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Mustelid Communication

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Synonyms

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Introduction

Mustelids are a large family, with 60 species found in Eurasia, Africa, Asia, North and South America (Koepfli et al. 2008). As shown in Table 1, the family contains eight subfamilies, with many fascinating species like the European badger (*Meles meles*), the sea otter (*Enhydra lutris*), and the wolverine (*Gulo gulo*), to name but a few.
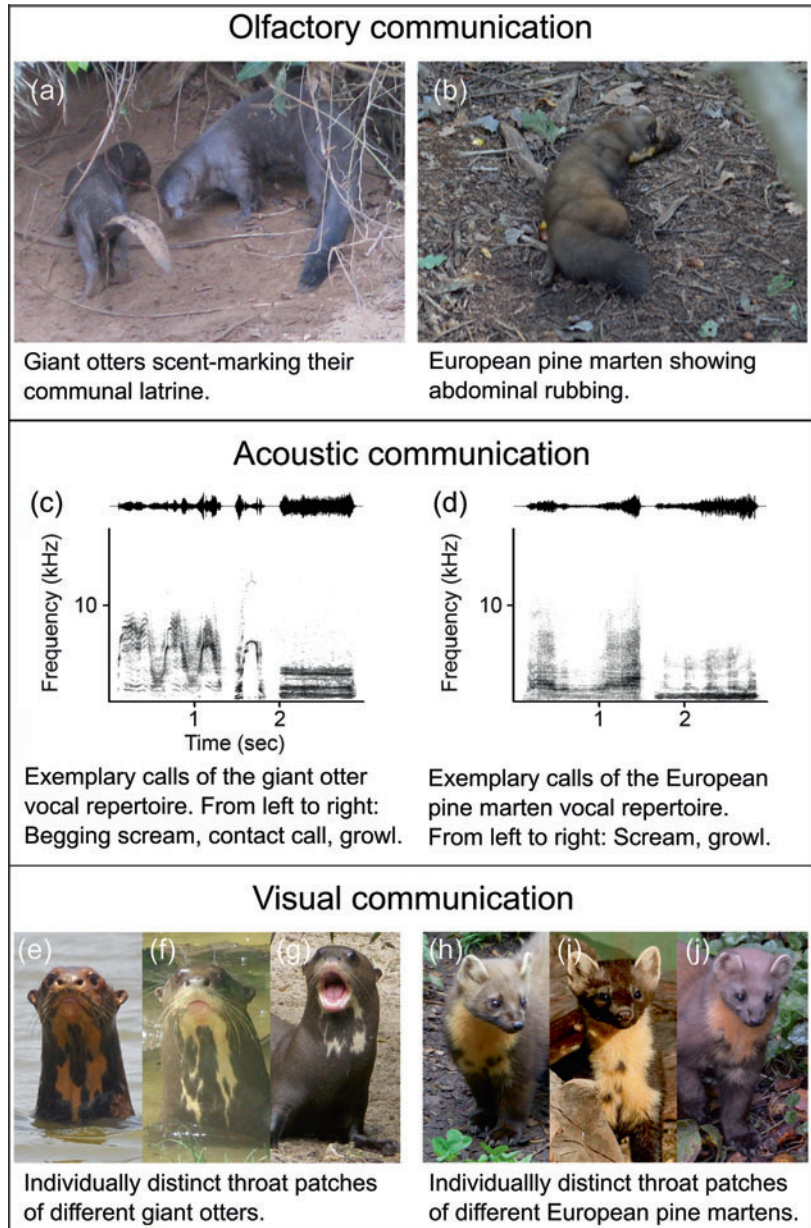
Communication in mustelids is closely related and dependent on the species' respective social system and habitat (Buesching and Stankowich 2017). The social and spatial organization of mustelids is highly variable between species, but there may be also variation in different populations of the same species (Kruuk 2006; Newman et al. 2011). Divergence of a pure solitary lifestyle is induced by environmental factors such as habitat, geographical distribution, ecomorphology, resource dispersion, or season (Johnson et al. 2000). The socio-spatial organization of mustelids is based on the "classical" system of one male territory encompassing distinct female territories. Several variations of and exceptions from this basic pattern exist as well (Kruuk 2006).

As knowledge on mustelids accumulates, several species which formerly have been described as purely solitary turn out to be more social, or have at least a much more flexible social lifestyle (e.g., Newman et al. 2011).

Each communication channel has its advantages and disadvantages. One may be more useful than the others, depending on when, where, and which information needs to be transmitted. Compared to acoustic signals, chemical markings persist for an elongated time, thereby allowing conspecifics or co-occurring species to gather information even in the physical absence of the sender. In a habitat where olfactory cues cannot be deposited, acoustic communication may be favored (Fig. 1). This is especially true for the

Mustelid Communication, Fig. 1 Mustelid communication in three sensory channels. Olfactory communication: two examples of scent-marking postures; acoustic communication: spectrograms of vocalizations showing frequency over time; visual communication: throat patterns likely used for visual (Picture credits **a**, **c**, **d**, **f**, and **g** by Christina Mumm, **b** and **j** by Pia Weidenmüller (written license), **e** by Hannah Heither (written license), **h** by user 422737 on pixabay (CC0 license), **i** by user Ellis Lawrence on flickr (CC BY-SA 2.0 license). Recordings: **c** by Christina Mumm, **d** by Tierstimmenarchiv Berlin)

Olfactory communication

(a) Giant otters scent-marking their communal latrine.

(b) European pine marten showing abdominal rubbing.

Acoustic communication

(c) Exemplary calls of the giant otter vocal repertoire. From left to right: Begging scream, contact call, growl.

(d) Exemplary calls of the European pine marten vocal repertoire. From left to right: Scream, growl.

Visual communication

(e) (f) (g) Individually distinct throat patches of different giant otters.

(h) (i) (j) Individuallly distinct throat patches of different European pine martens.

Mustelid Communication, Table 1 Subfamilies and number of genera and species in the family of mustelids. Each genus is shown with one exemplary species. The number of all genera and species is given in the subheadings for each subfamily (genera/species). All subfamilies are depicted with one representative species. Taxonomy following Koepfli et al. 2008

Subfamily: Galictinae (4/6)		
Galictis Ictonyx Poecilogale Vormela	Greater grison (*G. vitatta*) Striped polecat (*I. striatus*) African striped weasel (*P. albinucha*) Marbled polecat (*V. peregusna*)	 Marbled polecat
Subfamily: Helictidinae (1/5)		
Melogale	Chinese ferret-badger (*M. moschata*)	 Chinese ferret-badger
Subfamily: Lutrinae (6/13)		
Aonyx Enydra Lontra Lutra Lutrogale Pteronura	Asian small-clawed otter (*A. cinerea*) Sea otter (*E. lutris*) North American river otter (*L. canadensis*) European otter (*L. lutra*) Smooth-coated otter (*L. perspicillata*) Giant otter (*P. brasiliensis*)	 Eurasian otter
Subfamily: Martinae (3/10)		
Eira Gulo Martes	Tayra (*E. barbara*) Wolverine (*G. gulo*) European pine marten (*M. martes*)	 European pine marten
Subfamily: Melinae (2/4)		
Arctonyx Meles	Hog badger (*A. collaris*) European badger (*M. meles*)	 European badger

(*continued*)

Mustelid Communication, Table 1 (continued)

Subfamily: Mellivorinae (1/1)		
Mellivora	Honey badger (*M. capensis*)	Honey badger
Subfamily: Mustelinae (3/20)		
Lyncodon Mustela Neovison	Patagonian weasel (*L. patagonicus*) Stoat (*M. erminea*) American mink (*N. vison*)	Stoat
Subfamily: Taxidiinae (1/1)		
Taxidea	American badger (*T. taxus*)	American badger

Picture credits: Marbled polecat by Volker Röhl on Wikipedia; Chinese ferret-badger by Chien-Jen Wang; Eurasian otter by Gellinger on Pixabay; European pine marten by Maxmann on Pixabay; European badger by Chris Parfitt on Flickr; Honey badger by Derek Keats on Flickr; Stoat by Jo Garbutt on Flickr; American badger by Northwest Power and Conservation Council on Flickr

subfamily of otters. With the exception of sea otters (see below), they show a semiaquatic lifestyle and only use scent-marking on land (Kruuk 2006).

Olfactory Communication

Olfactory communication has a multipurpose function. It is regarded as the most important communication channel for mustelids, probably because all mustelids are territorial and scent-mark their territories to announce ownership. It further allows mustelids to signal information on reproductive state, as well as information on identity and food resources. To exchange more detailed information, the animals may vary frequency and location of markings.

Territorial scent-marking can be done by the deposition of feces, urine, or a combination of both (i.e., excremental marking, see Fig. 1a), as well as through gland secretion (i.e., secretional marking). Secretion may be produced in anal, ventral, foot, or subcaudal glands and applied by body rubbing, anal drag, or scratching (see Fig. 1b). Gland secretions can also be used to mark conspecifics. In some species, territorial scent-marking is enhanced by visually marking the surroundings, e.g., by scratching the ground or trees (e.g., Hutchings and White 2000; Leuchtenberger and Mourão 2009). Otter spraints consist of feces, anal gland secretion, and often of

a third compound, the "jelly." Not much is known about this slimy substance, the only available information is that it "is secreted somewhere in the intestine itself" (Kruuk 2006). Chemical composition varies among feces, urine, and gland secretion, thereby allowing for the transmission of differential information (Clapperton 1989).

Deposition of scent is not random in time and space (Kilshaw et al. 2009). For scent-marking, the animals select prominent places, on stones, under bridges, or on other landmarks, which are frequently revisited (Hutchings and White 2000). Otters may even chose marking places which are relatively far and visit them repeatedly (Kruuk 2006). Furthermore, European badgers do not only carefully select marking places, but also the positioning of scent inside each place (Stewart et al. 2002). As badger territories contain more than one latrine site, the animals systematically revisit several places to refresh their scent marks (Kilshaw et al. 2009).

Social species like European badgers and giant otters (*Pteronura brasiliensis*) make use of communal latrines – enlarged areas for the deposition of excremental and secretional marks from all group members. Giant otters regularly clear off the vegetation at communal latrines. Otters in general show an elaborate marking behavior because the deposition of excremental and secretional marks can be accompanied by a scent-marking "dance." Giant otters, as well as spotted-necked otters (*Lutra maculicollis*), and North American river otters (*Lontra canadensis*) show dance-like stepping postures, accompanied by intense sniffing. Giant otters use their forepaws for dancing, while spotted-necked otters and North American river otters use their hind legs. Some species may also smear feces from different individuals with their paws or tail to create a typical group odor (e.g., Buesching et al. 2016; Leuchtenberger and Mourão 2009; Rostain et al. 2004).

In several mustelids scent-marking frequency shows seasonal changes, mainly with a peak in the mating season. Mustelids scent-mark within their territory ("hinterland latrines") or at territorial borders ("boundary latrines"). Both types have different functions, which are best described

in badgers. The use of different latrine sites depends on population density and season. In high-density populations, European badgers form social groups, whereas in low-density populations, groups mainly consist of a pair and their offspring. Larger groups have more latrines inside their home range, but space is limited in high-density populations, so that these groups usually occupy smaller areas. They invest mainly in boundary latrines; however, their function in territorial defense is not fully understood (Buesching et al. 2016). Nevertheless, European badgers can discriminate between feces from neighboring and alien groups and react more aggressively towards the scent of alien groups. Smaller badger groups in low-density populations may use larger areas, but their ability of marking is limited by the number of individuals. Therefore, small groups may neglect boundary latrines and the use of hinterland latrines peaks during mating time. Latrine use is even abandoned seasonally, when home range size is enlarged. This shows a trade-off between group size and the area a group is able to defend, either in terms of limited space or in terms of limited number of individuals marking the latrines (Buesching et al. 2016). Population density also affects the main information provided at latrines: they likely function to signal territoriality in high-density populations, but reproductive state and other individual information in low-density populations (Zhou et al. 2015). In low-density populations of Japanese badgers (*Meles anakuma*), information provided at both latrine types eases information exchange about presence, identity, and hormonal state of females, and Japanese badgers visit boundary latrines most often during mating season (Kaneko et al. 2009). Hog badgers (*Arctonyx collaris*), which are described to be solitary, use latrines for a different reason: they signal the location of food resources (Zhou et al. 2015). This behavior is also found in coastal Eurasian otters (*Lutra lutra*), which mark food patches and freshwater pools to signal their use of these resources (Trowbridge 1983). Scent-marks allow them to inform conspecifics that the resource is already depleted, and avoid direct competition and confrontation. Besides its importance for signaling territoriality and reproductive

state, excremental markings may also aid in spatial orientation. For instance, Eurasian otters mark locations where their trails change direction (Trowbridge 1983).

The only mustelid in which excremental marking is absent is the sea otter. This exception is due to its exclusive aquatic lifestyle, differing from all other otters, which have a semi-aquatic lifestyle. Instead of scent marking, male sea otters defend their marine territories during the mating period by patrol swimming, splashing, and direct chases of rivals (Kruuk 2006).

Secretional marking is also important in territoriality, spatial organization, and individual information exchange. Dominant males of European badger groups intensify secretional marking of females during mating season (Kruuk et al. 1984). Individually distinct odor cues are found in several mustelids. Ferrets (*Mustela putorius furo*) do not only distinguish the deposition time of conspecific odor, but also discriminate between different individuals because the composition of volatiles is individually distinct. The combination of this information enables ferrets (and likely all other mustelids) to learn movement patterns of conspecifics, adjust their activities accordingly, and thereby avoid direct aggressive encounters.

Even though mustelids may encode individual identity in all available signal modalities, most studies focus on olfactory communication. Experiments on olfactory discrimination or recognition in mustelids are restricted to a few species, and older studies often tested only one focal animal, thereby providing descriptive indications rather than reliable statistical data for further comparisons.

Volatile compounds produced by mustelids differ between species, and show sufficient variation to encode sex, age, and individual identity (Brinck et al. 1983). Identity cues can either be encoded by presence or absence of certain compounds and/or through the amount and composition of the chemical compounds. For instance, gland secretions of Siberian weasels (*Mustela sibirica*) and the urine of ferrets contain sex-specific chemical compounds, while steppe polecat (*Mustela eversmanni*) secretions encode sex in

the relative abundance of different compounds (Zhang et al. 2002; Zhang et al. 2005).

Group or family odors can be created by secretional marking of conspecifics; cubs, mates, or other group members are normally labeled by body rubbing (Duplaix 1980). Group odors can be combined with individual distinct odors as well. For instance, European badgers use the scent from their subcaudal gland to create a group odor and to share individual information, especially about their reproductive state (Buesching et al. 2003). They distribute their group odor through mutually marking each other, but deposit their individually distinct odor by sequential allo-marking, i.e., one badger rubbing its scent onto the fur of other group members (Buesching et al. 2003).

The function of scent cues may also be influenced by composition of social groups. North American river otters, for instance, show a flexible social organization. When females rear their young, they may build family groups, sometimes with elder helpers, or stay solitary, while males may form temporary groups of up to 30 individuals (Lariviere and Walton 1998). Group-living females use scent cues for territorial maintenance and solitary individuals use them for avoiding direct encounters with conspecifics (Ben-David et al. 2005). Whereas in male groups, scent cues help to maintain a dominance hierarchy (Rostain et al. 2004).

In areas where different mustelid species co-occur, interspecies competition seems to be low due to different habitat and dietary preferences or foraging strategies (Hussain et al. 2011). Nevertheless, interspecific territoriality and social dominance are most likely communicated via olfactory cues.

Several mustelid species, e.g., the striped polecat (*Ictonyx striatus*) and the African striped weasel (*Poecilogale albinucha*), can produce chemical defensive sprays (Apps et al. 2015; Larivière 2001), comparable but not as strong as those known from skunks (*Mephitidae*). Other mustelids, such as the American mink and the honey badger (*Mellivora capensis*), do not directly spray, but also produce deterrent secretion when threatened (Brinck et al. 1978; Vanderhaar and Hwang 2003). The respective volatile

compounds are produced in anal glands, and are foul and strongly smelling (Apps et al. 2015; Larivière 2001).

Currently, no information on the mustelids' sense of smell is available but it is conceivable that their olfactory perception is highly sensitive, given the importance of odor cues for social communication.

Acoustic Communication

Many mustelids are extremely vocal and often engage in screaming, hissing, chuckling, squeaking, and squealing. Mustelids may signal identity cues, intention, stay in contact or beg for food via the acoustic channel. Some vocalizations also play a role in territorial defense. Nevertheless, peer-reviewed publications of the vocal repertoire exist for only 12 species and anecdotal descriptions are available for only 14 more (for an example of European pine marten calls see Fig. 1d). The acoustic communication of the remaining 34 species has not been studied so far (Table 2). There are no publications on acoustic communication in Helictidinae, and Taxidiinae. Most descriptions are found for the subfamily of otters. Outstanding in terms of vocal complexity are two representatives of the otters: the Asian small-clawed otter (*Aonyx cinerea*) and the giant otter (*Pteronura brasiliensis*).

To date, giant otters are the best studied mustelid concerning acoustic communication. Several authors described the vocal repertoire to consist of 15–19 distinct vocalizations (see some examples in Fig. 1c). This elaborate repertoire is further enlarged by gradations between calls. Like in many other otter species, such as sea otters, or Asian small-clawed otters, several giant otter vocalizations show enough variation in acoustic cues to provide individual differences and the potential for vocal discrimination and recognition (Leuchtenberger et al. 2016; Mumm and Knörnschild 2014). Giant otters use contact calls and hums for group cohesion and can discriminate between different individuals based on these vocalizations alone (Mumm et al. 2014). Correspondingly, Asian small-clawed otters derive

sufficient information from their contact calls to distinguish their mates from unknown individuals (Lemasson et al. 2013). Group screaming (a territorial vocalization) and snorts (a type of alarm call) provide acoustic information on group identity, thereby aiding giant otters in territorial defense. Moreover, acoustic parameters of snorts encode the sex of the calling individual, an aspect which is not prominently reflected in the physical appearance (Leuchtenberger et al. 2016; Mumm and Knörnschild 2017).

Some studies describe vocalizations of cubs. Apparently, innate precursors of the adult vocal repertoire are found in all species studied to date. Giant otter cubs emit adult-like vocalizations from birth on and combine them in long babbling bouts, presumably to practice. Some cub calls are age-specific and disappear during development (Mumm and Knörnschild 2014). American mink cubs are also vocally active from birth on. However, studies on hearing development in ferrets and mink cubs could show that hearing starts not earlier than around 30 days of age (Brandt et al. 2013; Moore and Hine 1992).

Hearing ranges and thresholds are known for six mustelid species. The hearing ranges of semi-aquatic otters and minks are largely comparable, while ferrets and stoats have a broader range. Best hearing lies between 1 kHz and 16 kHz (compare Brandt et al. 2013; Ghoul and Reichmuth 2012; Heffner and Heffner 1987). Overall, the hearing capacity of mustelids is comparable to other carnivores (Ghoul and Reichmuth 2012; Heffner and Heffner 1985). In tests for hearing and sound localization accuracy, least weasels performed better than their prey species (rodents), which underlines the selective pressure on carnivores for good sound detection abilities in order to localize their prey (Heffner and Heffner 1987).

Visual Communication

Fur coloration and body postures are apparent in several mustelid species, but vision is poorly studied, with only seven publications on five species (three otter species, European polecat, and ferret).

Mustelid Communication, Table 2 Publications describing the adult vocal repertoire of mustelid species

Subfamily	Species	Nr. of vocalizations	Detailed description of vocalizations	Reference
Galictinae	Marbled polecat (*Vormela peregusna*)	3	No	Gorsuch and Larivière (2005)
	African striped weasel (*Poecilogale albinucha*)	6	Yes	Channing and Rowe-Rowe (1977)
	Greater grison (*Galictis vitatta*)	6	No	Yensen and Tarifa (2003)
	Striped polecat (*Ictonyx striatus*)	6	Yes	Channing and Rowe-Rowe (1977)
Lutrinae	Smooth coated otter (*Lutrogale perspicillata*)	>3	No	Larivière and Hwang (2005)
	Hairy-nosed otter (*Lutra sumatrana*)	3–8	No	Wright et al. (2008)
	Congo clawless otter (*Aonyx congicus*)	7	No	Jacques et al. (2009)
	European otter (*Lutra lutra*)	7	Yes	Gnoli and Prigioni (1995)
	Sea otter (*Enhydra lutris*)	10	Yes	McShane et al. (1995)
	African clawless otter (*Aonyx capensis*)	11	No	Larivière (2001)
	North American river otter (*Lontra canadensis*)	11	Yes	Almonte (2014)
	Spotted-necked otter (*Hydrictis maculicollis*)	12	No	Reed-Smith et al. (2014)
	Asian small-clawed otter (*Aonyx cinerea*)	7–17	Yes	Lemasson et al. (2014), Tramm (2012)
	Giant otter (*Pteronura brasiliensis*)	15–19	Yes	Leuchtenberger et al. (2014), Mumm and Knörnschild (2014)
Martinae	Fisher (*Martes pennanti*)	>3	No	Powell (1981)
	Tayra (*Eira barbara*)	>4	No	Poglayen-Neuwall (1974)
	Beech marten (*Martes foina*)	5	Yes	Lodé (1991)
	American marten (*Martes americana*)	7	Yes	Belan et al. (1978)
	European pine marten (*Martes martes*)	8	No	Kvalheim (1982)
Melinae	European badger (*Meles meles*)	10	Yes	Wong et al. (1999)
Mellivorinae	Honey badger (*Mellivora capensis*)	>6	No	Vanderhaar and Hwang (2003)
Mustelinae	Long-tailed weasel (*Mustela frenata*)	3	Yes	Svendsen (1976)
	American mink (*Neovison vison*)	>4	No	Larivière (1999)
	Steppe polecat (*Mustela eversmanni*)	6	Yes	Farley et al. (1987)
	Black-footed ferret (*Mustela nigripes*)	7	No	Clark et al. (1986)
	European polecat (*Mustela putorius*)	9	Yes	Gossow (1970)
	Stoat (*Mustela erminea*)	9	Yes	Gossow (1970)
	Weasel (*Mustela nivalis*)	9	Yes	Gossow (1970)

Only one, but a very interesting study deals with visual cues in mustelids (Newman et al. 2005).

The otter eye is equivalent to that of other terrestrial mammals. Same visual acuity in air and underwater is achieved by an accommodation process which offsets loss of corneal refractive power underwater. The retinal resolution angle is about 14′ in Asian small-clawed otters (Balliet and Schustermann 1971), and 7′ in sea otters (Mass and Supin 2000), which is close to the angle of 5′ in pinnipeds. European polecats and ferrets have a resolving angle of 16′ (Neumann and Schmidt 1959). The amplitude of accommodation in sea otters is 60D and thereby comparable to that of humans (58D) (Murphy et al. 1990). Thus, we think that the often proposed poor visual abilities of mustelids can no longer be supported.

Fur coloration in mustelids reaches from inconspicuous unicolor (as in the Lutrinae), over contrasting black-and-white (as in the Galictinae) to a vivid coloration in the marbled polecat or the yellow-throated marten (*Martes flavigula*). Several species have facial masks, e.g., grisons and badgers, or individually distinct throat markings, e.g., giant otters and European pine martens (Fig. 1e–j) (Newman et al. 2005). Facial masks and throat markings may have different functions: facial masks are most likely a warning signal since they are found in species which produce defensive sprays and anal gland secretion in threatening situations (Newman et al. 2005). Throat markings, on the other hand, probably play a role in individual communication. Many mustelids stand on their hind legs when monitoring their surroundings, and giant otters periscope out of the water when detecting unknown or threatening objects (Duplaix 1980). This behavior gives conspecifics ample opportunity to see the throat pattern. Nevertheless, it remains to be tested whether mustelids make use of throat markings for visual or multimodal individual recognition.

Multimodal Communication

Not much is known about the information mustelids can derive by combining signals in different modalities. Asian small-clawed otters are the only mustelid species for which multimodal discrimination of conspecifics has been tested experimentally (Lemasson et al. 2013). Females are able to discriminate their male partners from unfamiliar males based on scent and vocalizations. They did not react to life-size photographs, which may either show the minor importance of visual cues or their inability of visual discrimination.

Conclusion

Mustelids use different modalities for communication. Like many mammals, they exchange information about territorial ownership, hormonal state, and individual cues like group membership, or sex and age. The mostly solitary lifestyle in this family may account for the importance of signals which do not require direct contact for communication. This is achieved via olfactory markings. Nevertheless, visual communication in terms of fur coloration and body postures also plays a role in mustelid communication. The more social the species, the more important becomes the acoustic channel, allowing group members a fast and direct information exchange.

Despite the growing literature on social communication in mustelids, there is an obvious lack of knowledge about perception and processing of olfactory, acoustic, and visual cues. There are many limitations hampering experimental approaches for the study of communication and cognition in mustelids: several species are elusive, solitary, and/or protected; basic data on behavior and ecology is lacking; captive holdings have only a few or one individual; and animal training strongly depends on cooperation and attention span of focal animals. Furthermore, experimental design needs to be sophisticated, and properly adjusted to the respective species (compare Mumm et al. 2014; Trowbridge 1983). Nevertheless, mustelids are a highly promising family for future studies, especially regarding multimodal communication and self-recognition. Moreover, the variety of social organization in mustelids is well suited to investigate the positive feedback loop between social and communicative complexity.

Cross-References

References

Apps, P. J., Viljoen, H. W., Pretorius, V., & Rohwer, E. R. (2015). Volatile components of the anal gland secretion of the striped polecat *Ictonyx striatus*. *South African Journal of Zoology, 23*(2), 136–137. https://doi.org/10.1080/02541858.1988.11448091

Balliet, R. F., & Schustermann, R. J. (1971). Underwater and aerial visual acuity in the Asian "clawless" otter (*Amblonyx cineria cineria*). *Nature, 234*(5327), 305–306.

Ben-David, M., Blundell, G. M., Kern, J. W., Maier, J. A. K., Brown, E. D., & Jewett, S. C. (2005). Communication in river otters: Creation of variable resource sheds for terrestrial communities. *Ecology, 86*(5), 1331–1345.

Brandt, C., Malmkvist, J., Nielsen, R. L., Brande-Lavridsen, N., & Surlykke, A. (2013). Development of vocalization and hearing in American mink (*Neovison vison*). *The Journal of Experimental Biology, 216*(Pt 18), 3542–3550. https://doi.org/10.1242/jeb.080226

Brinck, C., Erlinge, S., & Sandell, M. (1983). Anal sac secretion in mustelids: A comparison. *Journal of Chemical Ecology, 9*(6), 727–745.

Brinck, C., Gerell, R., Odham, G., & Odham, G. (1978). Anal pouch secretion in mink Mustela Vison. Chemical communication in mustelidae. *Oikos, 30*(1), 68. https://doi.org/10.2307/3543523

Buesching, C. D., & Stankowich, T. (2017). Communication amongst the musteloids: Signs, signals, and cues. In D. W. Macdonald, C. Newman, & L. A. Harrington (Eds.), *Biology and conservation of Musteloids* (pp. 158–177). Oxford: Oxford University Press.

Buesching, C. D., Stopka, P., & MacDonald, D. W. (2003). The social function of allo-marking in the European badger (*Meles meles*). *Behaviour, 140*(8), 965–980. https://doi.org/10.1163/156853903322589597

Buesching, C. D., Newman, C., Service, K., Macdonald, D. W., Riordan, P., & Parmenter, R. R. (2016). Latrine marking patterns of badgers (*Meles meles*) with respect to population density and range size. *Ecosphere, 7*(5), e01328. https://doi.org/10.1002/ecs2.1328

Clapperton, B. K. (1989). Scent-marking behaviour of the ferret, *Mustela furo* L. *Animal Behaviour, 38*(3), 436–446. https://doi.org/10.1016/S0003-3472(89)80037-5

Duplaix, N. (1980). Observation on the ecology and behavior of the giant river otter *Pteronura brasiliensis* in Suriname. *La Terre et la Vie – Revue d'écologie, 34*(4), 496–620.

Ghoul, A., & Reichmuth, C. (2012). Sound production and reception in southern sea otters (*Enhydra lutris nereis*). *Advances in Experimental Medicine and Biology, 730*, 157–159. https://doi.org/10.1007/978-1-4419-7311-5_35

Heffner, R. S., & Heffner, H. E. (1985). Hearing in mammals: The least weasel. *Journal of Mammalogy, 66*(4), 745–755. https://doi.org/10.2307/1380801

Heffner, R. S., & Heffner, H. E. (1987). Localization of noise, use of binaural cues, and a description of the superior olivary complex in the smallest carnivore, the least weasel (*Mustela nivalis*). *Behavioral Neuroscience, 101*(5), 701–708. https://doi.org/10.1037/0735-7044.101.5.701

Hussain, S. A., Gupta, S. K., & de Silva, P. K. (2011). Biology and ecology of Asian small-clawed otter *Aonyx cinereus* (Illiger, 1815): A review. *IUCN Otter Specialist Group Bulletin, 28*(2), 63–75.

Hutchings, M. R., & White, P. C. L. (2000). Mustelid scent-marking in managed ecosystems: Implications for population management. *Mammal Review, 30*(3–4), 157–169. https://doi.org/10.1046/j.1365-2907.2000.00065.x

Johnson, D. P. D., Macdonald, D. W., & Dickman, A. J. (2000). An analysis and review of the sociobiology of the mustelidae. *Mammal Review, 30*(3–4), 171–196.

Kaneko, Y., Suzuki, T., & Atoda, O. (2009). Latrine use in a low density Japanese badger (*Meles anakuma*) population determined by a continuous tracking system. *Mammal Study, 34*(4), 179–186. https://doi.org/10.3106/041.034.0401

Kilshaw, K., Newman, C., Buesching, C., Bunyan, J., & Macdonald, D. (2009). Coordinated latrine use by European badgers, *Meles meles*: Potential consequences for territory defense. *Journal of Mammalogy, 90*(5), 1188–1198. https://doi.org/10.1644/08-MAMM-A-200.1

Koepfli, K.-P., Deere, K. A., Slater, G. J., Begg, C., Begg, K., Grassman, L., et al. (2008). Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology, 6*, 10. https://doi.org/10.1186/1741-7007-6-10

Kruuk, H. (2006). *Otters: Ecology, behaviour and conservation*. Oxford/New York: Oxford University Press.

Kruuk, H., Gorman, M., & Leitch, A. (1984). Scent-marking with the subcaudal gland by the European badger, *Meles meles* L. *Animal Behaviour, 32*(3), 899–907. https://doi.org/10.1016/S0003-3472(84)80168-2

Lariviere, S., & Walton, L. R. (1998). Lontra canadensis. *Mammalian Species, 587*, 1. https://doi.org/10.2307/3504417

Larivière, S. (2001). Poecilogale albinucha. *Mammalian Species, 681*, 1–4. https://doi.org/10.1644/1545-1410(2001)681<0001:PA>2.0.CO;2

Lemasson, A., Mikus, M.-A., Blois-Heulin, C., & Lodé, T. (2013). Social partner discrimination based on sounds and scents in Asian small-clawed otters (*Aonyx cinereus*). *Die Naturwissenschaften, 100*(3), 275–279. https://doi.org/10.1007/s00114-013-1022-9

Leuchtenberger, C., & Mourão, G. (2009). Scent-marking of giant otter in the southern Pantanal, Brazil. *Ethology, 115*(3), 210–216. https://doi.org/10.1111/j.1439-0310.2008.01607.x

Leuchtenberger, C., Sousa-Lima, R., Duplaix, N., Magnusson, W., & Mourão, G. (2014). Vocal repertoire of the social giant otter. *The Journal of the Acoustical Society of America, 136*(5), 2861–2875.

Leuchtenberger, C., Sousa-Lima, R., Ribas, C., Magnusson, W. E., & Mourão, G. (2016). Giant otter alarm calls as potential mechanisms for individual discrimination and sexual selection. *Bioacoustics, 25*(3), 279–291. https://doi.org/10.1080/09524622.2016.1157704

Mass, A. M., & Supin, A. Y. (2000). Ganglion cells density and retinal resolution in the sea otter, *Enhydra lutris*. *Brain, Behavior and Evolution, 55*(3), 111–119. https://doi.org/10.1159/000006646

Moore, D. R., & Hine, J. E. (1992). Rapid development of the auditory brainstem response threshold in individual ferrets. *Developmental Brain Research, 66*(2), 229–235. https://doi.org/10.1016/0165-3806(92)90084-A

Mumm, C. A. S., & Knörnschild, M. (2014). The vocal repertoire of adult and neonate giant otters (*Pteronura brasiliensis*). *PLoS One, 9*(11), e112562. https://doi.org/10.1371/journal.pone.0112562

Mumm, C. A. S., & Knörnschild, M. (2017). Territorial choruses of giant otter groups (*Pteronura brasiliensis*) encode information on group identity. *PLoS One, 12*(10), e0185733.

Mumm, C. A. S., Urrutia, M. C., & Knörnschild, M. (2014). Vocal individuality in cohesion calls of giant otters, *Pteronura brasiliensis*. *Animal Behaviour, 88*, 243–252. https://doi.org/10.1016/j.anbehav.2013.12.005

Murphy, C. J., Bellhorn, R. W., Williams, T., Burns, M. S., Schaeffel, F., & Howland, H. C. (1990). Refractive state, ocular anatomy, and accommodative range of the sea otter (*Enhydra lutris*). *Vision Research, 30*(1), 23–32. https://doi.org/10.1016/0042-6989(90)90125-5

Neumann, F., & Schmidt, H. D. (1959). Optische Differenzierungsleistungen von Musteliden: Versuche an Frettchen und Iltisfrettchen. *Zeitschrift für Vergleichende Physiologie, 42*(3), 199–205. https://doi.org/10.1007/BF00333611

Newman, C., Buesching, C. D., & Wolff, J. O. (2005). The function of facial masks in "midguild" carnivores. *Oikos, 108*(3), 623–633. https://doi.org/10.1111/j.0030-1299.2005.13399.x

Newman, C., Zhou, Y.-B., Buesching, C. D., Kaneko, Y., & Macdonald, D. W. (2011). Contrasting sociality in two widespread, generalist, mustelid genera, *Meles* and *Martes*. *Mammal Study, 36*(4), 169–188. https://doi.org/10.3106/041.036.0401

Rostain, R. R., Ben-David, M., Groves, P., & Randall, J. A. (2004). Why do river otters scent-mark? An experimental test of several hypotheses. *Animal Behaviour, 68*(4), 703–711. https://doi.org/10.1016/j.anbehav.2003.10.027

Stewart, P. D., Macdonald, D. W., Newman, C., & Tattersall, F. H. (2002). Behavioural mechanisms of information transmission and reception by badgers, *Meles meles*, at latrines. *Animal Behaviour, 63*(5), 999–1007. https://doi.org/10.1006/anbe.2001.1990

Trowbridge, B. J. (1983). Olfactory communication in the European otter (*Lutra I. lutra*), Aberdeen. Thesis. University of Aberdeen.

Vanderhaar, J. M., & Hwang, Y. T. (2003). *Mellivora capensis*. *Mammalian Species, 721*, 1–8. https://doi.org/10.1644/721

Wong, J., Stewart, P. D., MacDonald, D. W. (1999). Vocal repertoire in the European badger (Meles meles): structure, context, and function. *Journal of Mammalogy, 80*(2), 570–588.

Zhang, J. X., Soini, H. A., Bruce, K. E., Wiesler, D., Woodley, S. K., Baum, M. J., & Novotny, M. V. (2005). Putative chemosignals of the ferret (*Mustela furo*) associated with individual and gender recognition. *Chemical Senses, 30*(9), 727–737. https://doi.org/10.1093/chemse/bji065

Zhang, J.-X., Sun, L., Zhang, Z.-B., Wang, Z.-W., Chen, Y., & Wang, R. (2002). Volatile compounds in anal gland of Siberian weasels (*Mustela sibirica*) and steppe polecats (*M. eversmanni*). *Journal of Chemical Ecology, 28*(6), 1287–1297. https://doi.org/10.1023/A:1016246120479

Zhou, Y., Chen, W., Buesching, C. D., Newman, C., Kaneko, Y., Xiang, M., et al. (2015). Hog badger (*Arctonyx collaris*) latrine use in relation to food abundance: Evidence of the scarce factor paradox. *Ecosphere, 6*(1), art 19. https://doi.org/10.1890/ES14-00155.1