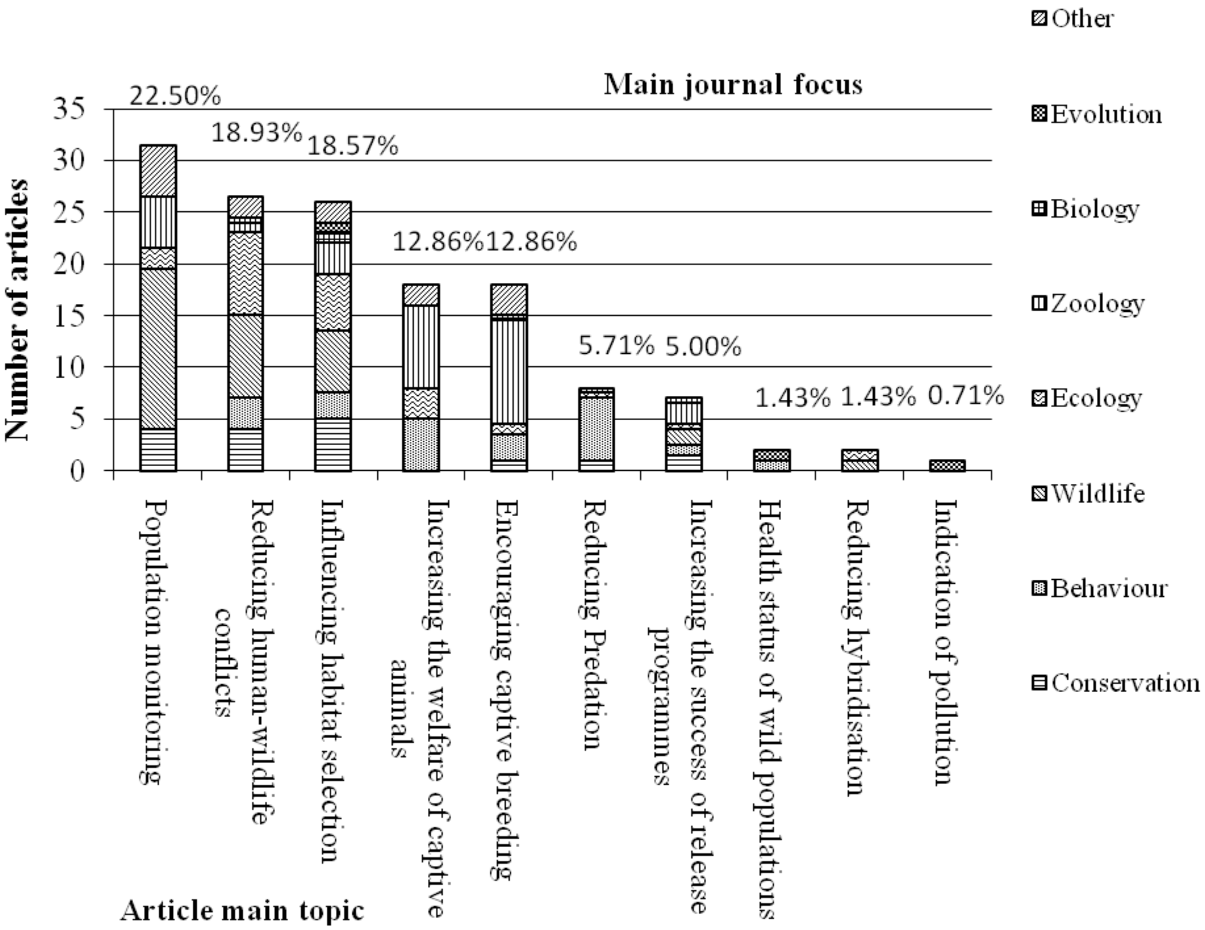
Order	**n**	**%**
Carnivora	79.5	58.03
Rodentia	19.5	14.23
Primates	12	8.76
Artiodactyla	9	6.57
Diprotodontia	6	4.38
Proboscidae	5	3.65
Chiroptera	2	1.46
Perissodactyla	2	1.46
Dasyuromorphia	1	0.73
Erinaceomorpha	1	0.73

Figure legends

Figure 1 Articles according to main topic and journal focus.

The number of articles (n=140) according to main conservation theme and journal focus. Welfare and captive breeding articles were mainly published by behavioural journals. Population monitoring, habitat selection and human-wildlife conflicts involving olfactory studies were mainly published in conservation journals.

Figure 1


Main journal focus
Number of articles
35
30
25
20
15
10
5
0
22.50%
18.93%
18.57%
12.86%
12.86%
5.71%
5.00%
1.43%
1.43%
0.71%
Population monitoring
Reducing human-wildlife conflicts
Influencing habitat selection
Increasing the welfare of captive animals
Encouraging captive breeding
Reducing Predation
Increasing the success of release programmes
Health status of wild populations
Reducing hybridisation
Indication of pollution
Article main topic
Other
Evolution
Biology
Zoology
Ecology
Wildlife
Behaviour
Conservation