Chapter 14:

The social function of latrines: A hypothesis-driven research approach

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Abstract

In many mammals, the function of latrine use is still debated. Suggested explanations can be broadly divided into resource defence, information centre/ advertisement, landmarks/ orientation, parasite control, or predator-prey interactions. Here, we develop a hypothesis-driven research framework based on the six categories of data that can be collected from latrines (spatial distribution patterns of latrines; temporal usage patterns of latrines; visit and contribution patterns of individual animals to individual latrines; behaviour of visitors to and/ or users of latrines; the longevity, volatility and life-span of the scent signals) to help investigate the role of latrine use in any focal species. We emphasise that, due to the complexity of the information content encoded in olfactory signals, in most mammals latrine use is likely multi-functional.

14.1 Introduction

Latrines are typically defined as accumulations of two to several hundred faeces resulting from the repeated use of the same defecation sites (Brown and Macdonald 1985). Faeces can be deposited in specially dug pits (e.g. European badgers *Meles meles*: Delahay et al 2000) or – more commonly - directly on the surface. Latrine use has been reported in most mammal orders (for reviews see e.g., Primates: Irwin et al. 2004; Rodentia: Ferkin this volume; Lagomorphs: Sneddon 1991; ungulates: Mueller-Schwarze 1987; Musteloidea: Buesching & Stankowich 2015; Carnovora: Buesching & Jordan in press; marsupials: e.g. Rubial et al. 2011; Insectivora: Poduschka et al. 1986) and has even been confirmed in dinosaurs (Fiorelli et al. 2013). Often these dedicated latrine sites are used not only for defecation and urination, but also for the deposition of glandular secretions, resulting in composite latrines or middens. In many species, latrines are shared by several animals belonging to the same family/ social group or to different (neighbouring) groups. Because conspecifics typically spend much time investigating excreta and secretions deposited by previous visitors (e.g. Stewart et al. 2002), the role of latrines in olfactory communication has long been accepted (Brown & Macdonald, 1985). Nevertheless, despite the ever expanding field of semio-chemical analysis, few ecological studies discussing the function of latrine use take into consideration the olfactory information content known to be encoded in the faecal, urinary and secretory scent-marks.

A variety of hypotheses have been suggested to explain latrine use in different species, which can be broadly divided into four categories pertaining to i) *resource defence* (encompassing territory, food, sleeping/ breeding sites, mates), ii) *information centre and reproductive advertisement,* iii) *landmarks aiding in orientation*, iv) *parasite avoidance*, or v) *predator–prey interactions* (for a detailed review of hypotheses pertaining to latrine function see Buesching & Jordan in press). However, while some of the proposed functions, such as the roles as information centres and individual reproductive advertisement signals, would require rather differentiated olfactory messages to be conveyed at latrines, others (e.g., parasite avoidance) would require latrines only to be identifiable as suitable sites for defecation. In addition, some functions (such as the marking of territories and sleeping dens, landmarks) would benefit from long-lasting olfactory signals deposited in (quasi-)permanent sites, others (such as reproductive advertisement, marking of abundant but transient food resources) would best be fulfilled by short(er)-term signals left at currently active locations, while predator avoidance would best be achieved if latrine smell could be kept to a minimum altogether. While some functions are thus mutually exclusive, others could easily be served simultaneously

In addition to the olfactory information content, five further categories of data can be collected when studying latrines: 1) their spatial distribution patterns; 2) their temporal usage patterns; 3) the visit and contribution patterns of individual animals; 4) the behaviour of visitors to and/ or users of latrines; 5) the longevity, volatility and life-span of the scent signals. The conclusions drawn about the function of latrines are thus very much influenced (and often restricted) by the data available.

Here, we aim to develop a research framework based on these six categories of data that might aid in testing specific hypotheses pertaining to the five broad theoretical paradigms that have been suggested to explain the function of latrines in the past.

14.2 Hypothesis-based predictions of latrine characteristics

14.2.1) Latrines as resource defence

Latrines are often explained as "advertisement of ownership" of one or several of four main resources (for a detailed discussion of the different hypotheses pertinent in this context, see Buesching & Jordan in press). Because, typically, only species that are either territorial or have stable home ranges use latrines, their function has been linked at least in part to territorial marking and the marking/ defence of the resources contained within, namely food, sleeping / breeding sites, and sometimes mates (although mates are more typically defended by direct aggression/ herding or allo-marking during mating/ courtship) in almost all species. The traditional interpretation as a "scent-fence" (e.g. Hediger, 1949), however, has been revised repeatedly since its conception to accommodate mounting observations in an ever increasing variety of species of territorial intrusions by non-residents, and has been reformulated for example as "scent matching hypothesis", which states that by comparing scent-marks encountered within the territory with the scent of the territory holder, intruders can avoid confrontation (e.g. Gosling & McKay, 1990) through scent-matching (Gosling, 1982). And so, latrines are proposed to help establish a power asymmetry between territory-holder and intruder (Maynard-Smith & Parker, 1976; Hammerstein, 1981; Gosling, 1982) according to the Payoff Asymmetry Hypothesis (Dawkins & Krebs, 1978; Krebs, 1982).

Either way, if latrine function is connected to territorial marking, we can predict the following (according to the five categories of data obtainable from latrines): Their **spatial distribution patterns** should optimise locations to intercept intruders and thus, dependent on costs of patrolling borders and faecal restraint (Buesching et al. 2016b), latrines should be located predominantly along (or near) the perimeter and to a lesser degree throughout the hinterland. Substrate and microclimate of latrine sites should be chosen to maximise detection (i.e., signal range increase through air flow/ elevation) and signal longevity (e.g., by preventing scent marks from drying out). Their **temporal usage patterns** should peak when intrusion threat is most intense, and should be correlated with intruder encounters (especially interlopers threatening territory integrity). The **visit and contribution patterns of individual animals** should reflect primary marking activity by territory owners, be sex-dependent in species where intrusion or territoriality is sex-biased, and be higher in individuals with more to gain by territorial defence (e.g. breeding/dominant individuals). The **scent signals** should be of low volatility and potentially contain anti-microbial components to enhance signal longevity while simultaneously minimising marking costs. Scent-profiles should allow association between territory owner(s) and defended areas. Consequently, in gregarious species, scent profiles should be group-specific (but could allow assessment of group-size through inclusion of individual-specific characteristics), whereas in solitary species signals should be individual-specific, allowing olfactory discrimination between group (own) odour from neighbours and strangers, and thus the identification of residents via scent matching. The **behaviour of visitors to and/ or users of latrines** should indicate that intruders avoid scent-marked areas/retreat on encountering scents (scent-fence) or modify their interaction with owner(s) when match territory scent to individual scent (scent-matching hypothesis). Intruders should over-/countermark only when attempting to take over territories, although border latrines can be shared between neighbours.

Nevertheless, animals do not defend territories for space alone, but also for the resources that they encompass. Although the general predictions outlined above, are applicable to all 'resource marking' signals independent of the resource itself (i.e., territory or food/ breeding/ sleeping sites etc.), **latrine location** should be close to the respective resource (den, food patch etc), and the **olfactory signal characteristics** may be adapted (i.e., shorter signal lifespan) to reflect transient food sources, short-term den use etc. In the case of breeding dens (and dependent on social structure also sleeping sites), information about familiarity and kinship might be encoded to aid related individuals/ offspring as well as sexual/ social partners to recognise the 'owner' of the site. Particularly in the case of food marking, signal odour might encode information on the consumed food source, where marking can either function as resource defence (e.g. Irwin et al. 2004), as a signal to self and others that the respective resource has been depleted (*sensu* Eisenberg & Kleimann, 1972), or to attract conspecifics to share valuable food (e.g. Zhou et al. 2015), where **behavioural responses** of conspecifics to the signals will vary accordingly.

14.2.2) Latrines as information centre and reproductive advertisement

Faeces and urine are naturally pungent metabolic waste products. As such, they serve to excrete indigestible dietary components that can then be used to identify what the animal has been eating (Ali et al. 2004), as well as endocrinological metabolites from corticosteroids that indicate stress levels or sex-steroid derivatives that can be used to determine the animal's reproductive status (Palme et al. 2013). In addition, many species possess paired anal glands that open into the rectum and coat faecal deposits with glandular secretion that has been shown to encode a wealth of familial (e.g. Sun & Mueller-Schwarze 1998) and individual-specific (e.g. reviewed for musteloids in Buesching & Stankowich 2017) parameters that, together with other specialised scent glands (e.g. inter-digital glands: Wronski and Plath 2010; badger subcaudal gland: Buesching et al. 2002) provide a wealth of information about the latrine user.

Therefore, if latrines play a role in information exchange and individual advertisement (esp. in the context of reproduction), their **spatial distribution patterns** should maximise the likelihood of intercepting potential mates and/ or reproductive rivals. Information centre latrines could be expected to be clustered around breeding grounds, near trails or throughout foraging areas. Their **temporal usage patterns** should peak during the breeding season/ period of breeding pair formation. Marking activity should be increased when potential mates (or rivals) are present/ in the vicinity. The **visit and contribution patterns** should differ significantly between individuals and vary according to dominance, reproductive status, somatic health etc. The **chemical composition of the scent signals** should be highly volatile to ensure far-reaching signal output and encode sex difference, information on reproductive status and/ or other fitness-related parameters, individual identity and possibly information on genetic and social affiliation (e.g. kinship/ group-membership/ pair bond etc.). The relative placement of the scent-mark (top vs. lower) position can be important in signalling superiority (Jordan et al. 2011). Importantly, specific signal degradation pattern (e.g., Buesching et al. 2002) should encode information on signal age (i.e., time since deposition), to assess current signal validity (particularly in the case of female oestrus advertisement that might only be valid for a short time; i.e., hours more likely than days). The **behavioural responses** of conspecifics coming across these scent-marks should evidence heightened interest in all scent-marks, Responses should differ between individuals according to their respective physiological state (e.g., males in reproductive condition should react strongest/ be most interested in marks left by oestrous females often employing their vomero-nasal organ in a characteristic flehmen response: Hart 1983).Thus, reactions should be sex-specific and depend on the physiological/ reproductive characteristics of receiver, where reaction will vary with information content (i.e. individual characteristics of the marker. Prefer potential mates who mark more. Subsequent social/ reproductive interactions should be shaped by signal characteristics, where individuals that had overmarked scent of others should be preferred as mates and more likely to be avoided as antagonists.

14.2.3) Latrines as landmarks aiding in orientation

Latrines are often located at conspicuous landmarks, such as ditches, road- or bridge crossings (e.g. grey wolf: Barja *et al.*, 2004; North American river otters, *Lontra canadensis*: Roberts et al 2008), or particularly big trees (e.g. common genet: Espírito-Santo *et al.*, 2007). In many species they are connected with well-travelled paths leading from sleeping sites to foraging grounds or watering holes (e.g. review in Gorman & Trowbridge, 1989); an observation that has caused some authors to liken the function of latrines to sign posts along human roads.

If were to predominantly latrines serve as "notes to self" to aid individuals in orientation, their **spatial distribution patterns** should be highly dependent on individual movement patterns. They should be distributed throughout the territory/ home range, placed at biologically important features (e.g., cross roads in paths, important (but potentially difficult to locate) resource patches, hazardous areas, etc.). Particularly in unfamiliar/ difficult to navigate terrain, latrine position should be elevated to ensure far-reaching signals. Their **temporal usage patterns** should ensure continual scent diffusion while landmark is needed resulting in regular visitation and use, while some latrines in the same home range/ territory may become temporally or even permanently inactive/ disused. As these landmarks may not be important to all individuals using the same area, **visit and contribution patterns** should differ considerably between individuals as well as between latrines encompassed in the same home range/ territory. The **chemical composition of the scent signals** should encode individual identity to enable discrimination between own signal vs. signal from another conspecific. Other encoded information could include signal age, travel direction, or even the stress level (e.g., adrenaline/ cortico-steroid level) of the owner when the scent was deposited to warn/ remind itself (and/ or others) of an area-specific danger/ hazard. In these 'notes to self', **behavioural responses** should differ between the marking individual and others, where only the depositing individual should be aided by this latrine in its spatial orientation.

14.3.4. The role of latrines in parasite avoidance

Latrine use has long been suggested to reduce parasite load, particularly in primates including humans (reviewed in Curtis 2014; Weinstein et al. 2018). Nevertheless, there is currently no evidence that latrine use is actually associated with a measurable reduction in parasite load in wild mammals. In fact, in some species, such as latrines raccoons, *Procyon lotor*, likely have the opposite effect as evidenced by a series of studies on the spread of raccoon roundworm, *Baylisascaris procyonis* (e.g. Page *et al.*, 1998; Logiudice *et al.*, 2001), where data from proximity-logging collars at 15 latrine sites implicated raccoon latrines as major foci for the infection and spread of *B. procyonis* (Hirsch *et al.*, 2014).

If, however, latrine use has evolved as a way to avoid (re-) infection with gut parasites, their **spatial distribution** should reflect those areas in the home range/ territory that are least valuable in terms of resources. Particularly sleeping and feeding sites should be avoided in latrine placement. Ideally, latrine sites would be chosen not to confer local (microclimatic) protection/, but to provide adverse conditions for excreted parasites. The **temporal usage patterns** should coincide with periods of high parasitic loads/ infection risk and be related to the parasitic lifecycle. **Contribution patterns** should either not differ between individuals, or should be correlated positively with parasitic load of individuals (i.e., animals with lower-than-average parasite loads should avoid using latrines frequented by high-parasitic-load individuals). The **signal scent profile** can be very basic, simply indicating that this is a latrine. Thus, the **behaviour** of latrine visitors should be such as to minimise contact with excreta (and thus (re-)infection with parasites) and should exclude sniffing/ licking of marks/ faecal deposits by previous visitors.

14.2.5. The role of latrines in predator–prey interactions

A wide variety of prey species have been shown to avoid areas containing scent of their predators (e.g. Mella et al. 2014), and predators are typically attracted to the scent of their prey

(Hughes et al. 2010). Thus, both might benefit from hiding/ disguising their scent to avoid detection (e.g. reviewed in Banks et al. 2014), and even smaller predators might benefit from avoiding detection by larger predators in cases of intra-guild competition (e.g., Hughes et al. 2009).

If prey species defecate in latrines to avoid detection by predators or if predators use latrines to avoid detection by their prey ("eavesdropping"), **spatial distribution** should reflect the need to 'hide' the (smell of) excreta. Thus, latrines should be located in difficult to reach habitat, not conducive to the specific hunting strategies of the respective predator species/ (or in the case of predator latrines the preferred habitats of their prey species) that minimises signal reach (i.e., visibility and scent diffusion). Overall number as well as size (in terms of area utilised) of latrines should be kept to a minimum, and latrines should not be located along obvious paths or land marks. In prey species, **usage** should increase with greater predation risk and **temporal patterns** should reflect predator activity with prey species using latrines predominantly when predators are resting, whereas predators should avoid using latrines during peak activity of their prey. **Contribution patterns** should either not differ between individuals, or predators on the hunt/ individual prey most vulnerable to predation and/ or having experienced predation should exemplify the latrine use patterns described in this section. **Signal scent** should be minimal and be of low volatility and short life-span, with prey species potentially mimicking scent characteristics of non-prey species and predators mimicking the scent of prey. Prey and predator **behaviour** at latrines should reflect the need to remain undetected through keeping visit duration and frequency to a minimum, without sniffing deposits by previous visitors and by not leaving glandular scent-marks in addition to the necessary ablutions. Particularly faecal deposits might be buried/ covered with material. Nevertheless, prey species should investigate predator latrines and *vice versa*.

14.3. Conclusion

Currently, the vast majority of studies reporting latrine use in a specific focal species present almost exclusively data on the spatial distribution patterns e.g., in relation to territory boundaries, land marks and resources and maybe digested food items (e.g. reviewed for carnivores in Buesching and Jordan in press). In contrast, only few studies investigate temporal variation in latrine usage of their study animals, and typically relate their findings to species-specific activity patterns and how these may be affected by e.g., human disturbance (e.g., Tsunoda et al. 2018). Even fewer studies provide insights into inter-individual differences in visit and contribution patterns, which are then typically related to status (e.g., Jordan 2007) and differences in home range use (e.g., Kilshaw et al. 2009). It is therefore hardly surprising that the most widely suggested function of latrines pertains to resource defence in the context of territoriality and food sources. In fact, if only spatial data are collected, basically any latrine use pattern can be interpreted as territorial marking, which led Gosling & Roberts (2001) and many others to argue that the collection of spatial data alone is insufficient to infer latrine function conclusively (Buesching & Jordan in press).

As illustrated by the example of the European badger *Meles meles*, pronounced bias in data collection can thus result in having to re-evaluate established theory when more (and different) data become available (reviewed in Buesching and Stankowich 2017): While for many years, badgers were believed to be strictly territorial (reviewed in Buesching & Macdonald 2001; Roper 2010), maintaining a perimeter scent-fence of so-called border latrines frequented by members of adjoining neighbouring social groups and a grid of group-specific hinterland latrines, more recently, when data on the chemical composition of latrine-based anal- (Tinnesand et al. 2015) and subcaudal scent-marks (Buesching et al. 2002, 2016a), but also on individual usage patterns (Kilshaw et al. 2009; Ellwood et al. 2017) became available, interpretation of border latrines changed from active (Delahay et al. 2000) to passive range exclusion (Stewart et al. 1997) and are now by many interpreted as information centres for self-advertisement (reviewed in Buesching & Macdonald 2001; Macdonald et al. 2015; Buesching et al. 2016b).

Nevertheless, most of the potential functions of latrine use discussed above are not mutually exclusive. And so, due to the complexity of information encoded in olfactory signals, it is likely that in most species latrines fulfil several of roles simultaneously. By designing studies to investigate the measurable parameters we identified in this chapter, predictions based on their characteristics will allow functional interpretations of latrine use in the target species to be drawn more effectively than at present.

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