The Last Mile: How to Sustain Long-Distance Migration in Mammals

JOEL BERGER

Teton Field Office, North American Program, Wildlife Conservation Society, Moose, Wyoming 83012, U.S.A., email jbwcs@earthlink.net

Abstract: *Among Earth's most stunning, yet imperiled, biological phenomena is long-distance migration (LDM). Although the understanding of how and why animals migrate may be of general interest, few site-specific strategies have targeted ways in which to best retain such increasingly rare events. Contrasts among 29 terrestrial mammals from five continents representing 103 populations indicate that remnant long-distant migrants have poor long-term prospects. Nonetheless, in areas of low human density in the Western Hemisphere, five social and nongregarious species, all from the same region of the Rocky Mountains (U.S.A.), still experience the most accentuated of remaining New World LDMs south of central Canada. These movements occur in or adjacent to the Greater Yellowstone region, where about 75% of the migration routes for elk (*Cervus elaphus*), bison (*Bison bison*), and North America's sole surviving endemic ungulate, pronghorn (*Antilocapra americana*), have already been lost. However, pronghorn still migrate up to 550 km (round-trip) annually. These extreme movements (1) necessitate use of historic, exceptionally narrow corridors (0.1–0.8 km wide) that have existed for at least 5800 years, (2) exceed travel distances of elephants (*Loxodonta africana*) and zebras (*Equus burchelli*), and (3) are on par with those of Asian chiru (*Pantholops hodgsoni*) and African wildebeest (*Connochaetes taurinus*). Although conservation planners face uncertainty in situating reserves in the most biologically valued locations, the concordance between archaeological and current biological data on migration through specific corridors in these unprotected areas adjacent to the Yellowstone system highlights their retention value. It is highly likely that accelerated leasing of public lands for energy development in such regions will truncate such migrations. One landscape-level solution to conserving LDMs is the creation of a network of national migration corridors, an action in the Yellowstone region that would result in de facto protection for a multispecies complex. Tactics applied in this part of the world may not work in others, however, therefore reinforcing the value of site-specific field information on the past and current biological needs of migratory species.*

La Última Milla: Como Sostener la Migración de Larga Distancia en Mamíferos

Resumen: *Entre los fenómenos biológicos más asombrosos, pero en peligro, de la Tierra está la migración de larga distancia (MLD). Aunque el entendimiento de cómo y porque migran los animales puede ser de interés general, pocas estrategias sitio-específicas han encontrado formas para retener tales eventos cada vez más raros. Los contrastes entre 29 mamíferos terrestres de cinco continentes que representar a 103 poblaciones indican que las MLD remanentes tienen perspectivas pobres a largo plazo. No obstante, en áreas con bajas densidades humanas en el Hemisferio Occidental, cinco especies sociales y no gregarias, todas de las misma región de las Montañas Rocallosas (E.U.A.) aun experimentan las MLD más acentuadas al sur de Canadá. Estos movimientos ocurren en la región de Yellowstone o adyacentes a la misma, donde se han perdido cerca del 75% de las rutas de migración de alces (*Cervus elaphus*), bisontes (*Bison bison*) y el único ungulado endémico sobreviviente de Norteamérica,* Antilocapra americana*. Sin embargo,* Antilocapra americana *aun migra hasta 550 km (viaje redondo) anualmente. Estos movimientos extremos (1) necesitan el uso de corredores históricos, excepcionalmente angostos (0.1-0.8 km de ancho) que han existido por lo menos por 5800 años, (2) exceden las distancias de viaje de elefantes (*Loxodonta africana*) y cebras (*Equus burchelli*) y (3) son similares a*

Paper submitted December 17, 2002; revised manuscript accepted July 16, 2003.

Conservation Biology, Pages 320–331
Volume 18, No. 2, April 2004

los de Pantholops hodgsoni *y* Connochaetes taurinus*. Aunque los planificadores de conservación enfrentan la incertidumbre de situar reservas en las localidades biológicamente más valiosas, la concordancia entre datos arqueológicos y actuales sobre migración por corredores específicos en estas áreas no protegidas adyacentes al sistema Yellowstone resalta su valor de retención. Es altamente probable que las migraciones se trunquen por el arrendamiento acelerado de tierras públicas para el desarrollo energético en tales áreas. Una solución a nivel de paisaje para conservar a las MLD es la creación de una red de corredores nacionales de migración, una acción que resultaría en la protección de hecho de un complejo multi-específico en la región de Yellowstone. Sin embargo, las tácticas empleadas en esta parte del mundo pueden no funcionar en otras, por lo cual se refuerza el valor de la información de campo sitio-específica sobre las necesidades pasadas y actuales de especies migratorias.*

Introduction

Despite increasing attention to biological conservation, most terrestrial surfaces on Earth remain unprotected. Consequently, extraordinary events that once occurred across vast landscapes, playing significant ecological roles, have been truncated. Long-distance migration (LDM) is one such event. Globally, spectacular LDMs still exist and involve volant taxa including diverse species of birds and butterflies (Brower 1995) and well-known cetacean journeys that traverse seas from Arctic to Mexican waters (Baker 1978). Many of the massive and historically described overland treks by herd-dwelling mammals, however, have been lost from Asian steppes, African savannas, and North American grasslands (Table 1). The development of effective strategies to maintain these events has been problematic.

Conservation planners, in trying to capture the essence of both ecological processes and diversity, continue to face uncertainty in reserve placement because landscapes vary in biological value (Groves et al. 2002), events beyond protected borders alter the efficacy of reserves (Newmark 1987, 1995), and changing environments impede knowledge about the relative importance of fixed areas on species persistence (Wilcove 1999). Although LDMs are far from the mainstream of conservation biology, and the movements of gregarious herds in Africa are well-chronicled (Fryxell & Sinclair 1988*a*; Williamson 1997), asocial species also migrate. These species are not typically associated with such movements and include Mountain tapirs (Downer 1996, 1997), black-tailed jackrabbits (Smith et al. 2002), and boreal moose, the latter covering round-trip distances of up to 390 km (Mauer 1998). (Scientific names for species used in analyses are provided in Appendix 1.) Other taxa of terrestrial vertebrates also undertake impressive migrations, including spotted frogs (*Rana luteiventris*) and newts (Pilliod et al. 2002), but how migration is linked with corridor use and especially population persistence has not been well studied (Simberloff et al. 1992; Beier & Noss 1998).

The broader issue, of course, is not whether migratory species are social or large or small, but whether and how to sustain migration so that it does not become a transitional or endangered phenomenon. A fundamental challenge to conservation-minded governments is how best to devise strategies that retain LDMs as part of a rich biological heritage. As a first step in bringing this fleeting ecological process to the conservation table, I offer (1) an analysis of where and which mammalian long-distance migrants have been lost and remain, (2) a potential correlate—body mass—of long-distance migrants, and (3) a relatively straightforward but site-specific conservation plan to retain the longest LDMs in the Western Hemisphere that involve species other than caribou.

Methods

Definitions and Rationale

Migration has been defined in various ways (Sinclair 1983; Rankin 1985). For my purposes a simple operational definition seems best: seasonal round-trip movement between discrete areas not used at other times of the year. For example, a mouse that moves from my house in winter to the outside woodpile during summer and back again would be migratory, and the one-way distance traversed is between house and woodpile. By contrast, a mouse that moves 15 km but not back again is not migratory (Maier 2002). Similarly, a wolverine (*Gulo gulo*) covering a 1000-km^2 region between mountain ranges throughout the year would not be migratory because it fails to show seasonal use of discrete ranges. Many researchers, although not specifically addressing questions about migration distance, have used measures to discern distinct areas of seasonal use (Pierce et al. 1999; Appendix 1), from which migration distances between them could be estimated. Other researchers evaluated distances between formal geometric centers of seasonally discrete home ranges (e.g., Kufeld et al. 1989; Nicholson et al. 1997).

A definition of *long-distance migration* is more troublesome because the distance traversed by species that differ in life-history traits may only be relative. Although

Table 1. Summary of selected major migrations confirmed or suspected lost in historic times, and remnants for three species within the Greater Yellowstone region (*n* is sample for total migration routes).

Continental			*Greater Yellowstone Ecosystem*	
species	*location*	*Reference*[a]	*species*	*percent lost* (n)[b]
Springbok[b]	karoo, Kalahari, South Africa, Namibia	1,2	pronghorn	78 (11)
Wildebeest[b]	Namibia, South Africa	2,3	bison	100 (14)
White-eared kob[c]	The Sudd, Sudan	4	elk	58 (36)
Bison[b]	Canda, U.S.A.	5		
African elephant[b]	Kenya	6		
Asian elephant[b]	India	7		
Saiga[b]	Kazakhastan, Russia, Mongolia	8		

[a] *1, Child & LeRiche 1967; 2, Gasaway et al. 1996; 3, Williamson et al. 1988 and Williamson 1997; 4, Fryxell & Sinclair 1988; 5, Roe 1970; 6, Waithaka 1994; 7, Sukumar 1989; 8, Milner-Gulland et al. 2001.*

[b] *Confirmed lost.*

[c] *Suspected lost.*

either ecological or life-history definitions of LDM may be estimated with allometric criteria to account for body size, my interest lies more in absolute rather than relative distance because conservation strategies have rarely, if ever, been based on relative measures of species size (Groves et al. 2002). With this as a caveat, both European and North American authors have offered provisional definitions that infer "long distance" when one-way movements exceed 10–12 km (Fuller & Keith 1981; Sandgren & Sweanor 1988). Here, I suggest that a long-distance migrant may be species or population dependent and let readers decide for themselves what is "long" and what is not pertinent to conservation objectives.

Choice of Species, Limitations of Data, and Analyses

I collated information on migration from both published and gray literature. I elected to include the latter given the immense number of state-agency reports and bulletins in the United States with information on radio collared animals and attendant analyses of movement patterns in relation to seasonal use. For example, 140 radio collared mule deer were studied at a Wyoming site for multiple years (Sawyer & Lindzey 1999), yet the mere exclusion of such data on migration simply because they were unpublished would represent the loss of significant information. I have not, however, attempted to summarize data from every agency report on movement patterns.

For some taxa (e.g., cervids, camelids), migration may be a polymorphic trait, with members of a population showing great fidelity to areas they either migrate to or remain within (Ortega & Franklin 1995; Bowyer et al. 1996; Nicholson et al. 1997). My measures on distance traversed reflect those of migratory segments of studied populations only, and these were estimated from data presented within the cited study or from the original calculations of the author. The reported measure is the mean for round-trip migrations. Where data stem from multiple populations, I calculated a species mean and, when relevant, standard errors (SEm) and 95% confidences intervals (CI).

Most studies of migration in terrestrial mammals are of hooved mammals (artiodactyls, perrisodactyls, and proboscideans; Appendix 1), but I also included those for carnivores and one lagomorph. For some species (mostly but not exclusively those from North America), multiple data sets exist that tend to reflect populations from geographically different regions. In other areas of the world, data are more restricted, especially when radio collars were not used. For comparative purposes, I included data on these latter migration distances when justified by the author and published in the peer-reviewed literature (e.g., Schaller 1998).

For the approximately 10.8 million ha of the Greater Yellowstone Ecosystem (GYE; Noss et al. 2002), the number of migration routes that have changed or been lost during the last 100 years were estimated by relying on recent historical records (i.e., trapper's journals; Schullery & Whittlesey 1995) and published and agency data. In the GYE this calculation has been possible because, at a coarse level, interest in migration has been great, yielding analyses of track counts, sightings, and estimates of travel routes since the 1950s. Efforts to mark visually (i.e., with neck bands or ear tags) and subsequently to radio-tag elk (Anderson 1958; Craighead et al. 1972) have now spanned portions of >5 decades (Smith & Robbins 1994; B. L. Smith personal communication). Although pronghorn and bison remain less studied, I based estimates of routes lost or retained on point counts of discrete winter and summer ranges. These derive from observations of these ungulates at past known locations, coupled with landscape-level analyses that involved the distribution and change of local human densities, agricultural practices, and winter snow depth. For instance, where towns replaced open habitat in what were once historic pathways (Fig. 1), a route was designated as

Figure 1. Example of the hard edge between a town and open habitat for wildlife (in this case, the National Elk Refuge and town of Jackson, Wyoming) and the blockage of migration (arrow) for bighorn sheep, elk, and pronghorn.

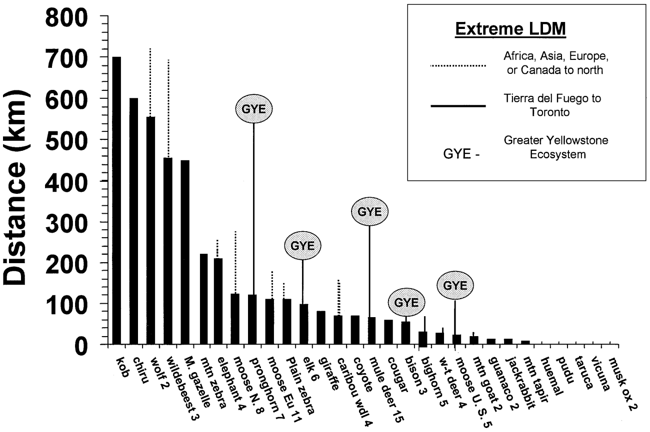

Figure 2. Mean and extreme (extended lines) long-distance migration round-trip distances for terrestrial mammals (excluding barren-ground caribou). Numbers after name are studies/species. If unnumbered, data are based on one study (see Appendix 1 for scientific names and references). Moose from geographically disparate regions are: N, Alaska and Yukon; Eu, Scandinavia; U.S., south of Canada.

"lost." Measures of chest height in pronghorn, bison, and elk relative to snow depth also enable crude prediction of winter occurrence (Telfer & Kelsall 1984).

Although analyses of the potential conduciveness of habitats to movement between two discrete points may be in error because the scale of inquiry affects interpretations (Bowyer et al. 1996) and it is impossible to be certain whether a movement corridor has been lost, I adopted a more conservative measure. Rather than assuming a route was lost, I included data only when discrete summering or wintering sites were known and one remained unused. For instance, the Gallatin Valley of Montana currently harbors a human population of over 40,000. Elk once crossed the valley but no longer can. Whether multiple migration pathways or a single one occurred historically is unknown. To be conservative, which undoubtedly underestimates real losses, I recorded only one lost route, although given the approximate size of Gallatin Valley—over 200,000 ha—and given that elk use summer ranges in at least four adjacent mountain ranges, it is likely that more than a single route has been truncated.

To evaluate whether life-history traits are associated with migration distance, I attempted to fit linear and nonlinear (quadratic, power, exponential) models to nontransformed and log-transformed data on migration distance (mean, median, and longest). Outliers for species or populations were excluded first, and then carnivores were removed to determine whether a global pattern emerged. Subsequently, I restricted analyses to potential migrations that still persist between the southern tip of South America and central Canada, a procedure that excluded more northern latitudes where human effects have been smaller (Sanderson et al. 2002*a*) and caribou mostly unhindered (Appendix 1, but see Mahoney & Schaefer 2002). Although comparative analyses with unequally weighted samples tend to use median values (Gittleman 1986) and measures of migration distance do not occur without error, mean and median distances were highly correlated for all studies ($r^2 = 0.918; p < 0.0001$); therefore, I used average values.

Results

The striking variation in body size that characterizes terrestrial mammals (Eisenberg 1981) is paralleled by migration distances that show great dissimilarities. Although wildebeest and Mongolian gazelles migrate more than 450 km (round-trip) (Fig. 2), for species that may differ in size by more than 40-fold, distances can be both small and similar. For example, mountain tapirs and black-tailed jackrabbits both move <12 km. By contrast, within-species variability can be great. Mule deer average 66 km (±12.7 [SEm]; 95% CI = 38–93; $n = 15$ studies), but in the Upper Green River Basin of Wyoming, distances exceed 285 km (Fig. 2). On a geographically broader scale are barren-ground caribou, with extreme LDMs ($\bar{x} = 1673 \pm 491$ km; $n = 3$; longest = 2500 km). Woodland caribou, however, move far less $\bar{x} = 71 \pm 28$; $n = 4$; Fig. 2).

Although the spatial area used by a species is often associated with its body size (Gompper & Gittleman 1991), this relation appears not to hold, even with the exclusion of such obvious outliers as barren-ground caribou (less than the 99.5% upper CI). Only an exponential model that was restricted geographically to the log mass of species occurring between Canada and the southern tip of South

America explained more than 15% of the variance in migration ($r^2 = 0.178$; $n = 15$; $p = 0.117$), and the explanatory value of this single variable is generally low. It did not improve when analyses were restricted further to only herbivores ($r^2 = 0.015$; $p = 0.986$). These findings, based on a more expansive sample, are consistent with the lack of relationship anticipated by others (Baker 1978; Sinclair & Arcese 1995), presumably because either local ecological conditions, population densities, or other factors are more important, or there is no simple association between body mass and migration distance.

It may be of more immediate relevance to conservation to gain an understanding of how migration has fared in areas with profound anthropogenic impacts. Omitting caribou and other species from the Arctic and other areas with relatively low human impacts (Sanderson et al. 2002*a*) enables a focus on remnant LDMs of the Western Hemisphere. Of 57 populations representing 17 species, the 5 with the extreme LDMs rely on lands within or adjacent to the Greater Yellowstone Ecosystem (GYE) (Fig. 2). Although the Yellowstone area has long been recognized for geothermal distinctiveness and, recently, a restored large-carnivore community (Clark et al. 1999; Noss et al. 2002), what previously has been unrecognized is its ability to support some ecological phenomena—especially the accentuated treks of pronghorn, elk, mule deer, moose, and bison (Fig. 2).

To improve insights into the type of planning necessary to conserve these LDMs, I examined the fates of historic and current routes (Craighead et al. 1972; Smith & Robbins 1994) traversed by three species: pronghorn, bison, and elk (Table 1). A conservative estimate of the frequency of routes truncated indicates that many have already been lost: pronghorn, 78% ($n = 11$); bison, 100% ($n = 14$); and elk, 58% ($n = 36$).

Discussion

Bottlenecks: a Link between the Holocene and Modern Threats

Effective conservation involves obvious complexities and approaches that vary from science and planning to policy and site-specific measures. It is this last category, however, that may be most relevant for achieving conservation of LDMs. Despite the loss of many spectacular treks (Table 1), the longest (caribou excluded) and perhaps most jeopardized in the Western Hemisphere occur in the GYE. Although causes vary for the loss of routes by migratory bison, elk, and pronghorn, four stand out: (1) little tolerance for bison outside protected areas, (2) concentrations of elk on 23 winter feeding grounds in Wyoming, (3) a 20% increase in the human population in the last decade to (currently) more than 370,000, and (4) associated loss of habitat, especially areas crucial to approximately 100,000 wintering ungulates in the southern part of this ecosystem. This last point is central if extreme and highly fragile LDMs are to be retained, especially as the effectiveness of conservation planning shifts from general paradigms to site-specific implementation (Groves et al. 2002; Sanderson et al. 2002*a*).

At the southern terminus of migration routes for pronghorn and mule deer from the GYE in southwestern Wyoming (Fig. 3), about 8500 energy-extraction sites exist on public lands, with up to 10,000–15,000 more forecast during the next decade. The potential to seriously alter winter habitats and subsequently sever migration is genuine. For pronghorns, the extreme LDM that connects the Upper Green River Basin to Grand Teton National Park faces additional challenges (Sawyer & Lindzey 2000) because it winds through at least four narrow corridors (A-D in Fig. 3), beginning with a 0.8-km constriction at an elevation of 2226 m.

This first bottleneck, officially known as Trapper's Point (A in Fig. 3), has existed for 5800–6800 years and is known from three mid-Holocene early Archaic procurement sites. Like today, it was used in the past by pregnant females during spring migration, an inference based on the presence of fetal bones of a size similar to those of pregnant pronghorn during late gestation (Miller & Saunders 2000). Toward the north, a second bottleneck (B) occurs along a 5-km-long sagebrush gap between floodplain and forest that narrows to a strip only 100–400 m wide. The additional two bottlenecks (Fig. 3) are C, a high-elevation hydrographic divide at 2774 m that is often filled with deep snow and distinguishes the Upper Green River Basin from the Gros Ventre Mountains, and D, 30–40 km farther west of C, a 100- to 200-m constriction between sandstone cliffs, road, and the Gros Ventre River.

That any LDM endures in this system is remarkable given increasing impediments to pronghorn treks at lower elevation that include at least 105 fences (Sawyer & Lindzey 2000; J.B., unpublished data), highways, housing subdivisions, and the proliferation of petroleum development in winter habitats. Critically, however, confidence in the existence of future migrations by both pronghorn and mule deer at the scale of past migrations is tenuous. Although much of the wintering areas and migration bottlenecks involve federal land in the Upper Green River Basin (Fig. 3), habitat protection is no longer assured because of possible incompatibilities with U.S. energy policies. Federal permits to drill are being fast-tracked under Presidential Order 13212, which expedites the review and approval of proposals to facilitate the rapid permitting of energy-related projects in the western United States (Berger 2003). Unlike the plethora of Alaskan studies designed to understand possible petroleum-related disruption to migratory caribou (Berger et al. 2001), no peer-reviewed scientific literature exists to assess possible energy-related effects on migration in the GYE.

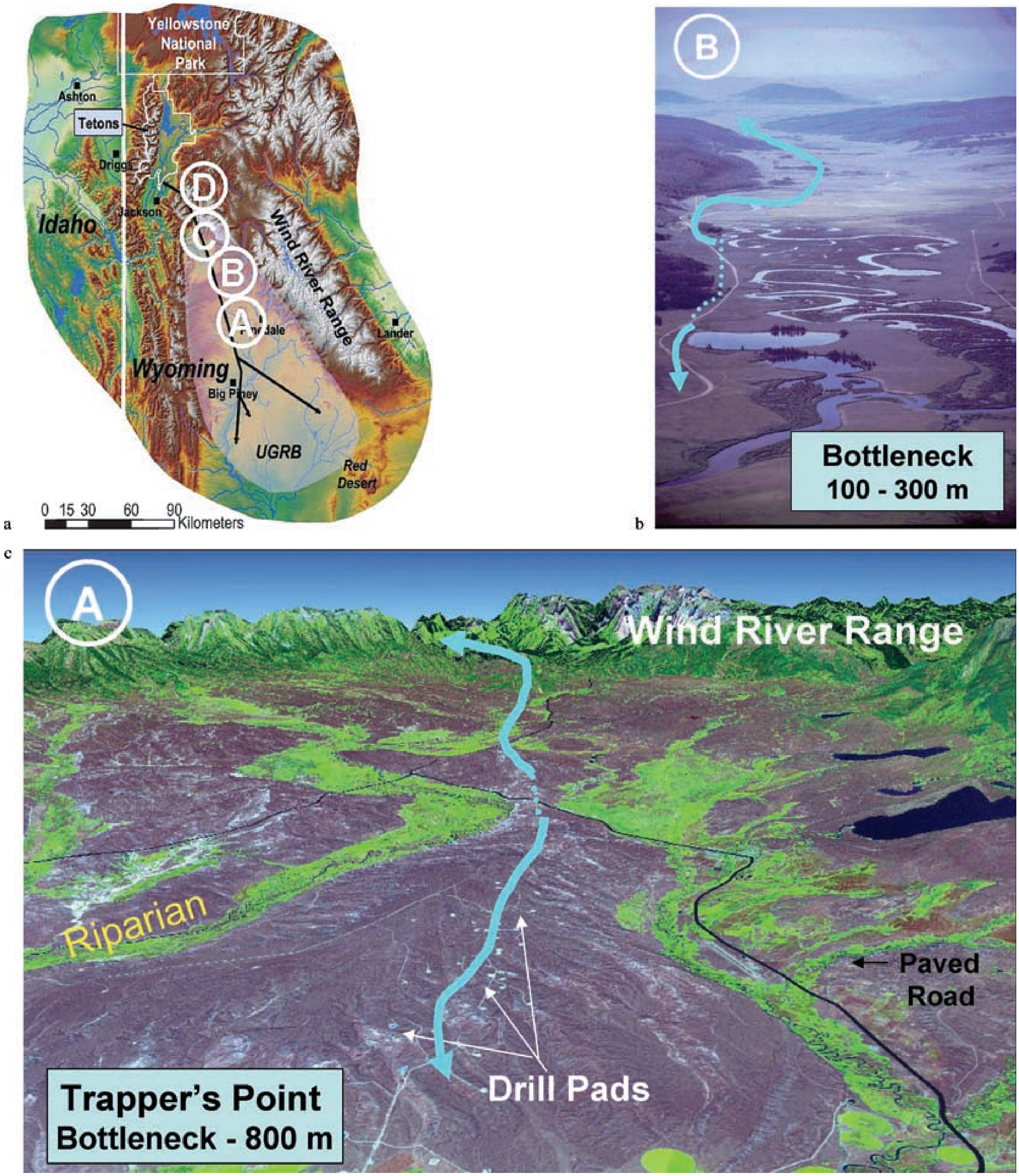

Figure 3. Location of pronghorn migration route in western Wyoming with placement of bottlenecks A to D (described in the text) as indicated in map and enhanced images of A and B (courtesy of Sky Truth and J. Catton, respectively). Solid lines reflect migration routes, and dotted lines are narrow pathways with maximal restriction (e.g., bottleneck) (UGRB, Upper Green River Basin).

Conclusions and a Simple Action Plan

Although American scientists, conservation advocates, private industry, and elected officials seemingly share in the goal of increasing domestic security, efforts to do so must involve serious attempts to develop alternate sources of energy while not sacrificing national or international biological treasures. Despite an association between energy consumption and loss of biodiversity (Ehrlich 1994), the protection of increasingly rare ecological events that include LDMs is possible (Brussard 1991).

Conservation efforts at the southern terminus of the GYE extend back to 1898, and, although largely ignored, have variously called for establishment of nationally designated parks, monuments, and landscapes (Dunham 1898; Wyoming Outdoor Council 2002). A more modest plan to conserve what few truly stunning LDMs remain between central Canada and Tierra del Fuego is to enhance protection for highly sensitive areas and bottlenecks. For the southern GYE these migration routes traverse existing U.S. public lands under the jurisdiction of the Bureau of Land Management (BLM) and U.S. Forest Service (USFS), and can receive real protection if a broader and more formally designated national wildlife migration corridor is instituted for all citizens. Precedents are numerous in the United States, including national scenic highways, historic trails, and rivers.

In this particular instance, details for a statutory migration corridor would need to be resolved. The BLM has the capacity to formally protect habitats by declaring them "areas of critical environmental concern" (ACEC), an idea once proposed between two reserves in the northern Great Basin Desert (Uselman 1998), and not unlike that proposed for connecting elephant refuges through communal lands in Zimbabwe (Osborn & Parker 2003). For the Upper Green River Basin, however, the designating of a formally protected corridor, rather than an ACEC, would represent a landmark victory nationally and internationally because not only would it offer greater protection but it would bring an ecological process, long-distance migration, to the attention of the public. As such, this proposal could sustain a macroscale phenomenon not repeated in grandeur between Tierra del Fuego and central Canada.

The use of process-driven approaches to conserve small and large areas has been effective (Brussard 1991; Sanderson et al. 2002*a*): for example, not only are Monarch butterflies (*Danaus plexippus*) now protected in central Mexico (Brower 1995), but the Serengeti ecosystem is defined by its migratory wildebeest (McNaughton & Banyikawa 1995). Although past boundaries of the GYE were generally denoted by wide-ranging species such as brown bears (*Ursus arctos*) (Craighead 1979; Noss et al. 2002), this species-centric approach may include an error of omission because the extreme LDMs of this region were not previously known. But whether the protection of critical corridors can be achieved by use of species or fleeting ecological processes (Sanderson et al. 2002*b*) is less important than achieving actions on the ground that will effectively result in protecting the remnant and narrow corridors currently used by migrating Upper Green River Basin ungulates. Although theory will help us understand more about the dynamics of connectivity in other systems, enough is known about the concordance between the pronghorn's use of corridors during the mid-Holocene and today to suggest that protective action should not be delayed. Otherwise, we will squander a biological legacy that may be enjoyed by our future descendants.

Acknowledgments

For support, comments, and other help, I thank P. Aengst, P. Arcese, V. Bleich, S. Cain, F. Camenzind, D. and S. Craighead, R. Deblinger, C. Downer, L. Dorsey, J. Ginsberg, R. Okensfells, F. Lindsey, M. Ortega, K. Redford, L. and S. Robertson, H. Sawyer, T. Segerstrom, A. R. E. Sinclair, B. L. Smith, D. Van Vuren, M. Taylor, and W. Weber; wildlife agencies from the states of Arizona, California, Colorado, Montana, and Wyoming; and the U.S. National Science Foundation, National Park Service, Greater Yellowstone Coalition (J. Catton), Sky Truth (J. Amos), and The Wilderness Society. K. Berger was instrumental in pointing out the value of the local Yellowstone migrations.

Literature Cited

Akenson, J. J., and H. A. Akenson. 1994. Bighorn sheep movements and summer lamb mortality in central Idaho. Symposium of Northern Wild Sheep and Goat Council **8:**14–27.

Anderson, C. C. 1958. The elk of Jackson Hole: a review of Jackson elk studies. Bulletin 10. Wyoming Game and Fish Commission, Cheyenne.

Baker, R. J. 1978. The evolutionary ecology of animal migration. Hoddes and Sloughton, Seven Oaks, United Kingdom.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs **114**.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs **135**.

Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology **12:**1241–1252.

Berger, J. 2003. Is it acceptable to let a species go extinct in a national park? Conservation Biology **17:**1451–1454.

Berger, J., A. Hoylman, and W. A. Weber. 2001. Perturbation in vast ecosystems in the absence of adequate science: Alaska's Arctic Refuge. Conservation Biology **15:**539–542.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1996. Sexual segregation in black-tailed deer: effects of scale. Journal of Wildlife Management. **60:**10–17.

Bright, J. L., and C. Van Riper III. 2000. Pronghorn home ranges, habitat selection, and distribution around water sources in Northern Arizona. Technical report series USGSFRESC/COPL/2000 18. U. S. Geological Service, Denver.

Brower, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly in North America: 1857–1995. Journal of Lepidopteran Society **49:**304–385.

Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management **56:**246–253.

Brussard, P. F. 1991. The role of ecology in biological conservation. Ecological Applications **1:**6–12.

Cain, S. L., T. J. Roffe, J. Berger, and C. Cunningham. 2001. Reproduction and demography of brucellosis-infected bison in the southern Greater Yellowstone Ecosystem. Annual progress report. National Park Service, Moose, Wyoming.

Carrel, W. K., R. A. Ocknefels, and R. E. Schweinsburg. 1999. An evaluation of annual migration patterns of the Paunsaugunt mule deer herd between Utah and Arizona. Technical report 29. Arizona Game Fish, Phoenix.

Child, G., and J. D. Le Riche. 1967. Recent springbok treks (mass movements) in southwestern Botswana. Mammalia **33:**499–504.

Clark, T. W., A. P. Curlee, S. C. Minta, and P. M. Kareiva. 1999. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut.

Craighead, F. J. 1979. Track of the grizzly, Sierra Club Books, San Francisco.

Craighead, J. J., G. Atwell, and B. O'Gara. 1972. Elk migrations in and near Yellowstone National Park. Wildlife Monographs **29**.

Cumming, H. G., and D. B. Beange. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. Journal of Wildlife Management **51:**69–79.

Dalke, P. D., R. D. Beeman, F. J. Kindel, R. J. Robel, and T. R. Williams. 1965. Seasonal movements of elk in the Selway River Drainage. Journal of Wildlife Management **29:**333–338.

Darby, W. R., and W. O. Pruitt Jr. 1984. Habitat use, movements, and grouping behaviour of Woodland caribou (*Rangifer tarandus caribou*) in southeastern Manitoba. Canadian Field Naturalist **98:**184–190.

Deblinger, R. D. 1980. Ecology and behavior of pronghorn in the Red Desert, Wyoming with reference to energy development. Ph. D. dissertation. Colorado State University, Ft. Collins.

Diaz, N. I., and J. Smith-Fluek. 2000. The Patagonian huemal: a mysterious deer on the brink of extinction. Literature of Latin America, Buenos Aires.

Downer, C. C. 1996. The mountain tapir, endangered 'flagship' of the high Andes. Oryx **30:**45–58.

Downer, C. C. 1997. Status and action plan for the mountain tapir (*Tapirus pinchaque*). Pages 100–122 in D. M. Brooks, R. E. Bodmer, and S. M. Matola, editors. Tapirs: status survey and conservation action plan. World Conservation Union, Morges, Switzerland.

Dunham, F. 1898. A winter game reserve. Recreation **9:**271–272.

Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66:**817–826.

Ehrlich, P. R. 1994. Energy use and biodiversity loss. Philosophical Transactions of the Royal Society of London Series B **344:**99–104.

Eisenberg, J. F. 1981. The mammalian radiations. University of Chicago Press, Chicago.

Eldridge, W. D., M. MacNamara, and N. Pacheco. 1987. Activity patterns and habitat utilization of pudus (*Pudu pudu*) in south central Chile. Pages 352–370 in C. M. Wemmer, editor. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C.

Fancy, S. G., L. F. Pank, K. R. Whitten, and W. L. Regelin. 1988. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology **67:**644–650.

Ferguson, M. A. D., and F. Messier. 2000. Mass emigration of Arctic tundra caribou from a traditional wintering range: population dynamics and physical condition. Journal of Wildlife Management **64:**168–178.

Forbes, G. J., and J. B. Theberge. 1995. Influences of a migratory deer herd on wolf movements and mortality in and near Algonquin Park, Ontario. Pages 303–314 in L. H. Carbyn, S. H. Fritts, and D. R. Seip. Ecology and conservation of wolves in a changing world. Circumpolar Polar Press, Edmonton, Alberta, Canada.

Franklin, W. L. 1982. Biology, ecology, and relationship to man of the South American camelids. Pages 457–490 in M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Special publication. Pymatuning Lab, University of Pittsburgh, Pennsylvania.

Fryxell, J. M., and A. R. E. Sinclair. 1988*a*. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution **3:**237–241.

Fryxell, J. M., and A. R. E. Sinclair. 1988*b*. Seasonal migration by white-eared kob in relation to resources. African Journal of Ecology **26:** 17–31.

Fuller, T. K., and L. B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management **45:**197–213.

Garrot, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Allredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management. **51:**634–643.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs **84**.

Gasaway W. C., et al. 1996. Persistent low densities of plain's ungulates in Etosha National Park, Namibia: testing the food regulation hypothesis. Canadian Journal of Zoology **84:**1556–1572.

Gittleman, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. The American Naturalist **127:**744–771.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia **87:**343–348.

Gray, D. R. 1979. Movements and behavior of tagged muskoxen (*Ovibos moschatus*) on Bathurst Island, Northwest Territories, Canada. Musk-Ox **25:**29–46.

Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice. BioScience **52:**499–512.

Gruel, G. E., and N. J. Papez. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Management **27:**414–422.

Hamlin, K. L., and Mackie, R. J. 1989. Mule deer: population ecology in a fluctuating environment. Job completion report. Federal aid W-120-R. Montana Fish, Wildlife, and Parks, Helena.

Hansen, C. G. 1965. Management units and bighorn sheep herds on the Desert Game Range, Nevada. Desert Bighorn Council Transactions. **9:**11–14.

Haugen T. M., and L. B. Keith. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management **45:**573–597.

Hofer, H., and M. East. 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. Pages 332–363 in A. R. E. Sinclair and P. Arcese, editors. Seregenti II. University of Chicago Press, Chicago.

Hoskinson, R. L., and J. R. Tester. 1980. Migration behavior of pronghorn in southeastern Idaho. Journal of Wildlife Management **44:**132–144.

Houston, D. B., E. G. Schreiner, B. B. Moorhead, and K. A. Krueger. 1990. Elk in Olympic National Park: will they persist over time? Natural Areas Journal **10:**6–11.

Johnson, R. L. 1980. Mountain goats and mountain sheep of Washington. Biological Bulletin (Washington) **18:**1–196.

Joubert, E. 1972. The social organization and associated behaviour in the Hartmann zebra, *Equus zebra hartmannae*. Madoqua **6:**17–56.

Kahurrananga, J., and F. Silkiluwasha. 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania in 1972 and recent trends. African Journal of Ecology **35:**179–185.

Knight, R. R. 1970. The Sun River elk herd. Wildlife Monographs **23**.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1989. Distribution and movements of female mule deer in the Rocky Mountain foothills. Journal of Wildlife Management **53:**871–877.

LeResche, R. E. 1974. Moose migration in North America. Naturaliste Canada **101:**393–415.

Leslie, D. M., and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildlife Monographs **66**.

Loft, E. R., J. W. Menke, and T. S. Burton. 1984. Seasonal movements and summer habitats of female black-tailed deer. Journal of Wildlife Management **48:**1317–1325.

Mahoney, S. P., and J. A. Schaefer, 2002. Hydroelectric development and the disruption of migration in caribou. Biological Conservation **107:**147–153.

Maier, T. J. 2002. Long-distance movements by female white-footed mice, *Peromyscus leucopus*, in extensive mixed wood forest. Canadian Field Naturalist **116:**108–111.

Mauer, F. J. 1998. Moose migration: northeast Alaska to western Yukon Territory, Canada. Alces **34:**75–81.

McCorquodale, S. M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management **63:**861–871.

McCullough, D. R. 1985. Long range movements of large terrestrial mammals. Contributions to Marine Science **27:**444–465.

McNaughton, S., and F. F. Banyikawa. 1995. Plant communities and herbivory. Pages 49–70 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago.

McQuivey, R. P. 1976. The status and trend of desert bighorn sheep in Nevada: McCullough Mountains. Federal aid, job report. Nevada Fish and Game, Reno.

Meagher, M. 1973. The bison of Yellowstone National Park. National Park Fauna Series **1:**1–161.

Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. Journal of Mammalogy **70:**670–675.

Merkt, J. R. 1987. Reproductive seasonaility and grouping patterns of the North Andean deer or Taruca (*Hippocamelus antisensis*) in southern Peru. Pages 388–401 in C. M. Wemmer, editor. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C.

Miller, M. E., and P. H. Saunders. 2000. The Trapper's Point site (48SU1006): early Archaic adaptations and pronghorn procurement in the Upper Green River Basin, Wyoming. Plain's Anthropologist **45:**39–52.

Milner-Gulland, E. J., M. V. Kholodova, A. Bekenov, O. M. Bukreeva, I. A. Grachev, L. Amgalan, and A. A. Lushchekina. 2001. Dramatic decline in saiga antelope populations. Oryx **35:**340–345.

Mitchell, G. J. 1980. The pronghorn antelope in Alberta. Alberta Department of Energy and Natural Resources, Edmonton.

Morgantini, L. E., and R. J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Canadian Field Naturalist **102:**12–19.

Murray, M. G. 1995. Specific nutrient requirements and migration of wildebeest. Pages 31–56 in A. R. E. Sinclair, and P. Arcese, editors. Seregenti II. University of Chicago Press, Chicago.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs **77**.

Newmark, W. D. 1987. Mammalian extinctions in western North American parks: a land-bridge island perspective. Nature **325:**430–432.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology **9:**512–526.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: trade-offs associated with migration. Journal of Mammalogy **78:**483–504.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology **16:**895–908.

Ockenfels, R. A., C. L. Alexander, C. Ticer, and W. K. Carrel. 1994. Home ranges, movement patterns, and habitat selection of pronghorn in central Arizona. Technical report 13. Arizona Game Fish, Phoenix.

Ortega I. M., and W. L. Franklin. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural **68:**489–500.

Osborn, F. V., and G. E. Parker. 2003. Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. African Journal of Ecology **41:** 68–74.

Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns for mountain lions: implications for social regulation and conservation. Journal of Mammalogy **80:** 986–992.

Pilliod, D. S., C. R. Peterson, and P. I. Ritson. 2002. Season migration of Columbian spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. Canadian Journal of Zoology **80:**1849–1860.

Rankin, M. A., editor. 1985. Migration: mechanisms and adaptive significance. Contributions to Marine Science **27:**1–868.

Reynolds, P. E. 1998. Dynamics and range expansion of a re-established muskoxen population. Journal of Wildlife Management **62:**734–744.

Roe, F. G. 1970. The North American buffalo, University of Toronto Press, Toronto.

Rudd, W. J., A. L. Ward, and L. L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? Wildlife Society Bulletin **11:**328–331.

Sandgren, F., and P. Y. Sweanor, 1998. Migration distance of moose populations in relation to river drainage length. Alces **24:**112–117.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002*a*. The human footprint and the last of the wild. BioScience **52:**891–904.

Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002*b*. A conceptual model for conservation planning based on landscape species requirements. Landscape and Urban Planning **58:**41–56.

Sawyer, H., and F. Lindzey. 1999. Sublette Mule deer study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie.

Sawyer, H., and F. Lindzey. 2000. Jackson Hole pronghorn study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie.

Sawyer, H., F. Lindzey, D. McWhirter, and K. Andrews. 2002. Potential effects of oil and gas development on mule deer and pronghorn populations in western Wyoming. Transactions of the North American Wildlife and Natural Resource Conference **67:**350–365.

Schaller, G. B. 1998. Wildlife of the Tibetan steppe. University of Chicago Press, Chicago.

Schoen, J. W., and M. D. Kirchhoff. 1985. Seasonal distribution and home range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. Journal of Wildlife Management. **49:**96–103.

Schullery, P., and L. Whittlesey. 1995. Summary of the documentary record of wolves and other wildlife species in the Yellowstone National Park area prior to 1882. Pages 63–76 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.

Semmens, W. J. 1996. Seasonal movements and habitat use of the Highland/Pioneer Mountains bighorn sheep herd of southwest Montana. Symposium of Northern Wild Sheep and Goat Council **10:**35–44.

Simberloff, D. J., A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology **6:**493–504.

Sinclair, A. R. E., 1983. The function of distance movements in vertebrates. Pages 240–258 in I. R. Swingland and P. J. Greenwood, editors. The ecology of animal movements. Oxford University Press, Oxford, United Kingdom.

Sinclair, A. R. E., and P. Arcese. 1995. Serengeti in the context of worldwide conservation efforts. Pages 31–46 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago.

Smith, B. L., and R. L. Robbins. 1994. Migrations and management of the Jackson Elk herd. Technical report series. Research Bulletin **199**. United States Department of Interior, Washington, D.C.

Smith, G. W., L. C. Stoddardt, and F. F. Knowlton. 2002. Long-distance movements of black-tailed jackrabbits. Journal of Wildlife Management **66:**463–469.

Sukumar, R. 1989. The Asian elephant: ecology and management. Cambridge University Press, Cambridge, United Kingdom.

Tchamba, M. N. 1993. Number and migration patterns of savanna elephants (*Loxodonta africana africana*) in Northern Cameroon. Pachyderm **16:**66–71.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology **65:**1828–1834.

Thompson, M. E., J. R. Gilbert, G. J. Matula, and K. I. Morris. 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. Alces **31:**233–245.

Thoules, C., and A. Dyer. 1992. Radio-tracking of elephants in Laikipia District, Kenya. Pachyderm **15:**34–39.

Uselman, S. 1998. ONDA proposes Pronghorn ACEC. Oregon Natural Desert Association **11:**1, 3.

Van Ballenberghe, V. 1977. Migratory behavior of moose in southcentral Alaska. International Congress of Game Biologists **13:**103–109.

Van Deelen, T. R., H. Campa III, M. Hamady, and J. B. Hausfler. 1998. Migration and seasonal range dynamics of deer using adjacent deer yards in northern Michigan. Journal of Wildlife Management **62:**205–213.

Van Vuren, D., and M. P. Bray 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 506–511.

Verlinden, A., and I. K. N. Gavor. 1998. Satellite tracking of elephants in northern Botswana. African Journal of Ecology **36:**105–116.

Waithaka, J. M. 1994. The ecological role of elephants in restructuring habitats. Ph.D. dissertation. Kenyatta University, Nairobi.

Walton, L. R., H. D. Cluff, P. C. Paquet, and M. A. Ramsey. 2001. Movement patterns of barren-ground wolves in the central Canadian Arctic. Journal of Mammalogy **82:**867–876.

Wilcove, D. S. 1999. The condor's shadow. W. H. Freeman, New York.

Williamson, D. 1997. The future of antelope migrations in a changing physical and socio-economic environment. Pages 59–68 in Proceedings of a convention on migratory species. United Nations Environmental Programme, Bonn.

Williamson, D., J. Williamson, and K. T. Ngwamotsoko. 1988. Wildebeest migration in the Kalahari. African Journal of Ecology **26:**269–280.

Wood, K. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Monograph. Montana Department of Fish, Wildlife, and Parks, Helena.

Wyoming Outdoor Council. 2000. Frontline report: saving the Red Desert: 50,000 antelope can't be wrong. Wyoming Outdoor Council, Lander, Wyoming. Available from www.wyomigoutdoorcouncil.org (accessed September 2002).

Zallunardo, R. A. 1965. The seasonal distribution of a migratory mule deer herd. Journal of Wildlife Management **29:**345–351.

Appendix 1. Summary of estimated round-trip migration by species, population, and site.

Species	*Scientific name*	*Location*	*Mean (km)*[a]	*Longest (km)*	*Reference*
Cougar	*Felis concolor*	Sierra Nevada, CA, USA	60		Pierec et al. 1999; V. Bleich, personal communication
Coyote	*Canis latrans*	Jackson Hole, WY, USA	70	80	K. Berger, unpublished data
Wolf	*Canis lupus*	Brooks Range, AK USA	370		Ballard et al. 1997
		Bathhurst region, NWT, Canada	743		Walton et al. 2001
Spotted hyena	*Crocuta crocuta*	Serengeti, Tanzania	120	160	Hofer & East 1995
Elk	*Cervus elaphus*	Banff, AB, Canada	73	138	Mogantini & Hudson 1988
		Yellowstone, WY, USA	70	220	Craighead et al. 1972
		Olympic, WA, USA	60		Houston et al. 1990
		Selway Drainage, ID, USA	<64		Dalke et al. 1965
		Sun River, MT, USA	96		Knight 1970
		Absaroka Divide, WY, USA	90		Rudd et al. 1983
		Jackson Hole, WY, USA	200	220	Smith & Robbins 1994
White-tailed deer	*Odocoileus virginianus*	Algonquin, ON, Canada	60		Forbes & Theberge 1995
		Cheery Creek, MT, USA	14	26	Wood et al. 1989
		Hiawatha Forest, MN, USA	10		Van Deelen et al. 1998
		Superior Forest, MN, USA	34		Nelson & Mech 1981
Mule deer	*Odocoileus hemionus*	Green River Basin, WY, USA	168	288	Sawyer & Lindzey 1999; Sawyer et al. 2002
		Salmon-Trinity Alps, CA, USA	42	70	Loft et al. 1984
		Cheery Creek, MT, USA	11		Wood et al. 1989
		Missouri River Breaks, MT, USA	12		Hamlin & Mackie 1989
		Klickkitat Basin, WA, USA	56		McCorquodale 1999
		Great Basin, NV, USA	141	280	Gruel & Papez 1963
		Silver Lake, OR, USA	60	256	Zallunardo 1965
		Piceance Basin, CO, USA	65	220	Garrot et al. 1987
		Lory State Park, CO, USA	58		Kufeld et al. 1989
		Transverse Ranges, ID, USA	52		Brown 1992
		Paunsaugunt Plateau, UT, USA	102	144	Carrel et al. 1999
		Kaibab Plateau, AZ, USA	45	116	Carrel et al. 1999
		Round Valley, CA, USA	134	192	Pierec et al.1999; V. Bleich, personal communication
		Admiralty Isle, AK, USA	15	90	Schoen & Kirchhoff 1985
		San Bernadino Mountains, CA, USA	23		Nicholson et al. 1997
Moose	*Alces alces*	Old Crow, YT, Canada	246	392	Mauer 1998
		Lower Koyukuk, AK, USA	84	136	Mauer 1998
		Upper Susitna, AK, USA	96	186	Ballard et al. 1991
		White Mountains, AK, USA	130	204	Mauer 1998
		Nelchina Basin, AK, USA	70	220	Van Ballenberghe 1977
		North Slope, YT, Canada	194	276	Mauer 1998
		Tanana Flats, AK, USA	120	280	Gasaway et al. 1983
		northeast Alberta, Canada	40		Haugen & Keith 1981
		Sorsele, Sweden	220	310	Sandgren & Sweanor 1998
		Slussfors, south Sweden	46		Sandgren & Sweanor 1998[b]
		Hornefors, Sweden	41		Sandgren & Sweanor 1998
		Klitten, Sweden	42		Sandgren & Sweanor 1998
		Tennanget, Sweden	68		Sandgren & Sweanor 1998
		Furudal, Sweden	156		Sandgren & Sweanor 1998
		Stottingfjallet, Sweden	118		Sandgren & Sweanor 1998
		Trehorningsjo, Sweden	149		Sandgren & Sweanor 1998
		Slussfors, north Sweden	144		Sandgren & Sweanor 1998
		Nordheden, Sweden	196		Sandgren & Sweanor 1998
		Rosvik, Sweden	66		Sandgren & Sweanor 1998
		Mooseleuk and St. Croix, ME, USA	14		Thompson et al. 1995
		northwest Minnesota, MN, USA	20		LeResche 1974
		northeast Minnesota, MN, USA	12		LeResche 1974
		Gravelly Mountains, MT, USA	14		LeResche 1974
		Teton, WY, USA	61	114	J. Berger, unpublished data
Musk ox	*Ovibos moschatus*	Bathurst Isle, NT, Canada	0		Gray 1979
		Arctic Refuge, AK, USA	0		Reynolds 1998
Caribou[c] (barren-ground)	*Rangifer tarandus*	Arctic Refuge, AK, USA	4355	5055	Fancy et al. 1988
		Central Arctic, AK, USA	3031		Fancy et al. 1988
		Baffin Isle, Canada	800		Ferguson & Messier 2000
Caribou (woodland)	*Rangifer tarandus*	Grand Cache, AB, Canada	136	300	Edmonds 1988
		Birch Mtn, Alberta, Canada	56	142	Fuller & Keith 1981
		Lake Nipigon, ON, Canada	92	160	Cumming & Beange 1987
		Aikens Lake, Manitoba, Canada	0		Darby & Pruitt 1984
Bison	*Bison bison*	Yellowstone, WY, USA	44		Meagher 1973, 1989
		Grand Teton, WY, USA	70	75	Cain et al. 2001
		Henry Mountains, UT, USA	50		Van Vuren & Bray 1986

continued

Appendix 1. (continued)

Species	*Scientific name*	*Location*	*Mean (km)*[a]	*Longest (km)*	*Reference*
Bighorn	*Ovis canadensis*	McCullough Mountains, NV, USA	60	64	McQuivey 1976
		River Mountains, NV, USA	7		Leslie & Douglas 1979
		Highland Mountains, MT, USA	19		Semmens 1996
		Salmon River Mountains, ID, USA	74	75	Akenson & Aksenson 1994
		Sheep Range, NV, USA	32		Hansen 1965
Mountain goat	*Oreamos americanus*	Mount Baker, Washington	12		Johnson 1980
		Barometer Mountain, WA, USA	29	29	Johnson 1980
Pronghorn	*Antilocapra americana*	Upper Snake River Plain, ID, USA	89		Hoskinson & Tester 1980
		Wupatki, AZ, USA	30		Bright & Van Riper 2000
		Cordes Junction, AZ, USA	30	80	Ockenfels et al. 1994
		Mingus Mountain, AZ, USA	26	40	Ockenfels et al. 1994
		Saskatchewan, Canada	220		Mitchell 1980
		Red Desert, WY, USA	128	164	Deblinger 1980
		Tetons, WY, USA	434	548	Sawyer & Lindzey 2000; Sawyer et al. 2002
Huemal	*Hippocamelus bisulcus*	Patagonia, Argentina	6		Diaz & Smith-Fluek 2000
Pudu	*Pudu puda*	Islote Rupanco, Chile	0		Eldridge et al. 1987
Taruca	*Hippocamelus antisenis*	La Roya, Peru	0		Merkt 1987
Guanaco	*Lama guanicoe*	Torres del Paine, Argentina	0		Franklin 1982
		Patagonia, Chile	24		Ortega & Franklin 1995
Vicuna	*Vicugna vicugna*	Pampa Galeras, Peru	0		Franklin 1982
Mountain tapir	*Tapirus pinchaque*	Sangay, Ecuador	9	10	Downer 1996, 1997
Mongolian gazelle	*Procapra gutturrosa*	Dornab, Mongolia	500		J. Ginsberg, personal communication
White-eared kob	*Kobus kob*	Sudd Region, Sudan	700		Fryxell & Sinclair 1988*b*
Wildebeest	*Connochaetes taurinus*	Serengeti, Tanzania	600–800		Murray 1995 & Web sites[d]
		Kalahari, Botswana	550		Williamson et al. 1988
		Tarangire, Tanzania	120		Kahurananga & Silkiluwasha 1997
Springbok	*Antidorcas marsupialis*	Karoo, South Africa	360, one way		Child & LeRiche 1967
Chiru	*Pantholops hodgsoni*	Chang Tang, China	600		Schaller 1998
Mountain zebra	*Equus zebra*	Namib Desert, Namibia	240		Joubert 1972
Plain's zebra	*Equus burchelli*	Tarangire, Tanzania	110		Kahurananga & Silkiluwasha 1997
Elephant	*Loxodonta africana*	northern Botswana	200		Verlinden & Gavor 1998
		Laikipia District, Kenya	200		Thoules & Dyer 1992
		Kalamalove Park, Cameroon	240		Tchamba 1993
		Waza Park, Cameroon	200		Tchamba 1993
Giraffe	*Giraffa camelopadia*	northern Serengeti	80		P. Arcese, personal communication
Black-tailed jackrabbit	*Lepus californicus*	Curlew Valley, UT, USA	12		Smith et al. 2002

[a] *Mean is the estimated round-trip distance (km) for migratory segment; otherwise, all data for that population are averaged.*

[b] *Based on means of four longest migration distances.*

[c] *Estimates are total annual movements (based on satellite data), but those in text reflect means between average annual home ranges (seasonal) in brochures of the U.S. Fish and Wildlife Service (Arctic National Wildlife Refuge).*

[d] *Web site: www.africaencounters.com/tanzania/serenget.htm; www.awf.org/wildlives/4547.*