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ECOLOGY

# *Learning to migrate*

## Hoofed animals, such as bighorn sheep and moose, learn migratory behaviors from other herd members

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Conditions for life are better in different places at different times of the year. Many animals—including birds, mammals, fishes, insects, and reptiles—take advantage of this temporal variation by migrating, sometimes over thousands of kilometers. But how do they know when and where to go, especially when released in an unfamiliar place? On page 1023 of this issue, Jesmer *et al.* (*1*) suggest that migratory ungulates—hoofed mammals—do something similar to that of tourists seeking local advice about places to eat: The ungulates' migration develops and persists through cultural transmission.

Spring starts earlier at lower altitudes and latitudes. A wave of green-up then moves higher or toward the poles, providing a gradient of highly nutritious vegetation over space and time. In mountains throughout the world, humans exploit this opportunity by moving livestock to higher grazing grounds from spring to summer. Reindeer herders also move their herds by hundreds of kilometers, imitating the long-distance migrations of tundra caribou. Wild migratory ungulates can feed over a long time on high-quality forage by following the onset of spring, or "surfing the green wave" (*2*). Better nutrition is one reason why migratory ungulates are much more numerous, and often physically larger, than sedentary ones, with important implications for ecology and the livelihoods of people that exploit them (*3*).

However, all migratory animals are extremely sensitive to human barriers to migration, such as fences and walls, including those at international borders. Because of the increasing prevalence of such barriers, many formerly migratory ungulates have become sedentary. In much of Europe, long-distance ungulate migrations likely disappeared centuries ago as humans changed the landscape. Migratory ungulates in Asia and Africa face ever more obstacles, and most bison in North America are inside large fenced areas because they are not tolerated on agricultural lands.

Because migratory ungulates are important ecologically and economically, governments, hunters, conservationists, and other people are interested in assisting their recovery, which requires knowledge on how migratory behavior develops. Jesmer *et al.* use a large sample of GPS-collared bighorn sheep and moose to investigate how the ability to migrate and surf the green wave varies with culturally transmitted local knowledge.

Most migratory ungulates are gregarious and likely learn when and where to go from their mother or other members of the herd. When a population is extirpated or reduced to so few animals that supplementation is required, translocation of animals from elsewhere may become a conservation option. But recently translocated ungulates must learn how to behave in their new environment because even short migrations may require crossing dangerous habitat. Bighorn sheep, for example, are at higher risk of predation away from the safety of cliffs, yet migration between seasonal ranges requires them to traverse risky habitats (see the photo and the figure). It turns out that to find the best seasonal ranges and surf the green wave, the animals mostly learn from others, sometimes over generations.

Migration requires knowing where the winter and summer ranges are. Surfing the green wave involves foraging at the best

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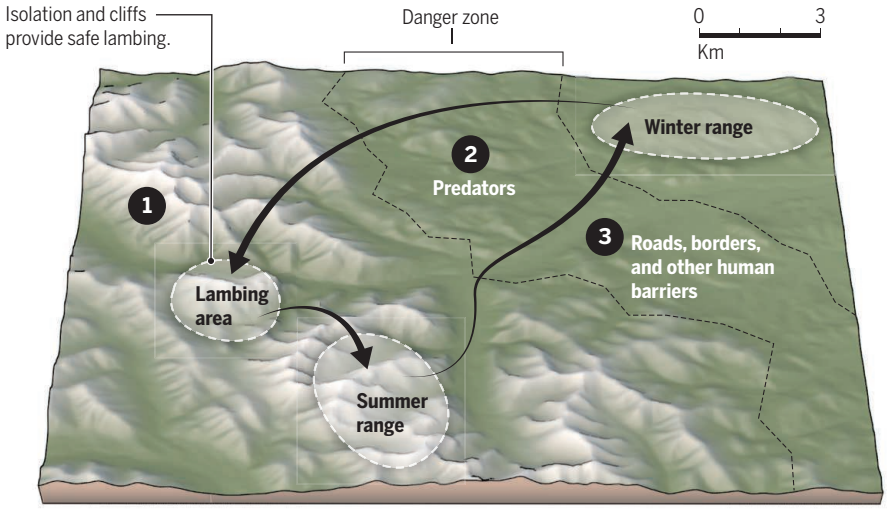
Bighorn sheep (*Ovis canadensis*) migrate in the mountains of the western United States.

## Dilemma of a migratory bighorn ewe

Migratory bighorn sheep must find a safe route from the winter range to the lambing area and then the summer range. Jesmer *et al*. show that the sheep's migratory knowledge is culturally transmitted.




**1 Seasonal changes**
The location of the best forage sites changes with the seasons. It takes several generations to find the best forage sites, a skill called green-wave surfing.

**2 Predation**
During migration, the sheep must avoid predators such as wolves and cougars. The best routes follow the cliffs and avoid the forest.

**3 Human barriers**
Roads, fences, border walls, reservoirs, and railways can force detours, block migration, or increase mortality risk.

spots along the route each day of the migration. Jesmer *et al*. compared the migratory habits and green-wave surfing skills of bighorn sheep and moose from native populations, reestablished populations following translocations a few generations ago, and animals recently moved into new areas. Most animals in established populations migrated and generally had high green-wave surfing skills, selecting the best places at the best times. In recently established populations, migratory skills improved over time. Newly translocated animals did not migrate, except for a few that followed migratory residents. The authors show that it can take 90 years, or 12 to 13 generations, for half of the descendants of translocated animals to become migratory. Surfing skills were correlated with the development of migration but improved less markedly over time. Even in native herds, surfing performance was lower than that expected of a theoretical omniscient ungulate that surfed the green wave perfectly.

Translocations can be successful. The numbers and range of bighorn sheep in North America and ibex in Europe are much greater than a century ago, mostly through translocations. However, many translocations failed (*4*). Some failures were due to exotic disease or poaching, but others were likely associated with inability to reestablish historic migratory habits. Lack of local knowledge can also increase the risk of predation; avoiding predation is often another major advantage of ungulate migration (*3*). Jesmer *et al*. show that reestablishment of migratory habits is possible but takes time, especially in the absence of locally born conspecifics.

Migration and green-wave surfing do not correlate perfectly; some animals migrate between seasonal ranges but do not stop in all the best spots along the way. There are many reasons for imperfect green-wave surfing. One is predation. Animals may avoid areas with good forage but high predation risk (*5*). Another is the constraint imposed by the low mobility of newborns. Before giving birth, many ungulates move to sites that maximize safety over nutrition, migrating to foraging areas after juveniles have developed adequate locomotor skills. Last, whereas migratory ability simply requires a knowledge of seasonal range location, surfing the green wave must incorporate year-to-year changes in plant phenology, which may require repeated sampling of forage in different sites, with heightened predation risk and locomotory costs.

Jesmer *et al*.'s findings have important implications for conservation. After reintroductions, migratory ungulates may need several generations to learn the location of seasonal ranges. Learning from resident conspecifics speeds up the process but requires social integration, and translocated individuals may not be accepted quickly by the local population (*6*). Gregariousness likely plays an important role: The highly gregarious bighorn sheep may develop traditions more quickly than the mostly solitary moose. Future research may apply social network techniques to better understand who learns from who and how cultural transmission spreads through a population in which animals differ in levels of local knowledge. Given individual differences in migratory behavior and in ability to surf the green wave, some individuals may be more important than others in transmitting cultural knowledge about these fitness-enhancing behaviors. As populations dwindle, the chance that those individuals may be lost increases, possibly leading to loss of migratory behavior. Once local traditions are lost, it may take decades before they are reestablished.

Migratory ungulates, like other migratory animals, are important for many ecological processes and as a source of food, recreation, and cultural values for many people. Jesmer *et al*. underline the importance of culture in their ecology. That culture is lost when populations go extinct. Cultural transmission of migratory behavior is a major conservation challenge that can be best met through identification of critical migratory routes and habitat protection at a very large scale. ■

GRAPHIC: C. BICKEL/*SCIENCE*

### REFERENCES

1. B. R. Jesmer *et al.*, *Science* **361**, 1023 (2018).
2. J. A. Merkle *et al.*, *Proc. R. Soc. B* **283**, 20160456 (2016).
3. J. M. Fryxell *et al.*, *Am. Nat.* **131**, 781 (1988).
4. F. J. Singer *et al.*, *Restoration Ecology* **8**, 6 (2000).
5. A. D. Middleton *et al.*, *Ecology* **94**, 1245 (2013).
6. M.-A. Poirier, M. Festa-Bianchet, *Biol. Conserv.* **218**, 1 (2018).

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