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REVIEW

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Global decline in aggregated migrations of large terrestrial mammals

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ABSTRACT: Knowledge of mammal migrations is low, and human impacts on migrations high. This jeopardizes efforts to conserve terrestrial migrations. To aid the conservation of these migrations, we synthesized information worldwide, describing 24 large-bodied ungulates that migrate in aggregations. This synthesis includes maps of extinct and extant migrations, numbers of migrants, summaries of ecological drivers and threats migrants confront. As data are often lacking, we outlined steps for science to address and inform conservation actions. We evaluated migrants against this framework, and reported their status. Mass migrations for 6 species are extinct or unknown. Most remaining migrants (n = 9) occur from 6 locations in Africa, with Eurasia and North America containing 6 and 4 remaining mass migrants, respectively (with caribou/reindeer *Rangifer tarandus* occurring in both regions). All migrants declined in abundance, except wildebeest and other migrants in the Serengeti-Mara Ecosystem (SME), white-eared kob and tiang in Sudan, and some caribou populations. Protected areas only contain migrations for 5 species in the SME, chiru on the Tibetan Plateau, and some caribou populations in North America. Most mass migrants track the seasonal and shifting patterns of greening vegetation over expanses of savannahs, steppes, and grasslands. Principal threats include overhunting and habitat loss from livestock, agriculture, and fencing that excludes animals from forage or water. Conservation science overlooks numerous migrations, so many have already disappeared and continue to do so. Key principles for conserving migrants, exemplified by the SME and Greater Yellowstone Ecosystem (GYE), include securing seasonal ranges, resource protection, government support and minimizing fences. This review forms a baseline for initiating conservation action for many ungulate migrations needing attention.

KEY WORDS: Mammals · Migration · Aggregation · Serengeti-Mara · Yellowstone · Ungulate · Global audit

INTRODUCTION

Migration, the seasonal and round-trip movement of animals between discrete areas (Berger 2004, Thirgood et al. 2004), is a behavior common to a diversity of taxa (Dingle 1996). A few migrations are well known, such as the movements made by 1.3 million wildebeest *Connochaetes taurinus* in the Serengeti-Mara Ecosystem (SME) of Tanzania and Kenya (Thirgood et al. 2004). Other migrations are obscure, such as those car-

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ried out by eland *Tragelaphus oryx* in Botswana (C. Thouless unpubl. data, R. Brett pers. comm.). Overall, our knowledge of migrations is low (Berger 2004), and human impact high (Vitousek et al. 1986, Pimm et al. 2001); this jeopardizes the conservation of many migratory species (Berger 2004).

Conservationists worry about the persistence of migrations (Wilcove & Wikelski 2008). Some issues are ecological, as mass migrants have positive feedback effects on grassland forage and indirect effects on ecosystem processes (e.g. increasing grassland production and raising nitrogen mineralization) (Caughley 1976, McNaughton et al. 1988, Frank 1998), and therefore losing migrations may result in ecosystem collapse. Economics also plays a part. For example, were there no wildebeest migration in the SME, herbivore populations would almost certainly decline, carnivore populations would follow, and Serengeti would lose tourism dollars. Without financing, resource protection would slacken and the natural ecosystem would disintegrate, as livestock, agriculture and other developments replaced it. Ethical issues are also involved. Eradicating migrations and relegating migrants to zoos or fenced parks represents one of the worst examples of destructive human impact. Their senseless destruction by a shortsighted few causes long-term losses in the natural spectacles for many. Humanity can and should advance society while maintaining such migrations.

Unfortunately, conservationists are largely unaware of which migrations are lost, which ones remain, the factors threatening the remainder, and tangible management solutions to protect the phenomenon. Consequently, we audited 24 large mammals that migrate or migrated in aggregations to evaluate their conservation status. Our efforts involved 6 components: (1) Preserving migrations means knowing where they remain and where they have been lost. Therefore, we mapped locations for extant and extinct aggregated migrations. (2) We summarized attributes pertinent for their conservation, namely the number of animals migrating and the distances traveled. (3) Conserving migrations requires knowing why they occur, so we examined ecological drivers. Site-specific studies of migratory ungulates identify the importance of gradients in rainfall, forage growth, and nutrient availability in driving seasonal migrations (Fryxell & Sinclair 1988a, Murray 1995, Boone et al. 2006). We investigated whether such resource gradients are widespread phenomena in migratory ecosystems. (4) We synthesized threats facing these migrations, examined their commonalities, and reported their consequences. (5) We evaluated all sources in a 6-step framework and reported the state of knowledge necessary to conserve these migratory species. (6) We described actions necessary to sustain mass migrations by exemplifying successes learned elsewhere. Overall, we provide a baseline for guiding and catalyzing conservation action for many migrations needing attention.

MATERIALS AND METHODS

We concentrated on terrestrial mammals with body mass >20 kg (Morrison et al. 2007). We then determined which species (including subspecies) are, or once were, migratory in aggregated masses. We defined an 'aggregation' as hundreds to thousands of animals that move or once moved in masses. We do not specify a clear threshold for group size or migratory distances.When mass migrations decline, the numbers of migrants and the distances traveled often fall. Quantifying a threshold requires credible historic and current data, which is lacking for most species and systems.

Given that most species have not been studied with respect to migration per se, we began with 'Walkers Mammals of the World' (Nowak 1999), with supplementary information for 20 African species (Estes 1991). Despite their shortcomings, these sources review the distribution, population status and natural history of these species. We used them to list mammals that migrate in aggregations, once migrated, or lack concrete data but for which natural history suggested potentially migratory behavior. For these species, we then examined scientific literature to determine where (or if) aggregated migrations remain, and information describing their attributes. Searches used 'Web of Science' and 'Google Scholar' engines, with terms including the species common name and scientific name alone or in combination with the word 'migration'. We also consulted gray literature, websites, scientists and game managers familiar with target species. From these sources, we digitized migratory areas based on their geographical locations, and summarized attributes, ecological drivers and threats for each migratory species.

Conserving mass migrations requires descriptive data, information to evaluate their status, and collaborations to foster their protection. This process forms a 6-step framework: (1) Mapping species movements to determine the locations that migrants go, and the routes taken to get there. (2) Determining migrants' habitat needs, namely seasonal ranges and transition areas between these ranges. (3) Mapping migratory habitats to determine their geographical location, and evaluating how much remains. (4) Identifying the factors threatening the sustainability of migratory habitats (or the migrants themselves), and where these threats are or are likely to occur. (5) Determining how much of the migratory route and migratory habitat is required to maintain a given population objective to ensure the sustainability of the mass migration. This should account for neighboring land uses and threats to routes or habitat. (6) Work with partners, wildlife managers, policy makers and opposing interest groups to better manage and conserve mass migrants, routes and habitat.

While these steps generally progress with increasing knowledge and details on migrations, some can be taken before completing previous steps. For example, Step 4 may happen without full knowledge covering Steps 1 to 3. Ideally, all 6 steps require scientific approaches, and if applicable, results should be presented in peer-reviewed literature. Steps 1 to 5 are relatively consistent between migratory systems, while Step 6, which seeks solutions, will likely vary depending on the species, situation and site.

We evaluated available sources describing mass migrants against this framework. Values represent our interpretation and we present them as relative measures. Results illustrate the state of information pertinent for conserving these migratory species.

RESULTS

Global audit

Twenty-four large mammal species (and subspecies) are known to migrate or to have migrated in aggregations — all ungulates. Mass migrations for 6 of these are extinct or their status unknown: springbok *Antidorcas marsupialis*, black wildebeest *Connochaetes gnou*, blesbok *Damaliscus dorcas*, kulan *Equus hemionus*, scimitar horned oryx *Oryx dammah*, quagga *Equus quagga*. Most migratory populations lack reports on their numbers, distances traveled, geographical routes, ecological drivers and threats. Where data exist, they are often over a decade old (Tables 1 & 2).

We plotted the geographical locations where aggregated migrations remain and, when documented, those lost (Figs. 1 & 2). Most migrants are African (n = 14). Migrations for the 9 remaining migrants occur in just 6 locations (Boma-Jonglei, Sudan; Serengeti-Mara Ecosystem, Tanzania/Kenya; Tarangire, Tanzania; Liuwa, Zambia/Angola; Chobe, Botswana and; Kalihari, Botswana) (Fig. 1). Protected areas in Africa only enclosed migrations within the SME. There are reports on 7 aggregated migrants (6 with migrations remaining) for Eurasia, and 4 for North America, with caribou/ reindeer *Rangifer tarandus* in both (Tables 1 & 2). Protected areas largely contain migrations of chiru *Pantholopos hodgsoni* on the Tibetan Plateau and some caribou populations in North America (Fig. 2). South America and Australia lack reports of mass migrations.

Ecological drivers

The ecological drivers of mass migrations and the threats that migrations confront are connected, as threats disable the drivers. Hence, we must first understand why mass migrations occur, in order to identify the threats, appreciate how they work, and arm ourselves to alleviate or pre-empt them. We identified 4 dominant factors driving mass migrations: seasonal availability of forage (quality/quantity), snow depth, use of traditional areas, and surface water availability. Forage moisture, a fifth factor related to forage quality, was only specifically documented for pronghorn *Antilocarpa americana*.

Migrants move from locations where food quality and quantity is poor or inaccessible to places where it is more abundant, nutritious and available. Most migrants seek young grass, because this is most digestible and high in protein (Hanley 1982). The quality and quantity of grass depends on the availability of water (rain in tropical and temperate savannas and grasslands, snowmelt in northern mountains and plains), which varies in timing, amount, and distribution across these species' ranges (Deshmukh 1984, Williamson et al. 1988). Animals track the seasonal and shifting distribution of their forage ('green flushes') and therefore become migratory (our Table 2, McNaughton 1985, Fryxell & Sinclair 1988a, Morgantini & Hudson 1988, Murray 1995, Boone et al. 2006, Mueller et al. 2008). This driver explains the movements of 17 migrants. When rainfall is the determining factor, this type of migration occurs in all of the African migrants for which we have data, and also for saiga *Saiga tatarica*, Mongolian gazelle *Procapra gutturosa*, kulan and pronghorn. Snowmelt across elevation gradients and the resulting vegetation response influences the movements of bison *Bison bison*, elk *Cervus elaphus* and caribou. Early references describe this qualitatively, with recent material quantifying the response (Table 2).

Deep snow obstructs migrants' access to forage in winter months. This driver affects migratory patterns in all of the North American and Eurasian migrants, by forcing them to move toward lower elevations or latitudes (Table 2). As above, migrants reverse movements during snowmelts, to capitalize on greening flushes of vegetation.

Changes in resource availability can be predictable or unpredictable, resulting in different migratory responses. The distribution of snow across elevations and interior (continental) regions is relatively predictable. Animals can conform to this regularity and become habituated to areas where forage is reliable over time. Hence, half of the northern migrants use traditional routes and ranges, often spanning generations

Table 1. Summary of historic and current aggregated migrations for terrestrial mammals, including distances traveled, numbers of migrants, and sources reporting non-migratory populations. The column, 'Mass migration', shows the location of migrants in Figs. 1 & 2 (no. in **bold** before literature source). Literature sources and geographical locations of migrations (in parentheses) given after

Scientific name	Common name	Location	Mass migration	
			Current	Historic
Alcelaphus buselaphus	Hartebeest	Africa	**1 -** Skinner & Smithers (1990) (Botswana)*, Estes (1991)*, **2 -** Verlinden (1998) (Kalahari, Botswana), **3 -** (1) (Kalahari, Botswana)*	**4 -** Swayne (1894) (Somalia), **5 -** Foster & Kearney (1967) (Nairobi, Kenya), **6** - (2) (Tsavo, Kenya)*, Skinner & Smithers (1990) (Botswana)*, (1) (Kalahari, Botswana)*, **7 -** (2) (Voi-Tsavo-Athi, Kenya)*
Antidorcas marsupialis	Springbok	Africa	**8 -** Skinner (1993) (Botswana (?)	Child & LeRiche (1969) (Botswana), Skinner (1993) (Namibia, South Africa), Skinner & Louw (1996) (Botswana, Namibia, South Africa)*, Skinner & Chimimba (2005) (South Africa)*
Connochaetes gnou	Black wildebeest	Africa		**9 -** Estes (1991) (South Africa)*, **10 -** Skinner & Smithers (1990) (South Africa)*, Estes (1991) (South Africa)*, Skinner (1993), Skinner & Chimimba (2005) (South Africa)*
Connochaetes taurinus	Blue wildebeest	Africa	**11 -** Williamson et al. (1988) (Kalahari, Botswana), **12 -** Skinner & Smithers (1990) (Kalahari, Botswana)*, Bonifica (1993) (Kalahari, Botswana)*, **13 -** Kahurananga & Silkiluwasha (1997) (Tarangire National Park, Tanzania), **14 -** Verlinden (1998) (Kalahari, Botswana), (1) (Kalahari, Botswana)*, **15 -** Homewood et al. (2001) (Serengeti-Mara, Tanzania & Kenya), **16 -** Ottichilo et al. (2000) (Masai Mara, Kenya), **17 -** Serneels & Lambin (2001) (Serengeti-Mara, Tanzania & Kenya) , **18 -** Thirgood et al. (2004) (Serengeti, Tanzania), **19 -** (2) (Amboseli, Kenya)*, **20 -** (3) (Angola & Zambia)*, **21 -** (4) (Chobe, Botswana)*	**22 -** Berry (1997) (Etosha, Namibia), **23 -** Foster & Kearney (1967) (Nairobi, Kenya), Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*, Borner (1985) (Tarangire, Tanzania), **24 -** Whyte & Joubert (1988) (Kruger, South Africa), Gasaway et al. (1996) (Etosha, Namibia), Thirgood et al. (2004), (2) (Amboseli - Nairobi)*, **25 -** (5) (Voi-Tsavo-Athi)*,
Damaliscus dorcas	Blesbok	Africa		**26 -** Estes (1991) (South Africa)*, Skinner & Smithers (1990) (South Africa)*, Estes (1991) (South Africa)*, Skinner & Chimimba (2005) (South Africa)*
Damaliscus lunatus	Tiang (topi)	Africa	**27 -** East (1999)*, (6) (Boma-Jonglei, Sudan)*	East (1988)*
Equus burchellii	Burchell's zebra	Africa	**28 -** Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*, **12 -** Skinner & Smithers (1990) (Kalahari, Botswana)*, **13 -** Kahurananga & Silkiluwasha (1997) (Tarangire National Park, Tanzania), **20 -** (3) (Angola & Zambia)*, (7) (Botswana)*, (4) (Botswana)*	Grzimek & Grzimek (1960) (Kruger, South Africa), Ebedes (1970) (Etosha, Namibia)*, Smuts (1972) (Kruger, South Africa)*, Sinclair & Norton-Griffiths (1979)*, **29 -** Whyte & Joubert (1988) (Kruger, South Africa), **30 -** Gasaway et al. (1996) (Etosha, Namibia), Kahurananga & Silkiluwasha (1997), **31 -** (2) Lake Nakuru - Laikipea (Kenya)*, **25 -** (5) (Voi-Tsavo-Athi)*
Equus quagga quagga	Quagga	Africa		**32** - Estes (1991) (South Africa)*, Estes (1991) (South Africa)*, Skinner & Chimimba (2005) (South Africa)*
Gazella thomsonii & G. t. albonotata	Thompson's gazelle & Mongalla gazelle	Africa	**33 -** Campbell & Borner (1995) (Serengeti-Mara, Tanzania & Kenya)*, East (1999) (Boma-Jonglei, Sudan)*, **27 -** (6) (Boma-Jonglei, Sudan)*	**34 -** (2) Lake Nakuru - Laikipea (Kenya)*
Kobus kob	White-eared kob	Africa	**35 -** East (1999) (Boma-Jonglei, Sudan)*, **27 -** (6) (Boma-Jonglei, Sudan)*	Fryxell & Sinclair (1988b)
Nanger granti	Grant's gazelle	Africa	**28 -** Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*, Estes (1991) (Serengeti, Tanzania)*	Walther (1972) (Serengeti, Tanzania), Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*

sources. The numbers 1 to 18 in parentheses indicate an unpublished source, listed as a footnote to the table. An asterisk indicates literature which may not have undergone peer review

Current migration distance (round trip, km)	Historic migration distance (round trip, km)	Numbers migrating		Non-migratory reference
		Current	Historic	
Inferred ~400 (Skinner & Smithers 1990)*	?	~40 000 (Botswana, Verlinden 1998) ~34000 (1)*	1000s (Eastern & Southern Africa) Swayne (1894) , 10 000+ (Botswana, Smithers 1971)	Estes (1991)*, Murray & Brown (1993)
~20. Presently, most likely 0 (Skinner 1993)	?	Cited in Skinner (1993) (2000–3000 [Namibia] Wakefield 1988), one 600 (if it remains) (Skinner 1993)	15 000 (Kalahari) Child & le Riche (1969). Following cited in Skinner (1993): 100 000 (Karoo) Thompson (1827), 5000–15 000 (Karoo) Barrow (1804), 40 000 (Kalahari) Livingstone (1857)	Skinner (1993), Gasway et al. (1996)
0 (Estes 1991)*	?	0 (Estes 1991)*	100 000s - Skinner & Smithers (1990), 1000s - South Africa's Karoo (Skinner 1993)	Estes (1991)*
200–600 (Verlinden 1998), ~600 (calculated from Thirgood et al. 2004), 400 (3)*, ~200 (Sinclair & Arcese 1995 - Serengeti-Mara, Tanzania & Kenya)*	400–600 (Williamson et al. 1988), ~480 (1960s) calculated from Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*	1.3 million (Sinclair & Arcese 1995)*, 8000–16 000 (Verlinden 1998), 25 000 (Serneels & Lambin 2001, Homewood et al. 2001, Ottichilo et al. 2001), ~25 000 (3)*	~60 000 (Botswana — inferred from Verlinden 1998); 10 000 (between 1970–1972; Kahurananga 1981), 3000–7000 (1960–1970s; Sinclair & Norton-Griffiths 1979) (Serengeti, Tanzania)*, 6000 (Whyte & Joubert 1988) (Kruger)	Thirgood et al. (2004)
0 (Estes 1991)*	?	0 (Estes 1991)*	1000s - South Africa's Karoo (Skinner & Smithers 1990, Skinner 1993), 1000s (Estes 1991)*	Estes (1991)*
?	?	~150 000 (East 1988)*, 360 000 (East 1999)*, ~160 000 (6)*	?	Skinner & Smithers (1990)*, Ottichilo et al. (2000)
200 inferred (Sinclair & Norton-Griffiths 1979)*, 110 (Kahurananga & Silkiluwasha 1997), 400 (3)*	~240 calculated from Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*, 200–320 Namibia (Ebedes 1972) 400+ (Grzimek & Grzimek 1960), (Serengeti)	200 000 (Sinclair & Arcese 1995)*, 3000 (3)*, ~10 000 (18) Tarangire)*	6000 (between 1970–1972 - Kahurananga 1981), 23 000 (in 1955) (Gasaway 1996) (Etosha), ~200 000 1960–1970 (Sinclair & Norton-Griffiths 1979)	Estes (1991)*
0 (Hack et al. 2002)*	?	0 (Hack et al. 2002)*	1000s - South Africa's Karoo (Skinner 1993)	Extinct (Hack et al. 2002)*
~200 (Campbell & Borner 1995*, Fryxell et al. 2004, 2005)	~160 calculated from Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*	~150 000 (East 1988)*, ~350 000 (Campbell & Borner 1995)*, ~250 000 - (6)*	725 000 (Bradley 1977, cited in Sinclair & Norton-Griffiths 1979) (Serengeti, Tanzania)*	Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)*
300–400 (Fryxell & Sinclair 1988b)	300–400 (Fryxell & Sinclair 1988b)	~1 000 000 (East 1988)*, ~800 000 (6)*	>800 000 (Fryxell & Sinclair 1988b)	Estes (1991)*
?	?	188 (Campbell & Borner 1995)	Group size max ~400 (Walther 1972), 30 000 in 1960s & 52 000 in 1978 (Sinclair & Norton-Griffiths 1979)*	Estes (1991)*

(Table continued on next page)

Table 1 (continued)

Scientific name	Common name	Location	Mass migration	
			Current	Historic
Oryx dammah	Scimitar horned oryx	Africa		**36 -** Mallon & Kingswood (2001) (Chad & Niger)*, **37 -** CMS (2006b) (Mauritania-Morocco, Mali-Niger, Niger-Algeria, Mali-Burkina Faso, Niger-Chad, Chad-Sudan)*
Tragela-phus oryx	Eland	Africa	**33 -** Campbell & Borner (1995) (Serengeti-Mara, Tanzania & Kenya)*, **3 -** Verlinden (1998) (Kalahari, Botswana) & (1) (Kalahari, Botswana)*	?
Antilo-carpa americana	Prong-horn	North America	**1 -** Springer (1950) (Califorina, Oregon, Idaho, USA), **2 -** Hoskinson & Tester (1980) (Idaho, USA), **3 -** Mitchell (1980) (Alberta, Canada)*, **4 -** Ockenfels et al. (1994) (Arizona, USA)*, **5 -** Sawyer et al. (2002) (Wyoming, USA)*, **6 -** Berger (2004) (Wyoming, USA), **7 -** (9) (Arizona, USA)*	Berger (2004)
Bison bison	Bison	North America	Van Vuren & Bray (1986), **8 -** Gates et al. (2001) (Alberta, Canada)*, **9 -** (10) (Yellowstone, USA)*	Dary (1974) (USA)*
Cervus elaphus	Elk	North America	Picton (1960) (Montana, USA), Craighead et al. (1972) (Wyoming, USA), Rudd et al. (1983) (Wyoming, USA), Brown (1985) (Idaho, USA)*, **10 -** Morgantini & Hudson (1988) (Alberta, Canada), **11 -** Houston et al. (1990) (Washington, USA), **12 -** Smith & Robbins (1994) (Wyoming, USA)*, Toweill & Thomas (2002) (Canada & USA)*	Skinner (1925) (Wyoming, USA), Craighead et al. (1972), Berger (2004) (Wyoming, USA)
Rangifer tarandus	Caribou/ reindeer	North America & Eurasia	**13 -** Pullianen (1983) (Finland), Fancy et al. (1989) (Alaska, USA), Boudreau (2003) (Alaska, USA)*, Gardner (2003) (Alaska, USA)*, Tobey (2003) (Alaska, USA)*, **14 -** Ulvevadet & Klokov (2004) (Canada, Russia, USA)*, **15 -** (11) (Canada, Russia, USA)*, (12)*, (13)*, (14)*, **22 -** Baskin & Danell (2003) (Russia), **23 -** Clark et al. (2006a,b) (Mongolia)	Ulvevadet & Klokov (2004)*, Baskin & Danell (2003) (Russia)
Capreolus pygargus	Siberian roe deer	Eurasia	**16 -** Danilkin (1996) (China, Russia)*	**17 -** Kirikov (1959) (Ukraine)*, Danilkin (1996)*, **24 -** Baskin & Danell (2003) (Ural)*
Pantholops hodgsoni	Chiru	Eurasia	**18 -** Schaller (1998) (Chang Tang & Qinghai , China)*, Lian et al. (2005) (Kekexili, China)	Schaller (1998)*
Equus hemionus	Kulan/ khulan	Eurasia	?	**25 -** Baskin & Danell (2003) (Kazakhstan)*
Procapra gutturosa	Mongo-lian gazelle	Eurasia	Lhagvasuren & Milner-Gulland (1997) (Mongolia-China), Jiang et al. (1998) (Mongolia-China/Russia), Baskin & Danell (2003) (Mongolia-Russia)*, **26 -** Ito et al. (2005) (Dornogobi, Mongolia), **19 -** Ito et al. (2006) (Dornogobi & Omnogobi, Mongolia), **27 -** Olson et al. (2005), **28 -** Mueller et al. (2008) (Eastern Mongolia)	Jiang et al. (1998)
Saiga tatarica tatarica & S. t. mongolica	Saiga	Eurasia	Eregdendagvaa (1954), **20 -** Bekenov et al. (1998) (Kazakhstan), **21 -** Lushchekina et al. (1999) (Mongolia), Milner-Gulland et al. (2001) (Kazakhstan, Mongolia), **29 -** Baskin & Danell (2003) (Kalmykia, Russia)*, **30 -** CMS (2006a) (Russia)*, **31 -** Berger et al. (2008a), **32 -** Berger et al. (2008b) (Mongolia)	Eregdendagvaa (1954)*, Bekenov et al. (1998), Baskin & Danell (2003)*

(1) C. Thouless (unpubl.) & R. Brett (pers. comm.)
(2) J. O. Ogutu (pers. comm.)
(3) www.african-parks.org/apffoundation/index.php?option=com_content&task=view&id=48&Itemid=83
(4) M. van Vewalle (unpubl. thesis) & N. Owen-Smith (pers. comm.)
(5) J. O. Ogutu & M. Norton-Griffiths (pers. comm.)
(6) www.msnbc.msn.com/id/19191023/
(7) S. Mohsarif (pers. comm.)
(8) www.ultimateungulate.com/Artiodactyla/oryx_dammah.html
(9) R. A. Ockenfels (pers. comm.)

Current migration distance (round trip, km)	Historic migration distance (round trip, km)	Numbers migrating		Non-migratory reference
		Current	Historic	
0 (Mallon & Kingswood 2001)*	100s (CMS 2006b)	0 (Mallon & Kingswood 2001)*	1000's - (8)	Extinct in wild (Mallon & Kingswood 2001)*
400 (Campbell & Borner 1995)*	?	12000 in groups of 200 (Campbell & Borner 1995), (16) ~16000 (1)*	?	?
Means: 128 (Deblinger 1980)*, 89 (Hoskinson & Tester 1980), 220 (Mitchell 1980)*, 30 (Ockenfels et al. 1994)*, 30 (Bright & Van Riper 2000)*, 434 (Sawyer et al. 2005)	?	~40 (Mitchell 1980)*, 2000 (Sawyer et al. 2002)*	?	Hoskinson & Tester (1980), Sawyer et al. (2002)*
50 (Van Vuren & Bray 1986), 160 (Gates et al. 2001)*, max. 80 (10)*	?	~600 (McDonald 1981)*, ~300 (Van Vuren & Bray 1986), ~1900 (Larter et al. 2000), ~2151 (Joly & Messier 2001)*	?	Dary (1974)*
70 (Craighead et al. 1972), 73 (Morgantini & Hudson 1988), 60 (Houston et al. 1990), 200 (Smith & Robbins 1994)*	?	250–1000 (Craighead et al. 1972), 1000 (Morgantini & Hudson 1988), 400–1000 (Houston et al. 1990), ~11000 (Smith & Robbins 1994)*	?	Toweill & Thomas (2002)*
3031 (mean) (Fancy et al. 1989), 1000–1200 Taymyr (Russia), 600–700 Yakutia (Russia), 80–150, Altai (Russia) (Baskin & Danell 2003)	?	~200000 (Boudreau 2003)*, ~40000 (Gardner 2003)*, ~3000 (Tobey 2003)*, maximum observed group size during migration 20000 (Baskin & Danell 2003) (Taymyr, Russia)	?	Ulvevadet & Klokov (2004)*, Baskin & Danell (2003)
200–400 (Danilkin et al. 1992), Most ~ 200, max. 800–1000 (Danilkin 1996)*	?	25000–30000 (Danilkin et al. 1992) 10000 with bunches up to 200–1000 (Danilkin 1996)*	?	Danilkin (1996)*
500–600 (Schaller 1998)*	?	~2000, Some few 100s to 700 (Schaller 1998)*, ~3000 (Lian et al. 2005, Lian et al. 2007) (Kekexili only), ~100000 (17)*	?	Schaller (1998)*
?	?	?	Groups up to ~200 (Baskin & Danell (2003))	Reading et al. (2001), Kaczensky et al. (2006)*
100–1000s (Ito et al. 2005, 2006)	?	800000–900000 (Olson et al. 2005), maximum herd size 80000 (Lhagvasuren & Milner-Gulland 1997)	?	No large-scale migrations in Mongolia (Clark et al. 2006b*, Mueller et al. 2008)
150 (Eregdendagvaa 1954)*, 400–2400 (Bekenov et al. 1998), 300–800 in Kalmykia, 250–300 Volga-Ural, 300–400 Ustyurt, 500–600 Betpagdala-Turgay (Baskin & Danell 2003)*	?	1500 (Clark et al. 2006a, Wingard & Zahler 2006)*, <70000 (total) (CMS 2006a)*	?	?

(10) P. Gogan (pers. comm.)
(11) www.carmanetnetwork.com/display/public/home
(12) www.arctic-caribou.com/
(13) www.wkss.nt.ca/HTML/08_ProjectsReports/PDF/SeasonalMovementsFinal.pdf
(14) http://arctic.fws.gov/cariboumaps.htm
(15) http://library.thinkquest.org/16645/wildlife/grants_gazelle.shtml?tqskip1=1
(16) M. Borner (pers. comm.)
(17) http://news.nationalgeographic.com/news/2007/02/070206-tibet-antelope.html
(18) Tanzania Wildlife Research Institute (unpubl.)

Table 2. Summary of ecological drivers, threats, and state of knowledge necessary to conserve aggregated migrations for terrestrial mammals. Grasslands quality/quantity refers to forage 'green-up' as a result of rainfall or fire; vegetation green-up refers to a green-up spanning elevation gradients. #1 to 6 in 'State of conservation knowledge' refer to Steps 1 to 6 in the framework for conservation. Num-

Scientific name	Common name	Location	Ecological drivers				
			Grasslands quality/quantity	Surface water	Snow depth	Vegetation green-up	Traditional areas
Alcelaphus buselaphus	Hartebeest	Africa	Skinner & Smithers (1990)*, Estes (1991)*, Verlinden (1998)	Skinner & Smithers (1990)*			
Antidorcas marsupialis	Springbok[b]	Africa	Skinner & Smithers (1990)*, Skinner (1993), Skinner & Louw (1996)*, Verlinden (1998)				
Connochaetes gnou	Black wildebeest	Africa	Estes (1991)*, Skinner (1993)				
Connochaetes taurinus	Blue wildebeest	Africa	Talbot & Talbot (1963), Skinner & Smithers (1990)*, Kahurananga & Silkiluwasha (1997), Mduma et al. (1999), Boone et al. (2006)	Williamson et al. (1988), Verlinden (1998)			
Damaliscus dorcas	Blesbok	Africa	Skinner & Smithers (1990)*, Estes (1991)*, Skinner (1993)				
Damaliscus lunatus	Tiang (topi)	Africa					
Equus burchellii	Burchell's zebra	Africa	Smuts (1972)*, Skinner & Smithers (1990)*, Sinclair & Norton-Griffiths (1979)*, Gasaway et al. (1996), Kahurananga & Silkiluwasha (1997)	Smuts (1972)*, Skinner & Smithers (1990)*, Kahurananga & Silkiluwasha (1997)			
Equus quagga quagga	Quagga	Africa	Estes (1991)*, Skinner (1993)				
Gazella thomsonii & G. t. albonotata	Thompson's gazelle & Mongalla gazelle	Africa	Sinclair & Norton-Griffiths (1979)*				
Kobus kob	White-eared kob	Africa	Fryxell & Sinclair (1988b)	Fryxell & Sinclair (1988b)			
Nanger granti	Grant's gazelle	Africa	Walther (1972), (15)*				
Oryx dammah	Scimitar horned oryx	Africa					

bers 1 to 18 in parentheses indicate an unpublished source, listed as a footnote to Table 1. An asterisk indicates literature which may not have undergone peer review

Threat						State of conservation knowledge
Fencing	Livestock encroachment	Human encroachment (including agricultural expansion)	Over hunting/ poaching	Energy development	Transportation corridors	
Verlinden (1998)	Williamson et al. (1988), Verlinden (1998)					Verlinden (1998) (Kalahari, Botswana) - #1, (1) (Kalahari, Botswana)* - #1
Skinner & Smithers (1990)*, Estes (1991)*	Williamson et al. (1988), Estes (1991)* Verlinden (1998)	Skinner & Smithers (1990)*, Estes (1991)*	Skinner (1993)			0
Estes (1991)*	Estes (1991)*	Skinner & Smithers (1990)*, Estes (1991)*	Skinner & Smithers (1990)*			0
Berry (1997), Williamson et al. (1988), Whyte & Joubert (1988), Spinage (1992), Gasaway et al. (1996), Verlinden (1998)	Williamson et al. (1988), Homewood et al. (2001)	Williamson et al. (1988), Kahurananga & Silkiluwasha (1997), Homewood et al. (2001), Thirgood et al. (2004)	Gasaway et al. (1996), Thirgood et al. (2004)			Williamson et al. (1988) (Kalahari, Botswana) - #4, Bonifica (1993) (Botswana)* - #1, Kahurananga & Silkiluwasha (1997) (Tarangire National Park, Tanzania) - #4, Verlinden (1998) (Kalahari, Botswana) - #1, (1) (Kalahari, Botswana)* - #1, Homewood et al. (2001) (Serengeti, Tanzania) - #4, Serneels & Lambin (2001) (Serengeti-Mara, Tanzania & Kenya) - #5, Thirgood et al. (2004) (Serengeti, Tanzania) - #4, Boone et al. (2006) (Serengeti, Tanzania) - #2, Thirgood et al. (2008) (Serengeti, Tanzania) - #6
Estes (1991)*	Estes (1991)*	Estes (1991)*	Skinner & Smithers (1990)*			0
			East (1999)*			0
Berry (1980)*, Whyte & Joubert (1988)	Whyte & Joubert (1988)	Kahurananga & Silkiluwasha (1997)				Sinclair & Norton-Griffiths (1979) (Serengeti, Tanzania)* - #1, Kahurananga & Silkiluwasha (1997) (Tarangire National Park, Tanzania) - #4
Estes (1991)*	Estes (1991)*, Hack et al. (2002)*	Estes (1991)*	Estes (1991)*, Hack et al. (2002)*			0
						Campbell & Borner (1995) (Serengeti-Mara, Tanzania & Kenya)* - #1
						0
						0
	Mallon & Kingswood (2001)*		Mallon & Kingswood (2001)*			0

(Table continued on next page)

Table 2 (continued)

Scientific name	Common name	Location	Ecological drivers				
			Grasslands quality/quantity	Surface water	Snow depth	Vegetation green-up	Traditional areas
Tragelaphus oryx	Eland	Africa					
Antilocarpa americana	Pronghorn[a,c]	North America	Yoakum (1978)*, Hoskinson & Tester (1980), Ockenfels et al. (1994)*	Yoakum (1978)*	Hoskinson & Tester (1980)		
Bison bison	Bison	North America			Meagher (1989), Frank & McNaughton (1992)	Frank & McNaughton (1992)	
Cervus elaphus	Elk	North America			Rudd et al. (1983), Morgantini & Hudson (1988)	Houston et al. (1990), Morgantini & Hudson (1988), Frank (1998)	Morgantini & Hudson (1988)
Rangifer tarandus	Caribou/ reindeer[d]	North America & Eurasia			Ulvevadet & Klokov (2004)*, (11)*	Ulvevadet & Klokov (2004)*, (11)*	Ulvevadet & Klokov (2004)*, (11)*
Capreolus pygargus	Siberian roe deer	Eurasia			Danilkin et al. (1992), Danilkin (1996)*		Danilkin et al. (1992), Danilkin (1996)*
Pantholops hodgsoni	Chiru	Eurasia			Schaller (1998)*		Schaller (1998)*
Equus hemionus	Kulan/ khulan	Eurasia	Kaczensky et al. (2006)*	Baskin & Danell (2003)*, Kaczensky et al. (2006)*	Baskin & Danell (2003)*, Kaczensky et al. (2006)*		
Procapra gutturosa	Mongolian gazelle	Eurasia	Leimgruber et al. (2001), Mueller et al. (2008)		Jiang et al. (1998)		
Saiga tatarica tatarica & S. t. mongolica	Saiga	Eurasia	Bekenov et al. (1998), Baskin & Danell (2003)*	Bekenov et al. (1998)	Bekenov et al. (1998)		

[a]Uncharted ecological driver is forage moisture (Hoskinson & Tester 1980)
[b]Uncharted threat is rinderpest (Skinner 1993)
[c]Uncharted threat is brush and tree invasion (Ockenfels et al. 1994*)
[d]Uncharted threats are climate change & disturbing of calving areas (Ulvevadet & Klokov 2004*, www.carmanetwork.com/display/public/home)

Threat						State of conservation knowledge[c]
Fencing	Livestock encroachment	Human encroachment (including agricultural expansion)	Over hunting / poaching	Energy development	Transportation corridors	
		Campbell & Borner (1995)*	Campbell & Borner (1995)*			Campbell & Borner (1995) (Serengeti-Mara, Tanzania & Kenya)* - #1, (1) (Kalahari, Botswana)* - #1
Ockenfels et al. (1994)*, Berger (2004)		Hoskinson & Tester (1980), Ockenfels et al. (1994)*, Sawyer et al. (2002)*, Berger (2004)		Sawyer et al. (2002)*, Berger (2004)	Ockenfels et al. (1994)*	Ockenfels et al. (1994) (Arizona, USA)* - #4, Sawyer et al. (2002) (Wyoming, USA)* - #1, Berger (2004) (Wyoming, USA) - #5, Berger et al. (2006) (Wyoming, USA) - #5, (9) (Arizona, USA)* - #1
Berger (2001)			Dary (1974)*, Berger (2001)			Gates et al. (2001) (Alberta, Canada)* - #4, (10) (Yellowstone, USA)* - #5
Toweill & Thomas (2002)*, Berger (2004)		Houston et al. (1990), Toweill & Thomas (2002)*, Berger (2004)	Houston et al. (1990), Morgantini & Hudson (1988)	Berger (2004)		Craighead et al. (1972) (Wyoming, USA) - #3, Rudd et al. (1983) (Wyoming, USA) - #1, Brown (1985) (Idaho, USA)* - #1, Morgantini & Hudson (1988) (Alberta, Canada) - #3, Houston et al. (1990) (Washington, USA) - #4, Smith & Robbins (1994) (Wyoming, USA)* - #1
			Ulvevadet & Klokov (2004)*, (11)*	Ulvevadet & Klokov (2004)*, (11)*		Ulvevadet & Klokov (2004) (Canada, Russia, USA)* - #4, (11) (Canada, Russia, USA)* - #4, Baskin & Danell (2003)* - #1
		Danilkin (1996)*	Kirikov (1959)*, Danilkin (1996)*, Baskin & Danell (2003)*			Danilkin (1996) (China, Russia)* - #4
			Schaller (1998)*, Lian et al. (2005)			Lian et al. (2005) (Kekexili, China) - #2
Kaczensky et al. (2006)*	Reading et al. (2001), Kaczensky et al. (2006)*	Clark et al. (2006b)*	Reading et al (2001), Kaczensky et al. (2006)*, Clark et al. (2006)b*		Kaczensky et al. (2006)*	Kaczensky et al. (2006)* - #4
Ito et al (2005), Clark et al. (2006b)*	Yoshihara et al. (2008)		Reading et al. (1998), Clark et al. (2006b)*, Wingard & Zahler (2006)*		Ito et al. (2005), (2008)	Lhagvasuren & Milner-Gulland (1997) - #2, Jiang et al. (1998) - #1, Ito et al. (2006) (Dornogobi & Omnogobi, Mongolia) - #2, Yoshihara et al. (2008) - #4, Ito et al. (2008) - #4, Mueller et al. (2008) - #2
Bekenov et al. (1998)	Lushchekina et al. (1999), Berger et al. (2008b)		Bekenov et al. (1998), Lushchekina et al. (1999), Milner-Gulland et al. (2001), Berger et al. (2008a,b)		Berger et al. (2008b)	Bekenov et al. (1998) (Kazakhstan) - #4, Lushchekina et al. (1999) (Mongolia) - #4, Baskin & Danell (2003)* - #1 CMS (2006a)* - #4, Wingard & Zahler (2006)* - #4, Berger et al. (2008a,b) (Mongolia) - #1

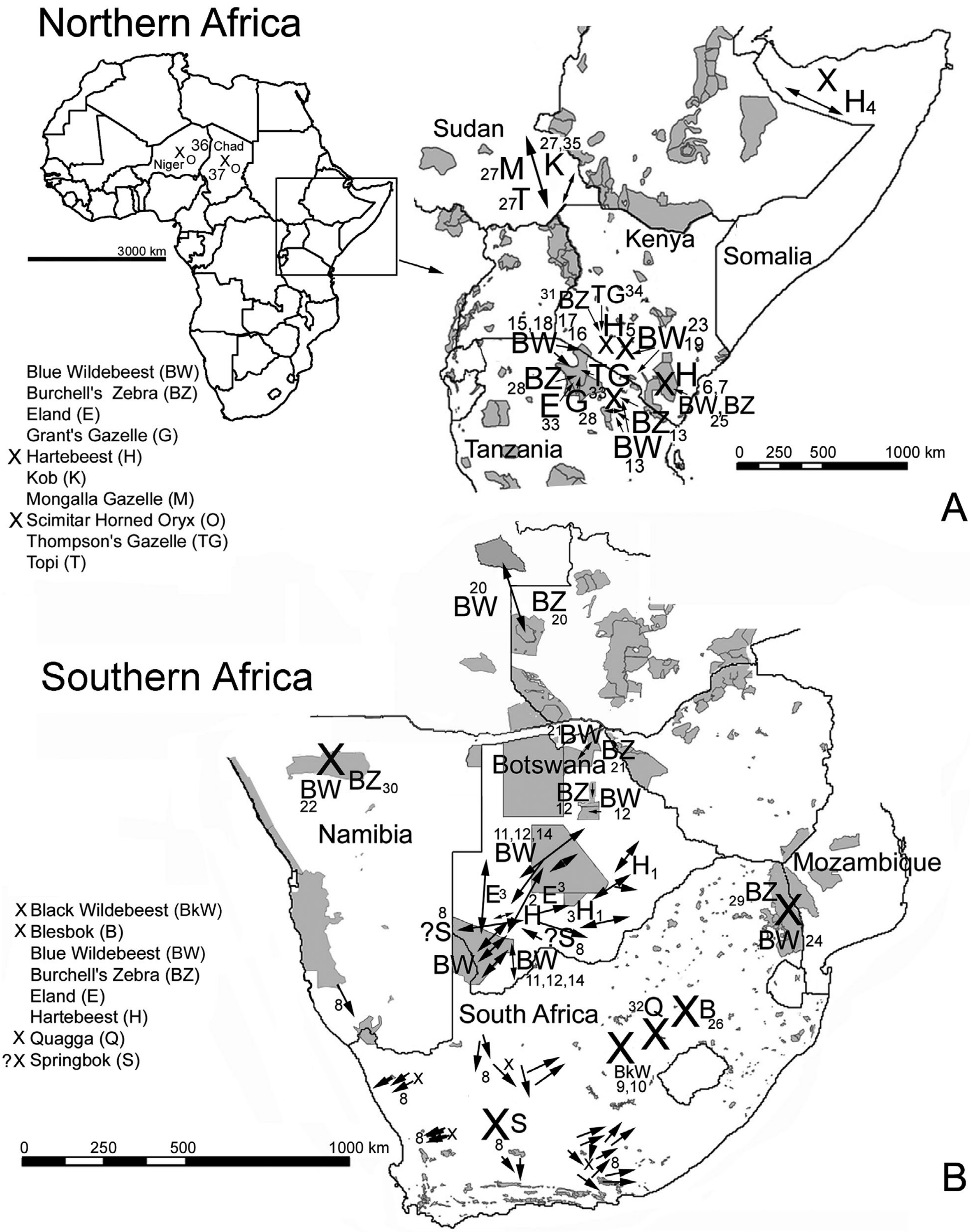

Fig. 1. Historic and current migrations in (A) northern and eastern Africa and (B) southern Africa for large mammals that move in aggregations. 'X' in the legend indicates that the species is no longer migratory. 'X' on the map shows where a species was historically migratory, but no longer is. Locations marked '?' represent migrations with an uncertain status. Lines with double arrows approximate locations with migratory routes. Lines with single arrows point to locations of current and historic migrations (for sprinkbok, these lines indicate 1-way movements. Numbers link to references and descriptions in Table 1. Light gray polygons are protected areas (WDPA Consortium 2005[1])

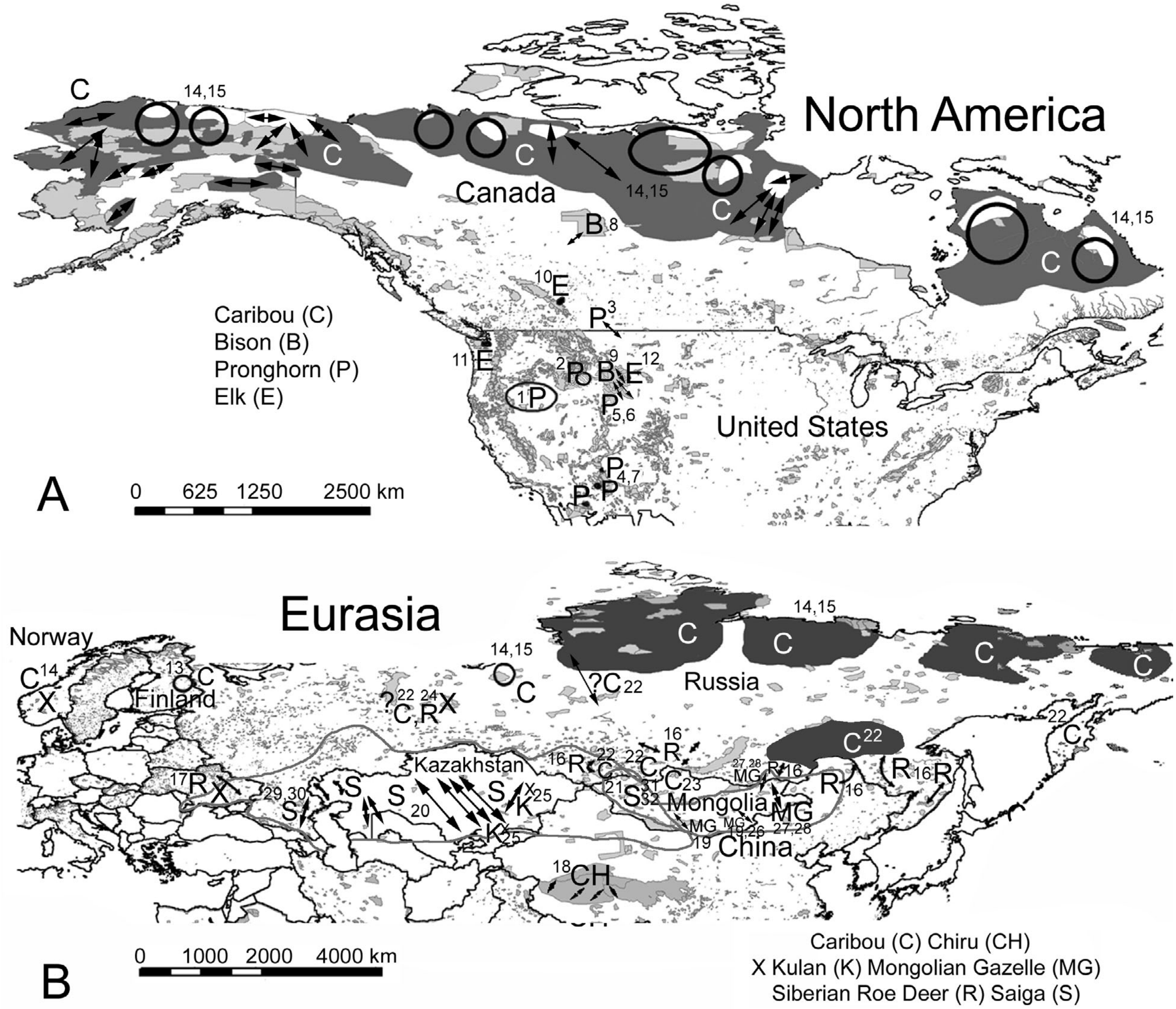

Fig. 2. Historic and current migrations in (A) North America and (B) Eurasia for large mammals that move in aggregations. Arrowed lines approximate locations of current and historic migrations. 'X' represents an extinct mass migration, and black circles/ovals mark migrations with routes unknown or variable. Locations marked '?' represent migrations with an uncertain status. Gray, unfilled polygons outlining areas of Kazakhstan and Mongolia represent the historic migratory range for saiga and Mongolian gazelle, respectively. Dark gray, filled areas in conjunction with caribou depict migratory ranges, and white areas within them in (A) calving grounds. Numbers link to references and descriptions in Table 1. Light gray, filled polygons are protected areas (WDPA Consortium 2005).

(elk, caribou/reindeer, Siberian roe deer *Capreolus pygargus*, chiru). In tropical grasslands and savannas, the timing of rainfall is relatively predictable, but the actual distribution and amount of rainfall is patchy (Williamson et al. 1988, Boone et al. 2006). Therefore, migratory routes in tropical ecosystems remain unfixed, as migrants deviate to patches of young grass from local rain or fire events (Williamson et al. 1988, Mueller et al. 2008).

Many grassland migrants can gain adequate moisture from forage, e.g. blue wildebeest *Conochaetes taruinus* (Williamson et al. 1988), springbok (Skinner 1993), pronghorn (Ockenfels et al. 1994). However, during severe droughts, grass desiccates, and species seek surface water. This is especially marked for hartebeest *Alcelaphus buselaphus*, blue wildebeest, Burchell's zebra *Equus burchellii*, white-eared kob *Kobus kob*, saiga, kulan and pronghorn (Table 2).

When forage is abundant, migrants move less, when it is sparse, they move more (Williamson et al. 1988,

[1]The WDPA is a joint product of UNEP and IUCN, prepared by UNEP-WCMC, supported by IUCN WCPA and working with Governments, the Secretariats of MEAs and collaborating NGOs. For further information: protectedareas@unep-wcmc.org

Mduma et al. 1999). During severely dry years, when many migrants seek surface water, movement distances are at their maximum (Williamson et al. 1988). Numbers also affect movement distances. When wildebeest populations in the SME were reduced by rinderpest to ~200 000 during the 1950s, their migratory routes were shorter than those of the current migration which comprises 1.3 million animals (Grzimek & Grzimek 1960, Thirgood et al. 2004). This did not occur with changes in annual rainfall, indicating that movement distances were associated with animal numbers (Sinclair & Norton-Griffiths 1979).

Threats

There are 2 principal ways to destroy a mass migration. First, kill a significant proportion of the migrants. Unsustainable hunting reduces migratory populations, contributing toward extirpation (e.g. scimitar horned oryx) and even extinction (e.g. quagga). Survivors may migrate shorter distances, or not at all, as migration distances decrease with lower numbers. If the population remains migratory, then they may no longer move in large masses, if such numbers no longer exist. Of the 20 mass migrants for which threats are listed, over-harvest is cited as a threat for 17 (Table 2).

The second principal threat is restricted access to food or water. This is an issue of habitat loss, which affects 17 of the mass migrants with listed threats (Table 2). Range can be taken directly, via agriculture, development (infrastructure, fossil fuels), or grazing livestock; fencing works indirectly, by barring access. Usually, agriculture and livestock secure the best lands, especially those which are productive during dry years. Several groups of migrants funnel into narrow corridors of 100s of meters wide (geographical, topographical or human induced), making routes prone to amputation (migration 'bottlenecks') (Kahurananga & Silkiluwasha 1997, Berger 2004, Berger et al. 2008a). Other migrants track traditional routes or ranges, and when access is denied or the range otherwise usurped, these migrants seem incapable of seeking essential resources elsewhere (Owens & Owens 1983, Williamson et al. 1988, Toweill & Thomas 2002). Transportation corridors (e.g. highways, railroads) often pose barriers for pronghorn, Mongolian gazelles, saiga and kulan (Ockenfels et al. 1994, Ito et al. 2005, 2006, Kaczensky et al. 2006, Berger et al. 2008b). Mass migrations usually extend beyond protected areas, which are simply too small to contain them. Hence, agriculture and development outside of parks often threaten migrations (Campbell & Borner 1995, Kahurananga & Silkiluwasha 1997, Homewood et al. 2001). Lack of adequate protection within parks also poses problems (Newmark 1987).

Climate change engenders longer-term threats. Concerns concentrate on migrants in higher latitudes where the pace and scale of habitat changes and the decoupling of climatic variables over disparate migratory ranges are highest, causing problems with mistimed migrations (Pulido 2007, Robinson et al. 2009). Migrants' abilities to adapt to changing environmental conditions are likely exacerbated by the other anthropogenic threats, such as habitat loss and fragmentation (Jetz et al. 2007)

Conservation knowledge

Africa, the continent with the most extinct and extant populations of migratory ungulates, has 17 reports containing information on the conservation of mass migrants, 60 % of which occur at Step 1 or 2 of the conservation framework assessed in this study. The average is about 1 report per migrant; however, more than half refer to wildebeest. Five of these reports refer to the SME, the sole location to attain Step 6 in the framework. Three remaining mass migrants in Africa have no conservation-based information. There are 18 reports for Eurasia, half of which cover Step 4, but not necessarily Steps 1 to 3. Siberian roe deer, chiru and kulan have only one report each describing any aspect of conservation. North America has the most advanced information (with fewest migrants), and 10 out of 16 reports reaching Step 3 or above (Table 2). The only North American efforts advancing to Step 5 are those for bison and pronghorn in the Greater Yellowstone Ecosystem (GYE).

Extinct migrations

Reducing migrants by over-harvest or removing range contributes to population declines, lowers the distances migrants travel, and can destroy the migration and species. In Africa, migrations of scimitar horned oryx and hartebeest have disappeared from the Sahara of Niger and Chad, and the Ogaden of Somalia and Ethiopia respectively (East 1988, Mallon & Kingswood 2001). Wildebeest migrations in the Athi-Kapiti Plains in southeast Kenya are extinct (J. Oguto pers. comm.). Wildebeest once migrated northeast of Etosha National Park in Namibia during dry seasons, but cordon fencing in 1973 closed all movements (Berry 1997); fencing, coupled with harvest on farms and communal lands, caused numbers to fall from 30 000 in 1964 to 2000 in 1993 (Gasaway et al. 1996). Burchell's zebra also declined by about 20 000 from 1953 to 1991 (Gasaway et al. 1996). Fencing in Kruger National Park in South Africa blocked wildebeest migration, and populations declined from 6000 to 750 (Braack 1973, Whyte & Joubert 1988). Historical (1850s) migrations of 10 000s of trekbokke (springbok, black wildebeest, blesbok, eland and quagga), no longer occur in the Karoo and Highveld of South Africa (Skinner & Chimimba 2005) and quagga are extinct as a species (Hack et al. 2002). Reports of extant mass migrations of springbok in Botswana are unconfirmed (Skinner & Louw 1996).

Reports describe mass migrations of Siberian roe deer up to the second half of the 19th century in the Ukraine, but these migrations are presumed lost, largely from over-harvesting (Kirikov 1959, Baskin & Danell 2003). Many details of Siberian roe deer migrations in Siberia are unclear (Danilkin et al. 1992, Danilkin 1996). Kulan reportedly migrated from NW Kazakhstan to Betpakdala in the southeast, but these regular migrations disappeared as kulan numbers dropped (Baskin & Danell 2003). The present status of kulan in Asia Minor countries such as Iran remains unclear. Saiga migrations used to be far more widespread up to the 18th century, going as far west as Romania, present-day Macedonia, and western Ukraine (Lushchekina & Struchkov 2001). Similarly, migrations of Mongolian gazelle were formerly common throughout Mongolia and parts of Russia and China (Jiang et al. 1998).

19th century hunters nearly exterminated migratory bison occupying the expansive grasslands of central North America (Dary 1974). Only 2 remnant populations of migratory bison remain, one in Yellowstone National Park in the USA and the other in Wood Buffalo National Park in Canada (Meagher 1973, Van Vuren & Bray 1986, Gates et al. 2001).

Threatened migrations

Many African ecosystems contain guilds of extant migratory species; we summarized these from north to south. Mass migrations of kob, tiang *Damaliscus lunatus* and mongalla gazelle *Gazella thomsonii albonotata* occur in the Boma-Jonglei Ecosystem in southern Sudan (Fryxell & Sinclair 1988b, East 1999). Many believed these migrations decimated by civil war, but recent surveys (2007) indicate ~1 million migratory ungulates in and adjacent to Boma National Park (www.msnbc.msn.com/id/19191023/?GT1=10056).

Mass migrations of wildebeest, Burchell's zebra, Grant's gazelle *Nanger granti*, Thomson's gazelle *Gazella thomsonii* and eland persist in the SME of Tanzania and Kenya (Sinclair & Arcese 1995, Thirgood et al. 2004). A separate population of wildebeest migrates from the Masai Mara National Reserve north to the Loita Plains. This population has declined from ~100 000 to ~25 000 over 20 years (late 1970s to late 1990s) because of habitat loss on the Loita Plains (Homewood et al. 2001, Ottichilo et al. 2001). Wildebeest, zebra and Grant's gazelle also migrate in the Tarangire Ecosystem, 200 km southeast of the SME (Borner 1985, Kahurananga & Silkiluwasha 1997). Migration routes to the west and north of Tarangire National Park are blocked by agriculture and there is considerable poaching pressure outside the park. Wildebeest populations declined from ~50 000 to ~5000 between 1988 and 2001 (TAWIRI 2001).

Populations of wildebeest and zebra migrate in masses between Liuwa Plains National Park (Zambia) and Kameia National Park (Angola). This migration is largely undocumented. Wildebeest and zebra also migrate in aggregations within the Chobe-Linyanti Ecosystem in northern Botswana (also largely undocumented; N. Owen-Smith pers. comm.). Severe drought in the 1980s killed many migratory eland, hartebeest (~10 000) and wildebeest (~80 000) in the Kgalagadi Transfrontier Park and the Central Kalahari Game Reserve in southern Botswana, as livestock use and veterinary fences block access to dry season refuges (forage and water) outside protected areas (Owens & Owens 1983, Spinage 1992, Verlinden 1998, C. Thouless unpubl. data, R. Brett pers. comm.); some 50 000 wildebeest starved around Lake Xau in 1983 alone (Williamson & Mbano 1988). Populations of non-migratory ungulates in the Kalahari have not shown similar declines.

Eurasia contains 2 subspecies of saiga: *Saiga tatarica tatarica* (mainly in Kazakhstan and Russia) and *S. t. mongolica* (in Mongolia). *S. t. tatarica* populations have collapsed (Milner-Gulland et al. 2001, CMS 2006a), with habitat loss and overhunting likely responsible for dividing remaining animals into 4 migratory populations (CMS 2006a). Recent studies have assessed the status and movements of *S. t. mongolica* in Mongolia (Berger et al. 2008a,b). This subspecies has also severely declined in numbers, and remaining migrations are threatened by increasing anthropogenic pressures.

Chiru migrate in the Chang Tang National Park on the Tibetan Plateau (Schaller 1998, Lian et al. 2005) and Mongolian gazelle migrate 1000s of kilometers across the steppes of Mongolia, China and Russia (Ito et al. 2005, 2006, Mueller et al. 2008). Both species were decimated by hunting during the 20th century, with chiru recently stabilizing at ~100 000 (http://news.nationalgeographic.com/news/2007/02/070206-tibet-antelope.html) and current estimates of Mongolian gazelle of ~800 000 (Olson et al. 2005). Some data on Mongolian gazelle movements are now available and suggest that populations may be more nomadic than migratory, which may make their conservation more difficult (Mueller et al. 2008).

Caribou/reindeer migrate in at least 13 populations in Alaska and Canada and at least 9 populations in Russia (Baskin & Danell 2003, Ulvevadet & Klokov 2004). Herds move between calving areas in the tundra and wintering areas in the taiga and migratory routes may change between years (Fancy et al. 1989, Baskin & Danell 2003, Ulvevadet & Klokov 2004). Some populations have declined whereas others have increased (Ulvevadet & Klokov 2004, www.rangifer.net/carma/). Increasing oil and gas exploitation threaten reindeer migrations on the Russian Taymyr peninsula and in southern Yakutia (L. Baskin pers. comm.).

Pronghorn and elk in western North America often display fidelity to migratory routes and winter range (Rudd et al. 1983, Sawyer et al. 2002, Toweill & Thomas 2002). Increases in fences and human habitation can shorten, impede and block these migrations (Ockenfels et al. 1994, Berger 2004). We did not find any information regarding mass migrations of the Eurasian red deer *Cervus elaphus*.

DISCUSSION

The principal conclusion drawn from this global audit is that mass migrations of mammals are under major threat throughout the world. Migrations of 6 of these mammals have been completely eradicated, and nearly all have lost some aggregated migrations. These are undoubtedly underestimates, given that reporting is poor, and other migrations probably existed in areas where humans now dominate landscapes. The main causes are unsustainable hunting and loss of seasonal ranges and/or migration routes through fencing, livestock, agriculture or human settlement. A number of migrations cross international borders, so solutions to mitigate threats rely on creative schemes often spanning countries and diverse cultures on site. Rarely has such work been done, and rarer still have efforts taken hold (Table 2).

Because the same factors threaten most migrations, the solutions for protecting them in a given location assist with conserving migrations elsewhere. Examples from 2 disparate migratory ecosystems, the SME and GYE, show that, given suitable commitment from governments, conservationists and scientists, conserving mass migrations is not an unrealistic ideal.

The SME is the world's largest (~2 million migrants) and most species-diverse extant migration (Sinclair & Arcese 1995, Thirgood et al. 2004). It may be the only ecosystem where migratory populations increased during the 20th century — in this case because of the eradication of rinderpest in the 1950s. Migratory populations are currently maintained through the protection of an intact ecosystem. The annual range for the migrants is largely contained within the protected area network, including wet and dry season ranges and transition zones (Thirgood et al. 2004). The entire range is without fences. Although illegal hunting removes ~40 000 wildebeest each year, this harvest is sustainable and the population is limited by food availability in the dry season (Mduma et al. 1999). Intensive activities by management authorities limit poaching (Hilborn et al. 2006). Ecotourism finances these activities, which are reinforced by long-term commitments from international conservation organizations. Maintaining these protected areas receives government support because of ecotourism's role in development (Thirgood et al. 2008). No other ecosystem containing migratory ungulates shares all of these attributes and it is perhaps no coincidence that the SME is the global flagship for successful conservation of migratory ungulates.

The GYE contains the longest and most diverse ungulate migrations in North America (Berger 2004). These migrations remain largely unprotected, with highways, housing, fencing, and energy extraction sites impeding movements both inside and outside protected areas (Berger 2004, Sawyer et al. 2005). Research projects focus on ungulate movements (routes, bottlenecks) to determine what constitutes migratory range and where this range is located, and establish population objectives to maintain and conserve these migrations (Berger et al. 2006). Solutions require implementing conservation plans far beyond protected area boundaries, such as purchasing conservation easements and reducing surface impacts to public lands, especially during migratory periods. Here and elsewhere, migration corridors can facilitate the movement of large mammal populations. For example, eland re-colonized Lake Manyara National Park (Newmark 1996) and projects envision elephants migrating between transboundary parks in southern Africa (van Aarde & Jackson 2007). As such, the myriad of conservation measures required to protect migrants in the largely unprotected GYE presents a marked contrast to the protected area-based conservation strategy in the SME.

Aggregated migrations vs. other types of movement

Many migrations are poorly known, which complicates abilities to distinguish between aggregated migrations and other forms of movement. Some migrations composed of relatively few individuals could represent disaggregated movements, or be remnants of mass migrations. Consequently, our list could be considered too inclusive if it included species that behave nomadically rather than as migrants. Alternatively, our collection could be considered restrictive. Elephants *Loxodonta africana*, for example, were excluded because there lacks literature describing their mass migrations, and experts state that they do not migrate in aggregations (I. Douglas-Hamilton & R. van Aarde, pers. comm.). Another view considers that elephants do make aggregated migrations; however, movements are widely spaced and coordinated through long-distance communication. (N. Owen-Smith pers. comm.).

Similar difficulties exist in defining other African ungulates. For example, Grevy's zebra *Equus grevyi* move in response to rainfall in northern Kenya, but such behavior is not a mass migration (Williams 2002, S. Williams pers. comm.). Lechwe *Leche leche* have been reported as migratory in the Chobe-Linyanti Ecosystem in Botswana (Child & von Richter 1969). Here, as elsewhere, lechwe inhabit floodplains and track seasonal changes in water levels. For example, ~40 000 lechwe aggregate on 100 km^2 of floodplain at Bangweulu in Zambia during the wet season (Thirgood et al. 1994). These aggregations dissolve in the dry season, as small groups disperse into permanent swamps. Hence, we do not consider such lechwe populations to migrate in masses.

In Eurasia, the goitered gazelle *Gazella subgutturosa* ranges from Mongolia and northwestern China to Israel and the Arabian Peninsula, and is highly nomadic throughout this range. We excluded this species, since clear references to mass migrations are lacking. However, few studies explore the spatial distribution of this species, and some populations could have fixed summer and winter ranges. Moreover, goitered gazelle have declined rapidly in numbers with >90% population reduction in many of their range states from the 1940s to 1980s (Mallon & Kingswood 2001), perhaps causing the disintegration of migrations into nomadic behavior. Goitered gazelle in central Asia seem to aggregate in winter and used to migrate 450–700 km, but due to reduced population sizes, the distances declined to 50–60 km (Baskin & Danell 2003). Other Eurasian and African species display similar behavior, and some may have migrated in masses in the past but no longer do (e.g. Bactrian camel *Camelus bactrianus*, Przewalski's horse *Equus caballus*, Tibetan gazelle *Procapra picticaudata*, addax *Addax nasomaculatus* and dama gazelle *Nanger dama*).

The recent study by Mueller et al. (2008) illustrates the fine border between migratory and nomadic behavior. The authors show that Mongolian gazelle in the eastern steppes of Mongolia display irregular seasonal movement patterns, escaping snow in winter and tracking vegetation quality in summer. This species, or at least this subpopulation, appears more nomadic, and less migratory, than earlier studies suggest. This begs the question whether or not the difference between nomadic and migratory behavior is an inherent species trait or whether it is driven by the regularity of climatic variation, as this example suggests. Other large-scale migrations, such as migrations in the SME, occur in regional areas with greater predictability in the timing and spatial patterns of rainfall (though highly variable at local scales). Future climate change might severely reduce this predictability and, hence, populations that we currently define as migratory could increasingly become nomadic. While in this paper we aimed at providing an audit of mass migrants using fixed ranges, obviously all migrants are worthy of conservation, irrespective of their movement patterns.

The fact that South America and Australia lack mammals that migrate in aggregations poses interesting ecological questions. For South America, increases in forest cover at the expense of grasslands during the mid-Holocene likely contributed to the loss of large-bodied mammalian fauna and migrations (de Vivo & Carmignotto 2004). The only large-bodied, migratory mammal known from South America is the guanaco *Lama quanicoe*, which makes altitudinal shifts across seasons (Nowak 1999). New work may reveal that these animals make aggregated migrations (The Patagonia Times 2008). Australia lost 43% of large bodied, herbivorous mammals (>5 kg) during the Pleistocene, compared to 13.5% in Africa (Owen-Smith 1987). This outcome likely affected the potential number of large-bodied mammals to migrate on the Australian continent.

Gray literature

This project reports facts from gray literature which we judged credible. Although it is not universally available or evaluated by peer review, we considered gray literature for 2 reasons. First, sometimes gray sources represent the best and only available knowledge on these migratory species and ecosystems. Second, we must learn and adapt using the best available information we have to inform society of the concern, and work toward maintaining the migrations that remain. For example, would it be better to report that kob migrations in Sudan are extinct based on older, peer-reviewed publications, rather than present recent, unpublished surveys stating otherwise? Certainly, peer-reviewed science should remediate the deficiencies, advance the understanding of these migrations, and monitor the effectiveness of conservation strategies aimed at protecting them. Our synthesis may also have missed important aspects of the literature that is difficult to access via standard scientific search engines, specifically literature from the vast Russian territory. In addition, data from the Asia Minor region, including countries such as Uzbekistan, Iran and Afghanistan, is severely deficient. These countries host potentially migrating species, such as goitered gazelle and kulan.

Veterinary policy

An increasing threat to animal migrations is that of international veterinary policy. We identify 2 main issues, the first being veterinary cordon fences. Since the late 1950s, these have been erected in Southern Africa to separate livestock from wildlife populations. These fences block migration routes and have devastating effects on ungulate populations (Owens & Owens 1983, Williamson et al. 1988, Martin 2005, Mbaiwa & Mbaiwa 2006). Their purpose is to limit disease transfer from wild to domestic ungulates in order to meet the high standards of disease management put forward by beef-importing nations (Taylor & Martin 1987, Martin 2005, Mbaiwa & Mbaiwa 2006). Ironically, the transfer of exotic diseases from domestic to wild populations is an increasing threat, and migratory ungulates might be especially sensitive due to their gregarious behavior, as likely exemplified by Mongolian gazelle (Lhagvasuren & Milner-Gulland 1997, Nyamsuren et al. 2006). Despite any clear evidence that these fences effectively control disease outbreaks, there are rising concerns that this method will be copied elsewhere, and hence threaten other migrations (e.g. Mongolia; Nyamsuren et al. 2006). The second issue is culling to control disease transfer to domestic stock. This policy has reduced migratory populations in the past (Newmark 2008), and threatens existing migratory populations now (e.g. Mongolian gazelle; Nyamsuren et al. 2006). We recognize the needs to control the spread of potentially dangerous zoonotic diseases; however, we seek novel solutions that retain ecological processes, such as mass migrations.

Conserving mass migrants

The Convention on Migratory Species works internationally to conserve migrations across taxa (www.cms.int/). They focus on species threatened with extinction, but include other species whose migrations would significantly benefit from international cooperation, including strictly migratory and nomadic species. The Convention currently lists 3 large mammals that migrate(d) in aggregations, the scimitar-horned oryx (Extinct in the Wild), *Saiga tatarica tatarica* (Critically Endangered), and the Mongolian gazelle (Least Concern) (IUCN 2008). Clear criteria for listing are absent. We also note that endangered chiru is unlisted (IUCN 2008). Other aggregated migrants, with migrations no longer existing, or with migrations declining faster than efforts to understand or conserve them, also remain absent (Table 2). We encourage this group (and others) to advance beyond species-level conservation planning to include preserving the migratory phenomenon itself (see also Wilcove & Wikelski 2008). Migratory behavior for these species can cease (and for some it has, Table 1) without species going extinct. Relegating these wide-ranging migrants to small zoos and parks because of poaching and extensive habitat loss from agriculture or livestock is inadequate on ecological and ethical grounds (e.g. ecosystem collapses and loss of the intrinsic ecology of such species). The Convention represents an international mechanism for change, and we urge their efforts in making changes happen.

Conserving mass migrants means preserving animals' freedom of movement in response to the temporal aspects of forage across seasonal extremes. This requires understanding basic parameters of the migration (e.g. location, numbers, routes, distances traveled), ecological drivers, habitat needs and threats. When migrants are excluded from forage and water resources , their numbers plummet and migrations disappear. Migrants remain at low population levels in small areas that have enough resources to maintain them.

This synthesis reviews the information currently available and pertinent for the conservation of mass migrations and highlights gaps to focus scientific attention. When addressed, proven methods such as protecting seasonal ranges, removing barriers, promoting ecotourism, securing long-term support from governments and NGOs, mitigating incompatible land uses and garnering conservation easements, can preserve the ecological, economic and aesthetic values of aggregated migrations.

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