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Rapid acquisition of memory in a complex landscape by a mule deer

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Whether attempting to escape harsh environmental conditions or securing access to mates, animals move in environments where resources are heterogeneous in time and space. Multiple factors shape the capacity for and execution of animal movement, including many physiological, behavioral, and neurological adaptations (Avgar et al. 2014). Animals that orient or return to particular locations must obtain, store, and use information about the spatial layout of their environment. Seasonal migration, one of the most dramatic and widely observed forms of movement, can take animals back and forth across hundreds of kilometers of landscapes that they see only twice a year. Consequently, many migratory animals likely possess the cognitive ability to process massive amounts of spatial information to complete their journeys. Although the cognitive and spatial processing abilities of some migratory animals have been studied at length (Dingle 2014), migratory ungulates are comparatively understudied. In particular, how quickly migratory ungulates develop knowledge of their landscape and their capacity to obtain it remains largely a mystery.

We observed a movement of a young mule deer (*Odocoileus hemionus*) that demonstrates an extraordinary capacity for rapid acquisition of information that was heretofore underappreciated in ungulates. In June 2017, we radio-collared a mule deer the day she was born in western Wyoming, USA. We tracked this deer, animal F210, as she matured throughout the summer and migrated at her mother's heel to their winter range (Fig. 1). We recaptured F210 in December and replaced her radio-collar with a GPS-collar (6-h fix rate). We simultaneously tracked F210's mother, who also was equipped with a GPS-collar (1-h fix rate). The following spring, F210 migrated north with her mother and arrived back on her summer range when she was almost 1-yr old. During her migration, F210 ascended and descended over 4,700 m along her 98 km migratory route at an average rate of 0.18 km/h (minimum = 0 km/h, maximum = 1.74 km/h). Shortly after returning to her summer range, however, she moved as if she were dispersing to a new location (Fig. 1). She traveled 94 km north over 10 d along a directed path away from her summer range. While moving away from her summer range, F210 traveled at an average speed of 0.42 km/h (minimum = 0 km/h, maximum = 1.55 km/h). Instead of remaining in a new area as we had expected, however, F210 returned to her summer range, returning along almost the same 94 km path over a period of 15 d. As she traveled back to her summer range, F210 moved at an average speed of 0.31 km/h (minimum = 0 km/h, maximum = 2.39 km/h). Throughout this walkabout, she traveled more than 180 km over complex topography that dropped into valleys (minimum elevation: 2,305 m) and crested mountain ridges (maximum elevation: 3,060 m; Fig. 2), in all ascending and descending over 7,000 m in elevation. Her walkabout was similar to her migratory route in distance traveled, but she moved over more varied terrain and at a faster pace. Despite slight deviations, she traveled along almost precisely the same, complex route she had traveled only once previously, indicating that she learned this new landscape within a single walkabout. F210's movement suggests that she possessed extraordinary cognitive abilities that allowed her to rapidly obtain and retain large amounts of spatial knowledge.

Movement characteristics are thought to be learned from conspecifics in ungulates (Jesmer et al. 2018), but it is unknown if F210's exploratory movement resulted from such interactions. We suspect the initial motivation behind this walkabout into uncharted terrain was associated with F210's mother becoming intolerant of her presence as she sought to seclude herself during parturition (Monteith et al. 2007). F210's mother gave birth to a new set of offspring on 8 June 2018, 8 d before F210

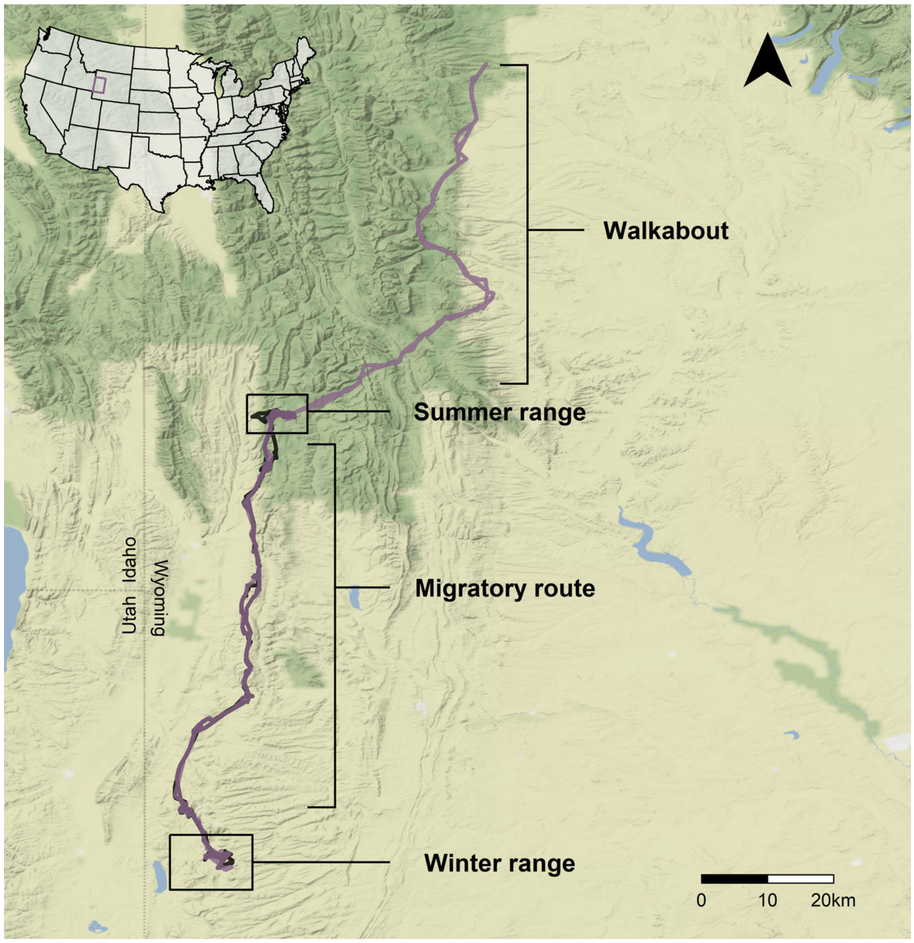

FIG. 1. Migratory route, seasonal range, and unexpected movement of a young female mule deer, F210 (purple), and her mother (black) in the Wyoming Range in western Wyoming (purple box in inset map), USA. Movements are based on information derived from GPS collars between summer 2017 and fall 2018.

left her summer range. Although F210's journey likely was done alone, it is possible that she may have been accompanied by another animal, as yearlings occasionally form groups with other yearlings (Bowyer et al. 2001). Nevertheless, of the 74 GPS-marked adults migrating in 2018, all finished migrating mid-May and none made additional walkabouts of this degree, indicating the unusual nature of F210's walkabout. Even if she had completed part or all of her walkabout with another animal, this observation still indicates that some mule deer complete complex exploratory movements early in life. Despite the possibility that she learned information about her initial movement from conspecifics, F210 likely learned and remembered her surroundings well enough to return along her same path on her return journey.

Seasonal migration can provide many benefits, such as the ability to escape harsh environmental conditions or access seasonally available resources (Milner-Gulland et al. 2011, Monteith et al. 2011), but the cognitive capacities that allow ungulates to move and reap these benefits are comparatively less understood. Some species, such as mule deer, exhibit extremely high fidelity to migratory routes and seasonal ranges, with the overwhelming majority of individuals using the same migratory route and seasonal ranges year after year (Sawyer et al. 2018). For an animal to display extreme fidelity in complex landscapes, memory and sophisticated cognitive abilities are likely key components to movement (Merkle et al. 2014). Further, because ungulate migration is thought to be culturally transferred between generations (Jesmer et al. 2018), mule deer potentially have the opportunity to solidify and refine migratory behaviors in their memory over multiple seasons or migratory events. Despite the intuitive appeal of these notions, both the cognitive capabilities for details related

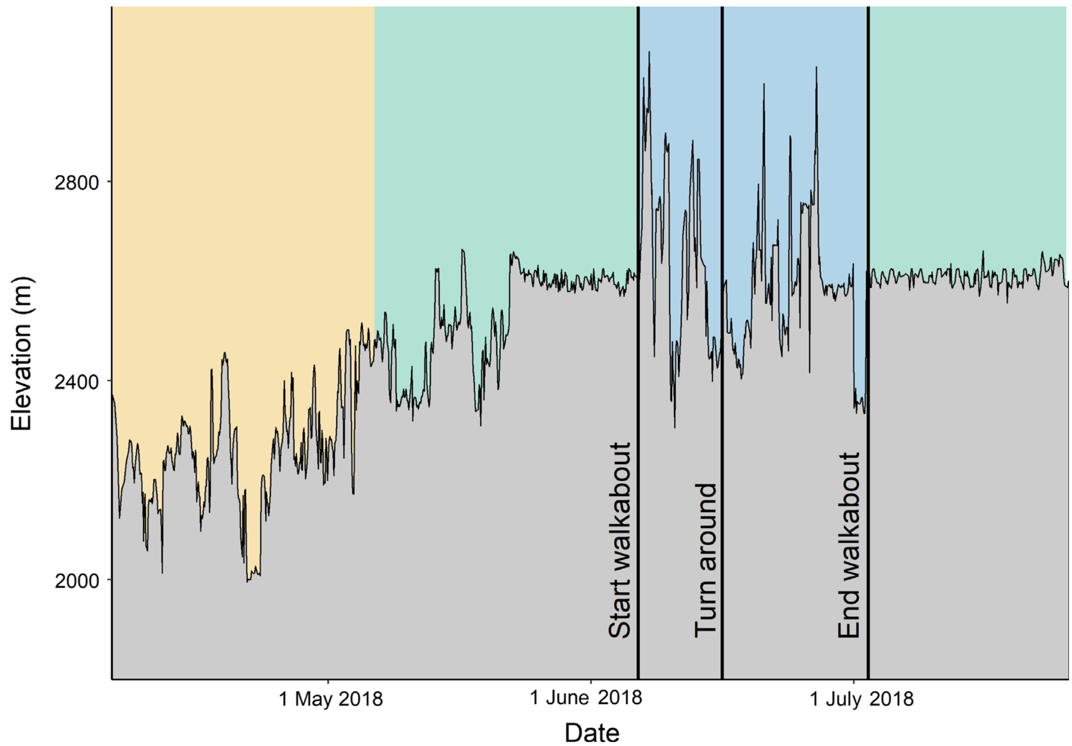

FIG. 2. Elevation profile of the movement of female mule deer F210 in western Wyoming, USA, April–August 2018. The area shaded orange corresponds to her spring migration, the green corresponds to home range movements, and the blue corresponds to her walkabout. Solid vertical lines indicate when she initially left her summer range on a walkabout (left), turned around and returned to her summer range (middle), and when she ended her walkabout on her summer range (right). Over this time, she traversed approximately 94 km from her summer range and, on her return trip, she followed almost exactly the same route she had previously taken.

to movement and the temporal window over which movement behaviors can be instilled remain open questions with regards to ungulates. F210's movement, however, seems to suggest that mule deer may have impressive cognitive abilities with regards to movement, such that they may need to experience migratory routes or seasonal ranges a single time to adopt them into their movement repertoire.

Whereas navigation and orientation, the mechanisms that allow animals to predictably migrate between summer ranges, have been studied extensively in migratory insects, fish, and birds, these mechanisms are comparatively less studied in ungulates. Zebras (*Equus burchelli antiquorum*), for example, remember the location of seasonal ranges and return to them, but the particulars of how they are able to return to those ranges is unknown (Bracis and Mueller 2017). Mule deer in Wyoming migrate through complex landscapes that contain a mix of mountain meadows, sagebrush (*Artemesia* spp.) flats, dense conifer forests, riparian areas, and rocky outcrops that vary substantially in elevation; in short, moving predictably and with fidelity through this landscape would not be simple. Mule deer possess the ability to base movements off of local cues in their environment (Merkle et al. 2016, Aikens et al. 2017), but other mechanisms could also explain their movement behaviors. Ungulates might move using various orientation and navigation abilities such as known reference points, compass orientation, a "cognitive map", or guidance from other animals (Dingle 2014), but conclusive evidence of any of these mechanisms is sorely lacking. Perhaps F210 used a far-off mountain ridge as a reference point or followed a scent or trail trodden by mule deer previously moving through the area. Alternatively, she may not have learned her landscape if topography were configured in such a way that only one route was a sensible option. Future studies, both experimental and observational, that explore the capacity for navigation and orientation will certainly be key to reveal how ungulates move predictably throughout their world.

As curious as these movements are, they will remain unevaluated unless we follow individuals through all stages of their life. By tracking F210's movements from the day she was born, paired with the history of her mother's movements, we observed this walkabout and placed it within a broader context. Although many studies of ungulate movement focus on adults, studying the "lost years" (Hays et al. 2016) early in life may yield exciting discoveries as to the development of memory and movement behaviors. Further, because walkabouts are relatively rare events, observing them hinges on multiple, longitudinal studies that incorporate a GPS-collaring element. Long-term, longitudinal data are rare and difficult to obtain, but they are critical to understanding the role and development of memory, navigation, and orientation in ungulate movement.

Although the characteristics of animal movements vary wildly depending upon the organisms, their life history, and the systems in which they live, many species have a suite of adaptations that permit potentially long, complex, or repeated movements (Milner-Gulland et al. 2011). These adaptations have long held scientists' attention, yet many elements remain perplexing. With regards to mule deer, the extent to which these animals build a map of their world is wholly unexplored, as are the underlying cognitive capacities. The single observation of F210's journey, however, lends overwhelming support for the role of rapid learning, memory, and the existence of an exquisite cognitive map in migratory ungulates.

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