The Olfactory Landscape Concept: A Key Source of Past, Present, and Future Information Driving Animal Movement and Decision-making

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Odor is everywhere, emitted across the landscape from predators, prey, decaying carcasses, conspecifics, vegetation, surface water, and smoke. Many animals exploit odor to find food, avoid threats, and attract or judge potential mates. Here, we focus on odor in terrestrial ecosystems to introduce the concept of an olfactory landscape: real-time dynamic olfactory contours reflecting the patchy distribution of resources and risks, providing a key source of information used by many animals in their movement and decision-making. Incorporating the olfactory landscape into current frameworks of movement ecology and animal behavior will provide a mechanistic link to help answer significant questions about where, why, and when many animals move, and how they do so efficiently in both space and time. By understanding how animals use the olfactory landscape to make crucial decisions affecting their fitness, we can then manipulate the landscape to modify ecological interactions and, ultimately, ecosystem consequences of these interactions.

Keywords: odor, olfaction, landscape ecology, animal movement, information

How animals detect and respond to the world around them has substantial ecological effects beyond individual fitness. Individual movement and decision-making collectively form complex webs of ecologically significant interactions, shaping the structure, dynamics, and evolutionary trajectory of populations, communities, and ecosystems (Nathan et al. 2008, Swingland and Greenwood 1983). Predators exert consumptive and non-consumptive effects on prey (Sheriff et al. 2020, Wirsing et al. 2021), with cascading effects on food webs and nutrient flows within ecosystems (Monk and Schmitz 2021e, Schmitz et al. 2010). Herbivores shape plant communities, affect fire regimes, and impact nutrient recycling processes (Daufresne 2021, Eldridge et al. 2017, Jia et al. 2018, Morgan 2021, Rouet-Leduc et al. 2021, Staver et al. 2021). Tapestries of competitive interactions across environments are formed by individuals moving in response to the presence or absence of con- and hetero-specifics (Forsman and Kivelä 2021, Seppänen et al. 2007). Many other critical ecological services, including pollination and seed dispersal, also often rely on animal movement (Tucker et al. 2021). Consequently, to predict patterns of movement in a landscape by animals to help explain a plethora of ecologically significant interactions, we must first take a step back and understand how animals interact with and navigate their surroundings.

Across a landscape, 'external factors' (both the physical environment and living organisms) are key drivers of animal movement and decision making (Nathan et al. 2008). Yet the information and sensory mechanisms animals use to detect and respond to these external factors are seldom discussed. Here we begin by deconstructing current frameworks of animal behavior and movement ecology to highlight a gap in our understanding of the information animals use to make non-random decisions. We argue that odor, as a major information source, and olfaction, as a navigational mechanism, provide a key mechanistic link between how many animal species identify, assess, and respond to their surroundings. We then describe a conceptual theory, the olfactory landscape, elaborate on its unique spatiotemporal flexibility, and argue it as a distinct channel of information allowing early and efficient navigation in many animals. Finally, we discuss manipulating the olfactory landscape to modify ecological interactions and explore potential future directions for its use in conservation and wildlife management.

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Although through decades of research, the significance of odor and olfaction in mediating a plethora of ecological interactions has been well demonstrated across both terrestrial and aquatic ecosystems, in this article we will focus on odor in terrestrial ecosystems to develop and demonstrate the olfactory landscape concept.

Information: a missing link in understanding animal movement and decision-making

Central to current frameworks of animal behavior and movement ecology (Abrahms et al. 2021, Boutin 2018, Gaynor et al. 2019, Lewis et al. 2021, Nathan et al. 2008), decisions to move are largely shaped by four 'F' landscapes (Dill 2017): 'Food' (e.g. distribution of resources, prey abundance, food quality, surface water availability), 'Fornication' (e.g. mating opportunities), 'Fear and disgust' (e.g. perceived levels of predation and parasitism risk (Doherty and Ruehle 2020, Laundré et al. 2010, Weinstein et al. 2018)) and 'Fighting' (e.g. territoriality and conspecifics). Ultimately, non-random decisions to move require the capacity to sense information about the spatiotemporal distribution of opportunities and threats across these four 'F' landscapes (Hein and McKinley 2012). However, the information animals use to detect and respond to these landscapes is rarely considered.

Movement of animals across these four 'F' landscapes is intrinsically linked to trade-offs between risk and reward - but how do animals know? Elk feed on lower quality food closer to the safety of the forest when wolves are nearby (Creel et al. 2009), zebra move into lower quality grazing areas and show significant nutritional losses in proximity to lions (Barnier et al. 2014), mandrills avoid parasite contaminated feces and refrain from interacting with infected individuals (Poirotte et al. 2017), elephants move to the greenest areas in the landscape to feed (Loarie et al. 2009), and bushbabies weigh up the relative cost of plant food toxin content and patch safety when foraging (McArthur et al. 2012). But, how do animals locate a foraging patch, or decide that it is or isn't worth visiting from afar? How do animals know when threats move in and out of an area, or when an area is safe to visit? Why do we sometimes observe prey species feeding in typically 'dangerous' areas, other than a lack of food in non-dangerous areas? How do animals determine if an individual is infected with parasites or if an area is contaminated? To answer these questions, we require an understanding of the information animals use to make informed decisions.

To date, our understanding of the information animals use to make movement decisions is largely based on physical habitat structure, spatial memory, and visual and audial properties. The importance of physical habitat in providing safety by visual concealment or alternatively in impeding escape (Brown 1992, Ripple and Beschta 2003), and the need for sight lines in animals creating and responding to landscapes of fear have been well documented (Banks et al. 1999, Embar et al. 2011, Shrader et al. 2008, Stears and Shrader 2015, van der Merwe and Brown 2008). Landscapes of sound, or 'soundscapes' are recognized as a key information source used in hunting, predator avoidance, foraging, and social communication strategies by many animals (Elmer et al. 2021, O'Connell-Rodwell 2007, Schmidt et al. 2008, Suraci et al. 2019, Suthers 1978). Spatial memory and past experience shape patterns of migration and space use (Fagan et al. 2013, Merkle et al. 2019). Although the importance of odor as an information source and olfaction as a key navigational mechanism has been recognized, this understanding has primarily come from localized studies, focusing on point-sources of information. Consequently, odor at a landscape context as a multilayered and ever-updating information source has been largely overlooked yet is likely fundamental in many animals deciding where to go, and what to eat.

The olfactory landscape concept

Odor is emitted from everything. Odor may be emitted deliberately (e.g. marking territory (Rafiq et al. 2020), signaling sexual state (Marneweck et al. 2017a), as an alarm cue (Joo et al. 2018, Verheggen et al. 2010)), or as an incidental consequence of metabolic processes. Odor also emanates from decaying carcasses (Peterson and Fuentes 2021), from parasite infected matter (e.g. feces) and individuals (Poirotte et al. 2017), from biotic sources such as vegetation (Holopainen and Gershenzon 2010, Šimpraga et al. 2019, Zu et al. 2020), and abiotic sources such as water (Wood et al. 2021), and smoke from fire (Doty et al. 2018, Mendyk et al. 2020, Stawski et al. 2015). Moreover, odor cues may be emitted directly (from the animal, plant, or water source itself) or deposited indirectly (e.g. as a scent mark, fecal matter, or urine). Deliberately emitted or otherwise, odor is everywhere and across the terrestrial landscape dispersion of odor concentrations through wind and air turbulence creates continuously updating contours of olfactory information (Moore and Crimaldi 2004, Riffell Jeffrey A. et al. 2008). As an information source, these dynamic olfactory contours reflect real-time patchy distributions of potential threats and opportunities and are available for all animals to access and then track to a source, ignore, or avoid, given they have the appropriate sensory architecture (figure 1).

There is a plethora of point-based examples of how animals exploit olfactory information. Odor is used to detect and avoid potential threats (Banks et al. 2016, Barnier et al. 2014, Cornhill and Kerley 2020) and locate prey (Hughes et al. 2010). It is used to attract, find and judge mate quality (Harris et al. 2019, Marneweck et al. 2017a, Tirindelli et al. 2009), and recognize conspecifics (Bonadonna and Sanz-Aguilar 2012). It is crucial in marking and maintaining territory (Rafiq et al. 2020, Stępniak et al. 2020) and determining home range distribution (Ranc et al. 2020). Odor has also been shown to be key in locating water (Wood et al. 2021), detecting vegetative food quality and toxicity (Brokaw et al. 2021, Finnerty et al. 2017, McArthur et al. 2019, Schmitt et al. 2018, Skopec et al. 2019) and in detecting and responding to smoke from fire (Doty et al. 2018, Mendyk et al. 2020, Stawski et al. 2015).

Figure 1. A snapshot of an olfactory landscape. At any one time, an animal is faced with overlapping odor contours emitted from sources of risk (predators, parasitic infected and/or territorial conspecifics) and reward (mating opportunities, food). These olfactory contours are dynamic in space and time, reflecting predator movements, changes in foraging resource quality and location, and territory shifts. For an animal navigating its surroundings, these dynamic contours of odor can be exploited, providing information on the spatiotemporal distribution of potential threats and opportunities. Consequently, across a landscape, these layers of odor provide a key mechanism for many animals to optimize decision making and movement patterns from afar.

This growing list of examples provides compelling evidence for the importance of odor as an informative cue, but studies to date typically only allow one dimension of the four 'F' landscapes to be examined. All decisions to move involve trade-offs in risk and opportunity, and consequently, these trade-offs cannot be made with only one dimension of information. To detect and respond optimally to ever-changing variation in risk and opportunity in an environment, animals require a regularly updating landscape scale perspective of information (Lima and Bednekoff 1999). By integrating these evidence points of odor as an informative cue, an entire landscape of olfactory information is apparent. Recognizing and incorporating the olfactory landscape into current frameworks of animal behavior and movement ecology will provide a mechanistic link to help answer significant questions about where, why, and when many animals move and respond to ever-changing distributions of resources and risk across the four 'F' landscapes, and how they do so efficiently in both space and time (figure 2).

Studies could be designed to better understand the olfactory landscape through two approaches. First, we may eventually be able to map the olfactory landscape as a whole, across the four 'F's in space and time. Yet, currently available technology continues to remain a key limiting factor in our ability to detect and describe airborne odors (Ivaskovic et al. 2021). In future, as more sophisticated sensory mechanisms are developed, we should be able to detect dynamic waves of olfactory information across landscapes and observe the behaviour and movement of animals responding to it. Second, we can use manipulative experiments to help understand the olfactory landscape and interactive effects of odors across the four Fs. With odor titration studies manipulating odors of one of the 'F' landscapes (e.g. adding predator scent cue), we could observe how this effects an animal's interactions with and response to odor information from other 'F' landscapes (e.g. herbivore responses to the food plants).

The olfactory landscape builds upon a distinct information channel

The spatial and temporal dynamics of odor provide information appropriate for early responses in animals. Across a landscape, odor cues can be long lasting and provide information across a range of distances (Celani et al. 2014, Marin et al. 2021, Orlando et al. 2020, Riffell Jeffrey A et al. 2014, Svensson et al. 2014). More mobile volatile components of odor can transport information about food (prey location, vegetation nutritional value, toxicity, surface water availably (Mella et al. 2018, Plotnik et al. 2019, Schmitt et al. 2020, Wood et al. 2021)), threats (predators, competitors, parasites, fire (Poirotte et al. 2017, Valenta et al. 2020) and habitat and reproductive components (kin, mate, and breeding colony location (Caspers et al. 2013, Leclaire et al. 2013, Padget et al. 2017) across potentially large areas. This means animals can receive and interpret this information from afar. Consequently, mobile odor cues enable a highly efficient means of decision-making, well before the odor sources are encountered, with the result that animals can respond early to reduce risk and increase rewards. Moreover, more stationary 'heavier' odor compounds can persist in a landscape long after the donor has departed, acting as 'olfactory billboards' advertising information left by the donor (Marneweck et al. 2018).

Communal defecation sites (latrines or middens) used by a wide range of mammals including coyote (*Carnis latrans*) (Ralls and Smith 2004), white and black rhino (*Ceratotherium simum* and *Diceros bicornis*) (Linklater Wayne L. et al. 2013, Marneweck et al. 2017a, Marneweck et al. 2018) and oribi antelope (*Ourebia ourebi*) (Brashares and Arcese 1999) are a key example of using such olfactory 'billboards'. These middens provide multipurpose olfactory communication

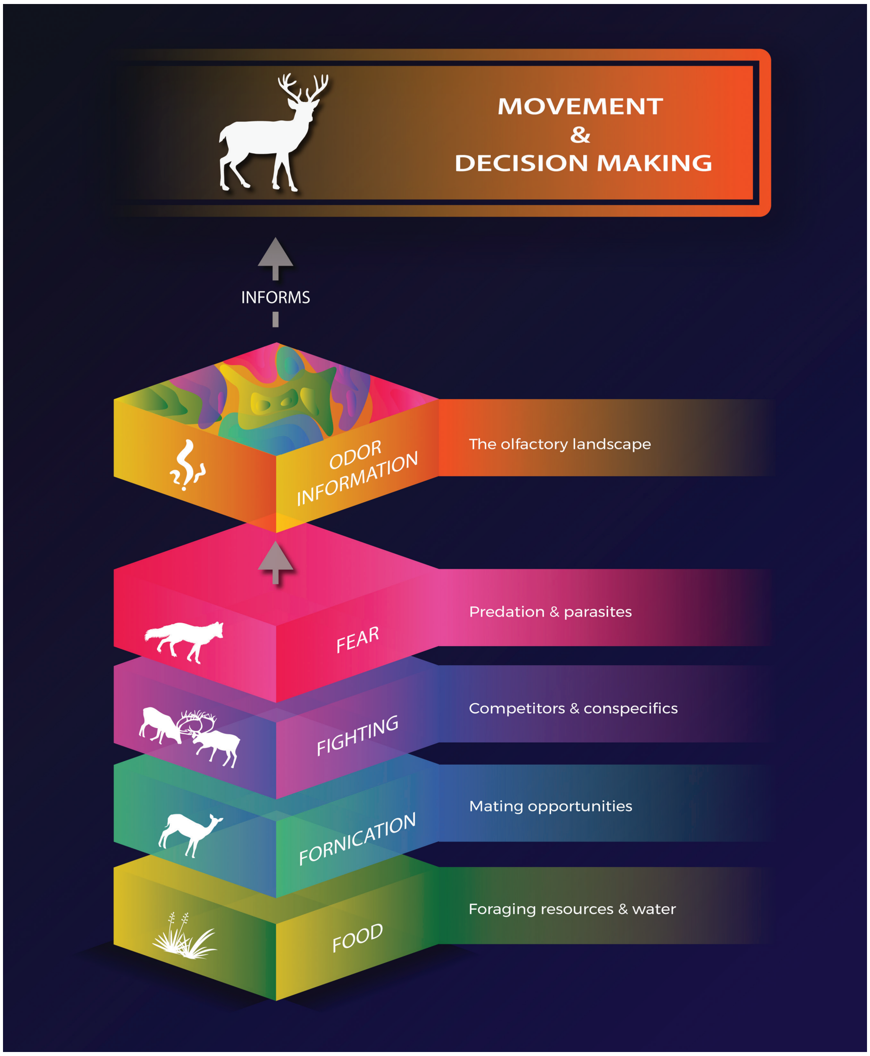

Figure 2. The four 'F' landscapes and the olfactory landscape. Current frameworks of animal behaviour and movement ecology focus on two major questions, 'why move?' and 'when and where to move?'. 'Why move' is informed by an animal's internal state (e.g., hunger and fear) (Nathan et al. 2008). 'When and where to move' is driven by the need to optimize fitness and avoid being eaten across fluctuating external physical landscapes of Food (foraging resources and water), Fornication (mating opportunities), Fighting (competitors and conspecifics), and Fear (predation risk and parasites). But, a missing link in these frameworks between 'why move' and 'when/where to move' is discussion around 'how?'. How does an animal know an area is safe to visit? How does an animal decide if an area has food worth moving to? Specifically, the sensory machinery animals use to sense and respond to information, and the information itself comprised of dynamic layers of volatile compounds indicative of resource and risk across these four 'F' landscapes is often left out of the equation. Odor is a major source of information answering the 'how's' of behaviour and movement for many animals. Across a landscape, dynamic olfactory contours are a consequence of emissions from everything. These dynamic olfactory contours can provide a real-time source of information, reflecting the spatiotemporal distribution of resource and risk across these four 'F' landscapes, informing many animals decisions to move.

hubs, advertising an abundance of information about territory, social rank, sex, and oestrus state. Irrespective of whether odor cues are highly mobile or relatively stationary, they degrade and change over time and distance (Marneweck et al. 2017b, Riffell Jeffrey A. et al. 2008, Riffell Jeffrey A et al. 2014). In doing so, odor cues can convey extra information useful in decision making, such as the proximity of an odor source, its age (Bytheway et al. 2013), ripeness (Nevo et al. 2020), or when it was deposited (Cavaggioni et al. 2006).

Consequently, odor can inform and update animals not only about the present, but also about the recent past, and the 'future'. Because odors linger and spread across the landscape, they can inform animals about the immediate presence and quality of food resources and threats (the present, e.g. predator body odors), on recent threats and resources (the past, e.g. predator or prey urine or conspecific scent marks) and can inform on threats and foraging opportunities from afar (the 'future', e.g. the smell of ripe fruit, the odor of predators in the distance) (Nevo et al. 2020). Whether an animal is navigating within a patch, between patches, or across entire landscapes (Senft et al. 1987), odor can therefore provide spatiotemporally dynamic information available for it to exploit when making decisions to move. Moreover, for animals using Bayesian optimization processes to make decisions (Hiratani and Latham 2020), dynamic olfactory landscapes offer 'live-streaming' updating of spatial memory 'maps', informing them of the past, present, and future distribution of resources and risk across the landscape.

Spatial memory, sight, and sound are other navigational tools, but every sensory system has its limitations. Visual information is curtailed in low light even for nocturnal animals, and fields of view can be obstructed in complex environments. Low frequency sound can travel far (O'Connell-Rodwell 2007), but all sound is momentary and cannot linger in the environment. Spatial memory and past experience may become too outmoded for animals navigating changing landscapes if not regularly updated, and non-existent when they explore novel areas. It is not surprising then, that the spatiotemporal flexibility of the olfactory landscape provides a key complimentary information source and a navigational mechanism that may even dominate other mechanisms and sensory systems for many animals interacting with the world.

Exploiting the olfactory landscape for novel wildlife management solutions

We can best manipulate animal movement and behavior by understanding the information they use to make decisions. Visual and audial sensory modalities have already been successfully exploited in passively managing and conserving wildlife. For example, ambush carnivore (lions and leopards) attacks on livestock (and subsequent retaliatory killings from landholders) were reduced when 'eyespots' were painted on the rump of cattle (McNutt et al. 2017, Radford et al. 2020). Audio playback of matriarchal family groups recordings successfully deter Asian elephants from raiding crops (Larsen and Eigaard 2014, Wijayagunawardane et al. 2016). At finer scales, odor is also used as a management tool. Unpalatable compounds are exploited as repellents and deterrents against herbivorous feeding damage (Gross et al. 2017, Miller et al. 2011, Oniba and Robertson 2019, Sullivan et al. 1988), livestock predation (Smith et al. 2000), and in attempts keep wildlife away from roads and railways (Bíl et al. 2018). Odorous baits are used as lures in attracting problem animals to traps. But, these fine scale solutions produce localized and short-term effects, aiming to stop the behaviors of already motivated animals (Garvey et al. 2020).

From a management perspective, approaches most likely to succeed involve working with animal motivations, rather than against them (Berger-Tal et al. 2011, Garvey et al. 2020, Price et al. 2022). Understanding how to alter an animals' perceptions of its surroundings (e.g. perceived threats or foraging opportunities) by selectively modifying the information available to an animal would allow for intervention at early stages of movement and decision making processes (Price et al. 2022). In manipulating the motivations and subsequent movement of individuals, we can modify targeted ecological interactions for conservation gain. Recognizing the olfactory landscape as a key information source many animals use to perceive and respond to their surroundings, provides scope to strategically modify this landscape to develop novel conservation approaches.

We are only just beginning to understand how to manipulate the olfactory landscape to alter the motivations of animals for conservation gain. Recent management approaches have shown the effectiveness of exploiting odor to manipulate animal learning and movement patterns. For example, olfactory 'misinformation' — unrewarding prey odor cues deployed across a New Zealand landscape — successfully led to a range of invasive predators ignoring 'unprofitable' prey cues of two threatened bird species, the South Island pied oystercatcher (*Haematopus finschi*) and the double-banded plover (*Charadrius bicinctus*). These approaches were as effective as lethal control (Norbury et al. 2021).

Manipulating the olfactory landscape to modify targeted ecological interactions provides promising and exciting new pathway for solving current and future conservation and management problems. Prey species reintroduction programs could employ similar olfactory 'misinformation' approaches as Price and Banks (2012) to reduce unwanted predation levels on vulnerable prey and also plants. Distributing the scents (e.g. dung, urine) of individuals that are to be re-released into protected areas as part of translocation programs may reduce aggression from resident individuals and promote safe settlement into new areas (Linklater Wayne L et al. 2006, Linklater Wayne L. et al. 2013). Problematic herbivores and granivores could be nudged away from areas of high ecological sensitivity (e.g. revegetation efforts, post fire recovery) or economical value (e.g. agriculture, forestry) by reducing perceived patch palatability (Santiapillai and Read 2010). Alternatively, with landscapes become increasingly fragmented globally, wildlife could be guided towards wildlife corridors, road culverts, and railway bridges using odors, helping to maintain and/or increase landscape connectivity and reduce wildlife mortality rates (Benítez-López et al. 2010, Haddad et al. 2015, Riggio and Caro 2017, Žák et al. 2020).

Conclusion

As a potential consequence of our own decision making being primarily informed by sight and sound (Atema 1996), we have under-recognized and overlooked the presence of dynamic olfactory landscapes as a key information source used by many animals in deciding where and when to move. The olfactory landscape is an ever-updating information source, reflecting real-time risk and reward distribution. In doing so, it offers a missing link in our understanding of how many animals identify, assess, and respond to patchy external factors they face. Integrating the olfactory landscape into animal behavior and movement ecology frameworks will allow us to better predict patterns of landscape use by animals, helping explain ecologically significant interactions whether predator-prey, plant-herbivore, or between con- and hetero-specifics. Moving forward, we hope that in presenting this conceptual theory we will stimulate new thinking around ways to manipulate the olfactory landscape in developing novel approaches to wildlife and conservation management.

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