

MIGRATION

Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals

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Ungulate migrations are assumed to stem from learning and cultural transmission of information regarding seasonal distribution of forage, but this hypothesis has not been tested empirically. We compared the migratory propensities of bighorn sheep and moose translocated into novel habitats with those of historical populations that had persisted for hundreds of years. Whereas individuals from historical populations were largely migratory, translocated individuals initially were not. After multiple decades, however, translocated populations gained knowledge about surfing green waves of forage (tracking plant phenology) and increased their propensity to migrate. Our findings indicate that learning and cultural transmission are the primary mechanisms by which ungulate migrations evolve. Loss of migration will therefore expunge generations of knowledge about the locations of high-quality forage and likely suppress population abundance.

From tropical savannas to the Arctic tundra, the migrations of ungulates (hooved mammals) can span more than 1000 km and are considered among the most awe inspiring of natural phenomena. Migration allows ungulates to maximize energy intake by synchronizing their movements with the emergence of high-quality forage across vast landscapes (1). Consequently, migration often bolsters fitness and results in migratory individuals' greatly outnumbering residents (2, 3). Despite their critical importance, migrations are increasingly imperiled by human activities (4). Thus, understanding how migrations are developed and maintained is critical for the conservation of this global phenomenon (5). Ecologists have long speculated that memory and social learning underlie ungulate migration (6–8). Bison (*Bison bison*) remember the locations of high-quality forage and transmit such information to conspecifics (9), whereas moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) adopt the movement strategies of their mothers (6, 7). Nevertheless, the hypothesis that social learning underlies the development and maintenance of ungulate migration has not been tested with empirical data.

Animal migrations arise through a combination of learned behavior and genetically inherited

neurological, morphological, physiological, and behavioral traits (5, 10, 11). When behavior is primarily a consequence of social learning and persists across generations—a phenomenon known as culture—information is transmitted from generation to generation (12). Culture is therefore regarded as a “second inheritance system,” analogous to the inheritance of genes that underlie innate behaviors (13–15). Thus, if social learning is the primary mechanism allowing animals to gain information regarding the seasonal distribution of high-quality forage, cultural transmission may be the principal force by which ungulate migrations have evolved in landscapes conducive to migration.

Ungulate migration is a strategy for exploiting altitudinal, longitudinal, and other topographic gradients of plant phenology that determine forage quality (16, 17). The ability of ungulates to synchronize their movements with phenological waves of nutritious, green plants—a behavior known as “green-wave surfing” (18)—can result in migratory movements far beyond an individual's perceptual range (19). Ungulates also can surf green waves of forage within year-round ranges, even in the absence of migration (1). Green-wave surfing may therefore represent a learned behavior that underlies migration, and such knowledge may accumulate over generations via cultural transmission (15, 20).

Across the American West, many bighorn sheep (*Ovis canadensis*) populations were extirpated in the late 1800s because of market hunting and transmission of disease from domestic sheep (*O. aries*) (Fig. 1). To restore lost populations, wildlife managers translocated individuals from extant, migratory populations into vacant landscapes where extirpated populations once existed (Fig. 1). These individuals therefore had no knowledge about the landscapes into which they were translocated (herein termed “novel landscapes”).

Thus, if migration does not stem primarily from a genetically inherited suite of traits, individuals should fail to migrate when first translocated into novel landscapes where migration would be a profitable strategy (21).

To test this prediction, we affixed global positioning system (GPS) collars on 129 bighorn sheep sampled from four populations that had been extant for >200 years (herein termed “historical populations”) (Fig. 1) and 80 bighorn sheep when the sheep were first translocated into novel landscapes (table S1). We defined migration as movement between distinct seasonal ranges and classified the movement of each collared individual as migratory or resident by using net-squared displacement (22) [supplementary materials (SM)]. We then quantified how green waves of forage propagated across individual landscapes (1000 to 3600 km²) by measuring the date each pixel in a rasterized time series of the normalized difference vegetation index (250-m spatial resolution, 8-day temporal resolution) peaked in forage quality (SM) (23). Using this rasterized measure of peak forage quality, we quantified the semivariance (the magnitude of the wave) in the date of peak forage quality across a range of spatial lags (the distance the wave traveled) (SM). Within historical populations, 65 to 100% of individuals migrated, whereas few (<9%; 7 of 80) individuals translocated into novel landscapes migrated (Fig. 2A). The migratory propensity of a population was not related to the magnitude of the green wave or the distance it traveled (fig. S1), meaning that landscape characteristics alone did not explain differences in migratory propensity among populations. The seven translocated individuals that migrated were translocated into existing populations of bighorn sheep (<200 individuals) that had been reestablished three decades before (SM), suggesting cultural transmission of migratory behavior among conspecifics (horizontal transmission). Because individuals from migratory populations failed to migrate when translocated into landscapes where they had no prior experience, genes are unlikely to be the primary agent underlying ungulate migration. Instead, migration may require extended periods of time for social learning and cultural transmission to occur.

To evaluate the hypothesis that green-wave surfing is a learned behavior, we first calculated the surfing ability of each GPS-collared individual as the absolute difference between the day an individual occupied a location and the day forage quality peaked at that location (23). We then controlled for the influence that local differences in latitudinal, elevational, and topographical features may have on an individual's ability to surf the green wave (23) by comparing observed green-wave surfing ability with those of a “naïve forager” that moved at random and an “omniscient forager” that had complete knowledge of phenological patterns (SM). By doing so, we were able to quantify how much knowledge individuals possessed about local patterns of phenology (fig. S2). We found that the surfing knowledge of bighorn sheep from historical populations was approximately twice that of transplanted

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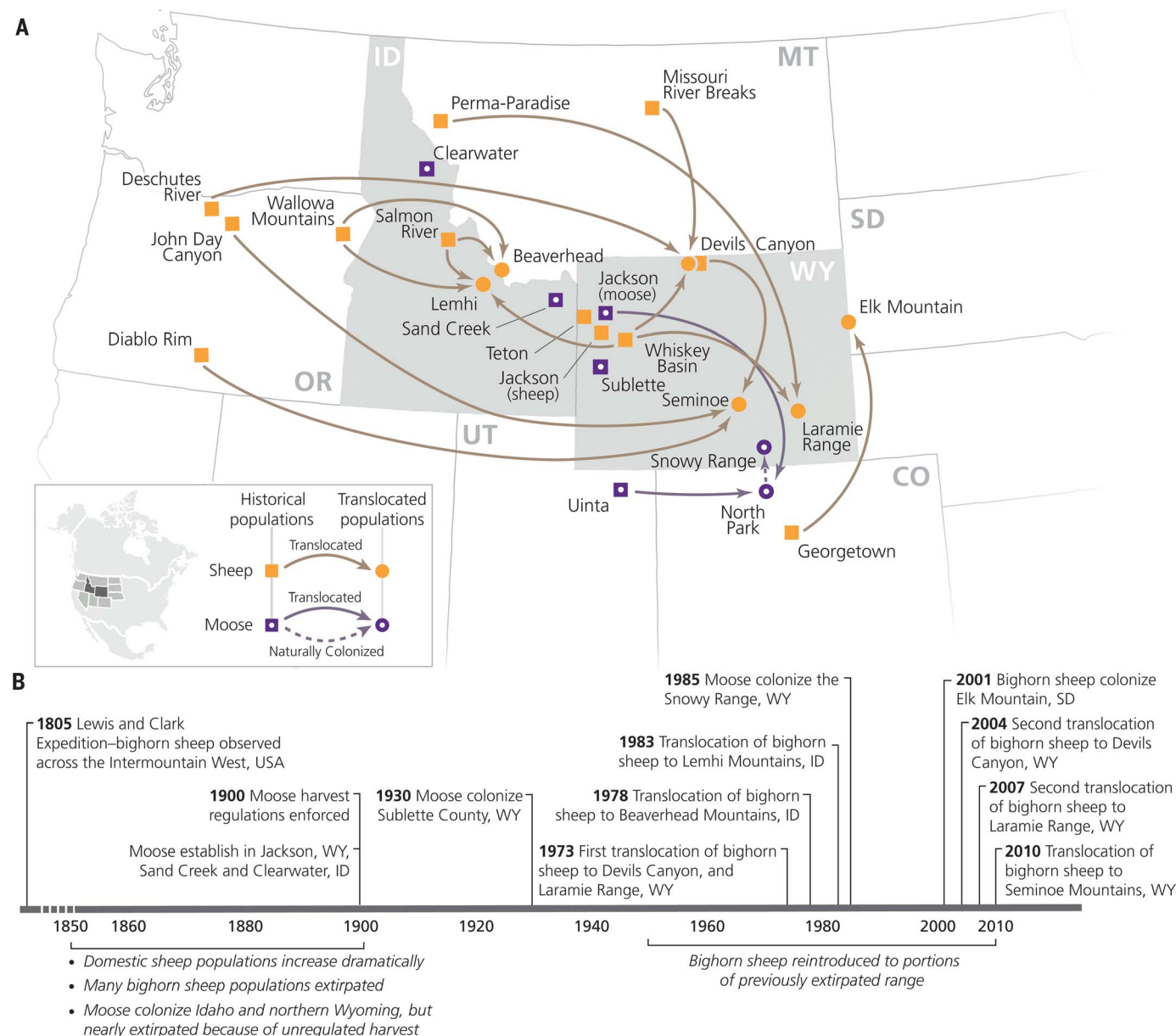


Fig. 1. Bighorn sheep and moose translocation history. (A) The subset of historical and translocated populations of bighorn sheep and moose used to assess the cultural basis of ungulate migration. (B) Timeline of bighorn sheep and moose translocations as well as other important

events in the history of these species since the settlement of western North America by European Americans. See SM for further details about translocation history. (Cartography by InfoGraphics Lab, University of Oregon.)

individuals (Fig. 2B), suggesting that knowledge about local green waves may improve over time as animals learn and culturally transmit information about the seasonal distribution of high-quality forage.

The hypothesis that ungulate migration is established and maintained by cultural transmission predicts that green-wave surfing knowledge and, subsequently, the propensity to migrate should increase as animals learn how to exploit landscapes and transmit that foraging information across generations (vertical transmission of information). To evaluate the influence of vertical transmission on surfing knowledge and migratory propensity, we expanded our analysis to include individuals from four additional popula-

tions of bighorn sheep (an additional 58 individuals) and five populations of moose (*Alces alces*; 189 individuals) that were GPS collared ~10 to 110 years after either translocation or natural colonization (Fig. 1, table S1, and SM). We found that the surfing knowledge of both bighorn sheep and moose increased as time since population establishment increased (Fig. 3A). As time passed and bighorn sheep and moose increased their surfing knowledge, their migratory propensities also increased (Fig. 3, B and C). Although population density and migratory propensity are sometimes correlated positively (24), migratory propensity did not change with substantial decreases in population density caused by epizootics,

habitat loss, and increased predation (25, 26). Together, these results demonstrate that ungulates accumulate knowledge of local phenological patterns over time via the “ratcheting effect,” wherein each generation augments culturally transmitted information with information gained from their own experience, a process known as cumulative cultural evolution (15, 20). Cultural transmission therefore acts as a second (nongenetic) inheritance system for ungulates, shaping their foraging and migratory behavior and ultimately providing the primary mechanism by which their migrations have evolved.

Across the globe, anthropogenic barriers have disrupted ungulate migrations, triggered declines

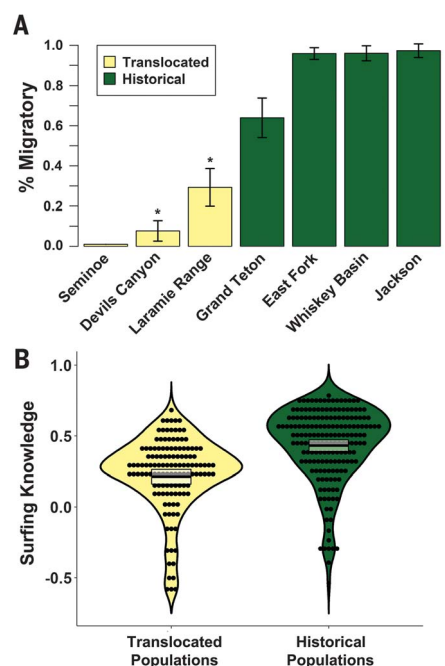


Fig. 2. Migratory propensities and green-wave surfing knowledge of seven translocated and historical populations of bighorn sheep.

(A) Migratory propensities (\pm SEM) of bighorn sheep translocated into novel landscapes compared with those of historical populations (>200 years old). Asterisks indicate landscapes where naïve individuals were translocated into populations previously established via translocation ~ 30 years before. (B) Relative to omniscient and naïve foragers on the same landscape, surfing knowledge was lower for translocated (yellow) bighorn sheep than for individuals from historical populations (green). Mean surfing knowledge (black horizontal bars) relative to that of an omniscient forager (set at 1.0) and associated 95% confidence intervals (white boxes) are presented. The surfing knowledge of individuals (black circles) in historical populations was significantly higher than that of translocated individuals (Mann-Whitney U Test, $W = 5863$, $P < 0.001$).

in population abundance, and even caused local extirpations (4). Our results provide empirical evidence that learning and cultural transmission underlie the establishment and maintenance of ungulate migration. Because ungulate migrations stem from decades of social learning about spatial patterns of plant phenology, loss of migration will result in a marked decrease in the knowledge ungulates possess about how to optimally exploit their habitats. Hence, restoring migratory populations after extirpation or the removal of barriers to movement will be hindered by poor foraging efficiency, suppressed fitness, and reduced population performance (2, 3). Thus, conservation of existing migration corridors, stopover sites, and seasonal ranges not only protects the landscapes that ungulates depend on (27, 28); such efforts also maintain the traditional knowledge

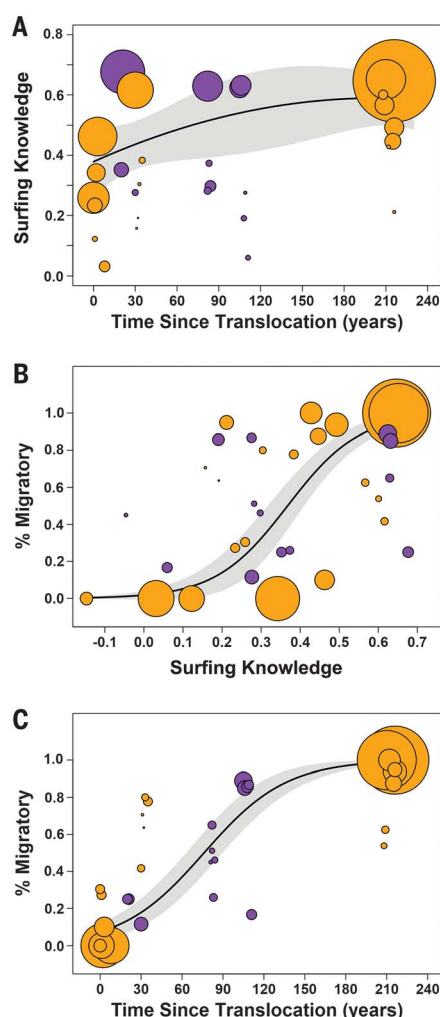


Fig. 3. Green-wave surfing knowledge and migratory propensity over time. (A) After translocation, populations of bighorn sheep (orange circles) and moose (purple circles) require decades to learn and culturally transmit information about how to best surf green waves, (B) eventually leading to the establishment of migration, which (C) takes many generations (the generation time for bighorn sheep and moose is ~ 7 years). Circles represent estimates of surfing knowledge and migratory propensity for a given population in a given year (i.e., a migratory event). Circle size depicts the amount of confidence (inverse variance) in each estimate. Black lines and gray shaded areas illustrate fitted generalized linear model predictions and their 95% confidence intervals. All relationships are significant at $P < 0.01$.

and culture that migratory animals use to bolster fitness and sustain abundant populations (13, 29).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6406/1023/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 and S2
Tables S1 to S3
References (31–78)

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Learning where and when

Large ungulate migrations occur across continents and inspire curiosity about how these animals know when to leave and where to go. Jesmer *et al.* took advantage of regional extinctions and reintroductions of several North American ungulate species to determine the role of learning in migrations (see the Perspective by Festa-Bianchet). Reintroduced populations of bighorn sheep and moose did not migrate as historical herds had. However, after several decades, newly established herds were better able to track the emergence of vegetation in the environment and were increasingly migratory. Thus, newly introduced animals learned about their environment and shared the information through social exchange.

Science, this issue p. 1023; see also p. 972

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