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Lagomorpha Navigation

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Synonyms

Behavior; Hare; Movement; Pika; Rabbit

Definition

Navigation – the theory and practice of charting a course to a remote goal (Schöne 1984).

Introduction

The daily movements of animals are governed by many factors including the need to find food, water, conspecifics, and favorable environmental conditions while trying to avoid predators, dominant ecological competitors, and unfavorable habitats and conditions. Animals use external cues such as odor (Gagliardo 2013), landmarks (Baader 1996), day length (Baoping et al. 2009), the position of the stars (Dacke et al. 2013), and the Earth's magnetic field (Chernetsov et al. 2017) to guide their movements in the landscape and the timing thereof.

The order Lagomorpha is comprised of two families, the hares and rabbits (Leporidae or leporids) and the pikas (Ochotonidae). The navigational capabilities of lagomorphs are poorly understood, with the few movement studies to have been conducted focusing on dispersal, home range behavior, foraging, and habitat use. Indeed, movement behavior has been entirely unstudied in most lagomorph species. Studying the navigational capabilities of small-to-medium-sized mammals can be challenging as the equipment required for fine-scale data collection (e.g., GPS collars) are often too heavy and/or have limited battery life. For example, the maximum weight for GPS collars is defined by the size of the subject. This is known as the "5% rule" (Cochran 1980); the weight of the collar should not exceed 5% of the focal animal's mass. For a very large hare weighing 5 kg, that would equate to a GPS collar weighing 250 g. The typical battery life for such a collar is around 500 days, though that is based on the recording of only a handful of "fixes" (i.e., records of the individual's location) per day – not enough for nuanced analysis of movement behavior such as navigational strategies (Handcock et al. 2009). The frequency of fixes required for such studies would exhaust the battery in only a few days. However, technological advances such as the use of micro-GPS and snapshot receivers (McMahon et al. 2017), as well as increasingly lightweight collars and improved

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batteries, mean that many obstacles are slowly being overcome. It is likely that future technological improvements and dedicated research will lead to a greater understanding of movement behavior and navigational strategies, particularly in larger lagomorphs.

Given the lack of navigation-specific literature, here I broadly summarize research on movement behavior, particularly in the context of home ranges, habitat use, and dispersal, in each group of lagomorphs.

Hares

Hares (genus *Lepus*; 32 species) are crepuscular/nocturnal open-habitat specialists with long hind legs which allow them to flee from potential predators at high speeds. They are poorly adapted for a digging and rest during that day in above ground depressions, known as forms. As they are not reliant on burrows for shelter and protection, hares generally range over much wider areas than most rabbits and certainly all pikas (see "► Lagomorpha Life History", Table 1). However, all hares and their offspring ("leverets") make use of emergent vegetation for concealment. For example, the Irish hare (*L. timidus hibernicus*), a subspecies of the mountain hare (*L. timidus*), favors open-field habitats (Dingerkus and Montgomery 2002) but is also associated with rough grassland which offers potential cover in the form of stands of rushes (*Juncus* sp.; Caravaggi et al. 2015). Similarly, woolly hares (*L. oiostolus*) favor montane grasslands for foraging but require intermediate shrub habitats for cover (Lu 2011). Researchers studying movements of translocated European hares (*L. europaeus*) found that, rather than establishing home ranges at release sites, the translocated individuals moved to find better habitats which were more similar to those from which they had been removed (Ferretti et al. 2010). Hares will also recurrently use a network of paths between foraging and/or resting sites (Caravaggi et al. 2016).

Dispersal, i.e., the movement of young out of the natal range (natal dispersal) or the movement of adults to another breeding area (breeding dispersal), is an important process with a key role in population dynamics. The benefits conferred by individuals moving within and between populations and into previously uncolonized habitats are such that dispersal is considered to underpin the persistence of many species (Avril et al. 2011). The causes of dispersal are poorly understood, though it is likely that inbreeding avoidance, mate competition, resource availability, and the density of conspecifics all play a role. The availability of cover vegetation may be a particularly important factor in determining the eventual settlement locations of dispersing females (Avril et al. 2011). Dispersal is ubiquitous and common among hares, though breeding dispersal occurs at lower frequencies than natal dispersal. Moreover, the proportion of young which disperse from the natal range, and the distances travelled, varies between and within species. However, movement behavior during dispersal can give clues to navigational capabilities. For example, dispersing leverets have been observed to use direct long-distance exploratory movements over 1 km before returning to the same resting location, over several days (Reid and Harrison 2010). This return behavior suggests a capacity for accurate navigation on a landscape scale.

The locomotor activity of hares often varies seasonally, with an increase in activity particularly around the start of the breeding season. During this time, individuals will move from their home ranges in search of mating opportunities. It is possible, perhaps even likely, that olfaction plays a role in the location of mates, though olfactory communication in hares is currently not a research priority. Locomotion may also be affected by perceived predation risk (i.e., lunar illumination) and local predator density and abundance (Rogowitz 1997); hares spend more time moving between habitat patches, reducing stationary foraging time in each patch.

Rabbits

There are ten genera of rabbits (*Brachylagus, Bunolagus, Capolagus, Nesolagus, Oryctolagus, Pentalagus, Poelagus, Pronolagus, Romerolagus, Sylvilagus*), with a total of 29 species. Rabbits differ physically from hares in that they have

comparatively shorter hind legs and shorter ears and are physically smaller (► Lagomorpha Life History, Table 1). Old World rabbits (all genera except for *Sylvilagus*) are diggers, creating underground holes, burrows, and communal warrens in which to rest, avoid threats (e.g., predation, poor weather), and raise their young (known as kits or kittens). In contrast, new world rabbits (*Sylvilagus* sp.) will either utilize holes or burrows dug by other species or raise their young in aboveground forms. The movement behavior of rabbits is poorly understood, with substantial knowledge gaps in all aspects.

Rabbits choose their home ranges with reference to the vegetative composition of the landscape, preferring areas with an abundance of vegetation which could be used for cover. For example, researchers in Spain found that the warrens of European rabbits (*O. cuniculus*) were strongly associated with the *Retama monosperma*, a dense flowering bush (Dellafiore et al. 2008). Rabbits make use of cover vegetation to provide shelter and concealment, often using the same paths through ostensibly safe habitats to reach foraging areas in their home ranges. European rabbits also live in underground warrens which may span a considerable area and have multiple entrances. Within their home range, therefore, European rabbits have a number of options which offer safety from potential threats. Flight to places of concealment is usually direct, suggesting that the animal is aware of its position relative to relevant landscape features.

The proportion of dispersing juveniles is often high, particularly in low-density populations, and, as with many mammal species, dispersing cohorts are often male-biased. However, levels of dispersal may be similar between the sexes when populations occur at high densities (Richardson et al. 2002). In many species, dispersing subadults barely venture beyond their natal home range; males are often more likely than females to make long-distance movements. For example, one male marsh rabbit (*S. palustris*) was recorded as having dispersed over 2 km from its place of birth, compared to most females which did not leave their natal ranges (Forys and Humphrey 1996). In contrast, a study of pygmy rabbits (*Brachylagus idahoensis*) found that females dispersed up to three times further than males (Estes-Zumpf and Rachlow 2009). Dispersal distance may be related to population density (e.g., European rabbit) (Richardson et al. 2002), with long-distance movements being more common in low-density populations.

Pikas

There are 30 species of pika, all of which are classified within a single genus, *Ochotona*. Pikas are the smallest of the lagomorphs (► Lagomorpha Life History, Table 1), with rounded bodies and ears and no visible tail. Pikas are broadly split into two groups: (i) rock- or talus-dwelling species and (ii) species of grassland or steppe habitats. The two groups have different social behaviors, though they do not differ in life history or ecology. As with other leporids, there is little information available on their movement behavior and navigational capabilities.

Steppe and grassland pikas are social, living in often high-density groups. In contrast, talus pikas are largely solitary and highly territorial. Nevertheless, the dispersal behavior of the two groups is similar. For example, both breeding and natal dispersal distances of plateau pika (*O. curzoniae*; a steppe species) and American pika (*O. princeps*; a talus-dwelling species) are often extremely short, rarely extending beyond two family ranges (Dobson et al. 1998). However, genetic analyses suggested that American pikas may occasionally disperse up to 2 km from their natal range and that intermediate movements may be common (Peacock 1997). Juvenile males are often the primary dispersers in plateau pikas, a pattern not observed in American pika.

The (re)colonization potential of pikas has been shown to be strongly influenced by the degree of habitat patch connectivity, as well as patch quality (Franken and Hik 2004). However, while juveniles are more likely colonize neighboring patches in fragmented habitats, dispersal rates are not necessarily compromised, with a mixture of short- and long-distance dispersal events resulting in a genetically contiguous metapopulation (Peacock and Smith 1997). Thus,

dispersing pikas likely use similar exploratory behaviors to those found in other lagomorphs, facilitated by emergent vegetation and landscape features (e.g., rocks). Researchers investigating the social behavior of the northern pika (*O. hyperborean*) have shown that the species exhibits spatial awareness and recall, with individuals recurrently returning to the same shelter and breeding pairs using multiple collective food caches (Gilwicz et al. 2005).

Conclusion

Navigational abilities are common features among animals. All lagomorphs exhibit behaviors which can be interpreted in terms of navigational skills, including foraging behavior and the utilization of burrows and/or vegetation for cover. Therefore, it is reasonable to assume that lagomorphs have long-term awareness and understanding of the composition of the habitats and microenvironments found within their home ranges. These cognitive maps (i.e., representations of an animal's environment which are used in decision-making; Tolman 1948) allow them to effectively navigate between foraging and resting areas within their home ranges and beyond such as when making exploratory forays beyond the natal range. However, navigation and movement behavior are understudied in lagomorphs, and, hence, data are scarce. There is scope to expand research in spatial cognition, e.g., mental mapping, into lagomorphs, thus giving researchers greater insight into population dynamics and habitat utilization and requirements, as well as potentially benefitting conservation and management processes.

Cross-References

- Home Range
- Lagomorpha Life History
- Mammalia
- Movement/Locomotion
- Spatial Memory

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