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Invited review: Ruminant ecology and evolution: Perspectives useful to ruminant livestock research and production

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ABSTRACT

The article reviews ruminant ecology and evolution and shows insights they offer into livestock research. The first ruminants evolved about 50 million years ago and were small (<5 kg) forest-dwelling omnivores. Today there are almost 200 living ruminant species in 6 families. Wild ruminants number about 75 million, range from about 2 to more than 800 kg, and generally prefer at least some browse in their diets. Nine species have been domesticated within the last 10,000 yr. Their combined population currently numbers 3.6 billion. In contrast to wild ruminants, domestic species naturally prefer at least some grass in their diets, are of large body weight (BW; roughly from 35 to 800 kg), and, excepting reindeer, belong to one family (Bovidae). Wild ruminants thus have a comparatively rich ecological diversity and long evolutionary history. Studying them gives a broad perspective that can augment and challenge the status quo of ruminant research and production. Allometric equations, often used in ecology, relate BW to physiological measurements from several species (typically both wild and domestic). They are chiefly used to predict or explain values of physiological parameters from BW alone. Results of one such equation suggest that artificial selection has increased peak milk energy yield by 250% over its natural level. Voluntary feed intake is proportional to $BW^{0.9}$ across wild and domestic ruminant species. This proportionality suggests that physical and metabolic factors regulate intake simultaneously, not mutually exclusively as often presumed. Studying the omasum in wild species suggests it functions primarily in particle separation and retention and only secondarily in absorption and other roles. Studies on the African Serengeti show that multiple species, when grazed together, feed such that they use grasslands more completely. They support the use of mixed-species grazing systems in production agriculture. When under metabolic stress, wild species will not rebreed, but rather will extend lactation (to nourish their current offspring). This bolsters the suggestion that lactation length be extended in dairy operations. Cooperation between animal scientists and ecologists could generate more valuable insight.

Key words: ecology, evolution, livestock research, ruminant

INTRODUCTION

As an applied field, animal science borrows variously from classical physiology, endocrinology, biochemistry, genetics, and nutrition, among other disciplines. It draws less often from ecological and evolutionary research. For ruminant livestock research, several excellent publications exist on these 2 overlooked subjects, including classic works such as those by Hofmann (1973), Clutton-Brock et al. (1982), Foose (1982), and Owen-Smith (1988) and more recent material compilations such as those by Vbra and Schaller (2000) and Prothero and Foss (2007).

In his general ruminant nutrition text, Van Soest (1994) presents a brief overview of ruminant ecology and evolution. As a brief overview, it necessarily lacks detail and synthesizes few explicit connections between ruminant ecology and evolution and applied livestock research. Some individual manuscripts (e.g., Walker, 1994; Knight, 2001) have drawn more detailed and direct connections. Although valuable in their own right, these manuscripts do not include a thorough introduction to ruminant ecology and evolution.

The aim of this review is to 1) summarize key points of ruminant ecology and evolution, and then 2) show where these points offer insight into livestock research and production, drawing on our original ideas and some isolated ones presented previously. The focus on nutrition and physiology in this review reflects our own expertise, not a lack of importance of other fields (e.g., reproduction, behavior, genetics).

ECOLOGY AND EVOLUTIONARY HISTORY OF WILD RUMINANTS

For the purpose of this review, a ruminant includes any artiodactyl (member of the mammalian order Ar-

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Figure 1. A greater Malay chevrotain (*Tragulus napu*), a member of the family Tragulidae and one of the most primitive ruminants. Note the small size (approximately 3 kg), short limbs, and absence of horns, all of which are characteristic of early ruminants. Enlarged upper canines are absent because this specimen is a female. Photo courtesy of Ellen S. Dierenfeld (Novus International Inc., St. Charles, MO).

tiodactyla) possessing a rumen, reticulum, omasum, or isthmus homologous to the omasum, and abomasum. Ruminants also possess certain skeletal features—such as loss of upper incisors, the presence of incisiform lower canines, and fusion of the cubiod and navicular bones in the tarsus—that are useful in fossil identification (e.g., Gentry, 2000) but that are not of primary consideration here.

Ruminant Families

The 6 extant (i.e., nonextinct) ruminant families include the Tragulidae, Moschidae, Bovidae, Giraffidae, Antilocapridae, and Cervidae. Table 1 provides a description of these families, including the number of species and genera (from Nowak, 1999).

The Tragulidae (chevrotains; 4 species) are small, reclusive, forest-dwelling, deer-like ruminants (Figure 1). They are the most primitive of all living families and have changed little morphologically over evolutionary history; this has led them to being called "living fossils" (Janis, 1984). Their primitiveness is demonstrated by their 1) very simple social behavior, 2) retention of a gallbladder and appendix (Janis, 1984), 3) lack of a true omasum (Langer, 1988), and 4) possession of many skeletal characters (e.g., short, unfused metapodials) considered ancestral (Webb and Taylor, 1980). Although still considered ruminants, the Tragulidae are not included in the same infraorder (Pecora) as other ruminant families (Moschidae, Bovidae, Giraffidae, Antilocapridae, Cervidae) because of these ancestral features.

The Moschidae (musk deer; 5 species) are small, Asiatic forest deer whose males possess a musk gland anterior to the genitals. Like tragulids, the moschids are hornless (other families possess horns or antlers), and the males have large upper canines instead. The remaining families, the Bovidae (e.g., cattle, sheep, goats, antelope; 140 species), Giraffidae (giraffe and okapi), Cervidae (true deer; e.g., white-tailed deer, red deer elk, caribou, moose; 41 species), and Antilocapridae (pronghorn), include species familiar to most readers. Standard mammalogy textbooks (e.g., Feldhamer et al., 2007) and encyclopedias (e.g., Nowak, 1999) provide additional information for all these families.

Five additional extinct families are generally recognized (Carroll, 1988): the Hypertragulidae, Leptomerycidae, Gelocidae, Palaeomerycidae, and Dromomerycidae. The Hypertragulidae, Leptomerycidae, and Gelocidae were small, hornless ruminants that probably most closely resembled moschids or tragulids (Webb and Taylor, 1980; Webb, 1998b). The Palaeomerycidae and Dromomerycidae were medium to large sized, with giraffe-like horns but deer-like limb proportions (Janis and Scott, 1987). Their ecological niche probably resembled that of a subtropical deer (Janis and Manning, 1998b).

Phylogeny and Evolution

The phylogeny of these families is not well resolved, but one possible scenario (a simplified and updated version presented by Gentry, 2000) is shown in Figure 2.

Table 1. Description of extant ruminant families, including number of genera and species and example species[1]

Family	Genera, no.	Species, no.	Example species
Antilocapridae	1	1	Pronghorn
Bovidae	49	140	Cattle, sheep, goats, antelope
Cervidae	17	41	Red deer, caribou, moose
Giraffidae	2	2	Giraffe, okapi
Moschidae	1	5	Muskdeer
Tragulidae	3	4	Chevrotains
Total	73	193	

[1] Data from Nowak (1999).

The Hypertragulidae are the most primitive and were thus probably the first to appear (Webb and Taylor, 1980), around 50 million years ago (Ma; Early Eocene) in Southeast Asia (Hernández Fernández and Vrba, 2005; Métais and Vislobokova, 2007). The Tragulidae and Leptomerycidae (or close ancestors thereof) arose shortly thereafter, again in Asia (Colbert, 1941; Métais et al., 2001), but quickly dispersed to North America (Webb, 1998b). During this time, tropical, closed-canopy forests were widespread (Janis, 1993) and temperatures were very warm (near their highest point in the last 65 million years; Zachos et al., 2001). The Gelocidae appeared at approximately 40 Ma (Middle Eocene), when the climate had already cooled (about 5°C relative to 50 Ma; Zachos et al., 2001) and temperate woodlands appeared (Janis, 1993).

When these first ruminant groups emerged, they were rabbit-sized (<5 kg; Métais and Vislobokova, 2007). Their skull and dental morphology (low-crowned teeth, small incisors, long and narrow skulls) were optimal for consuming fruits, shoots, and insects (Webb, 1998b). This evidence, in addition to the observed habitat and diet of living tragulid and moschid species (which are taken as rough analogs for these first groups), suggests that the first ruminants were small, reclusive, forest-dwelling omnivores (Webb, 1998b). The first ruminants did not ruminate or have a functional rumen flora (viz., for fiber fermentation) until about 40 Ma, as indicated by dental morphology (Janis, 1976) and molecular techniques (Jermann et al., 1995).

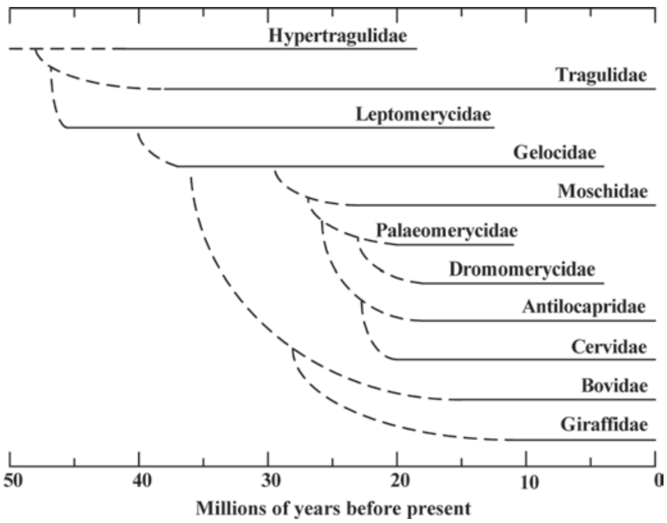

Figure 2. A phylogeny of ruminant families. Families included are the Hypertragulidae, Tragulidae, Leptomerycidae, Gelocidae, Moschidae, Dromomerycidae, Palaeomerycidae, Antilocapridae, Giraffidae, Cervidae, and Bovidae—that is, those recognized by Carroll (1988). Solid lines indicate age ranges documented in the fossil record [adapted from Métais et al. (2001) for Tragulidae; Webb (1998b) and Gentry (2000) for Gelocidae; and Gentry (2000) for all other families, assuming Archaeomeryx belongs to Leptomerycidae (Webb and Taylor, 1980)]; stippled lines indicate inferred age ranges and family relationships (adapted from Gentry, 2000).

The remaining families evolved about 18 to 23 Ma (Early Miocene) during a second radiation (Janis, 1982) in Eurasia (Antilocapridae, Cervidae, Moschidae, Dromomerycidae, Bovidae, Palaeomerycidae) and Africa (Giraffidae; Gentry, 2000). Many of these families (Moschidae, Dromomerycidae, Antilocapridae) dispersed to North America shortly after their emergence (Janis and Manning, 1998a,b; Webb, 1998b). By this time, the climate was drier (Janis, 1993) and had cooled substantially (the first Antarctic ice sheets had formed; Zachos et al., 2001) and open, temperate woodlands were the dominant flora (Janis, 1982, 1993). Dental wear patterns and craniodental morphology suggest these groups ate primarily leaves (Janis, 1982; Solounias and Moelleken, 1992) or grass and leaves (Solounias et al., 2000; Semprebon et al., 2004; Semprebon and Rivals, 2007; DeMiguel et al., 2008). The body mass of these groups was initially about 20 to 40 kg (Janis, 1982).

By about 5 to 11 Ma (Late Miocene), grasslands had expanded (Jacobs et al., 1999), and some species began including more grass in their diets, again as suggested by dental wear patterns and craniodental morphology (Semprebon et al., 2004; Semprebon and Rivals, 2007). At the end of this period (5 Ma), bovids and cervids migrated to North America (Webb, 1998a, 2000). Later (2 Ma; Latest Pliocene), deer would migrate to South America (Webb, 2000).

Distribution, Abundance, BW, and Dietary Preferences of Living Ruminants

Today, nearly 200 wild ruminant species exist (Nowak, 1999), most of which are Bovidae and Cervidae (Table 1). A conservative estimate places the world population of wild ruminants at 75.3 million, with 0.28 million tragulids, 0.28 million moschids, 44.6 million cervids, 29.1 million bovids, 0.15 million giraffids, and 0.88 million antilocaprids (Supplemental Table 1, http://www.journalofdairyscience.org/; Appendix). The majority of wild ruminants, in terms of species and population numbers, are thus bovids and cervids.

Following their distribution in the fossil record, living ruminants are natively found on all continents except Antarctica and Australia, although most species are found in Africa and Eurasia (Table 2, constructed from data in van Wieren, 1996). The Bovidae and Cervidae both enjoy an almost worldwide distribution, whereas the range of the remaining families is much more restricted (Table 2). Only the Cervidae are found in South America (Table 2).

Table 2. Native distribution of species (% of total within family) across continents and habitat and climate types[1]

	Continent[2,3]				Habitat			Climate		
Family	EA	AF	NA	SA	Forest	Ecotone	Open	Warm	Temperate	Cold
Antilocapridae	0	0	100	0	0	0	100	0	100	0
Bovidae	28.4	67.6	4.9	0	25.4	32.4	42.2	74.5	16.7	8.8
Cervidae	63.3	0[4]	13.3	30.0	50.0	30.0	20.0	46.7	46.7	6.7
Giraffidae	0	100	0	0	50.0	50.0	0	100	0	0
Moschidae	100	0	0	0	0	100	0	0	0	100
Tragulidae	75.0	25.0	0	0	100	0	0	100	0	0
Total	37.6	51.1	7.1	6.4	32.6	31.9	35.5	68.8	22.0	9.2

[1] Data from van Wieren (1996).

[2] EA = Eurasia; AF = Africa; NA = North America; SA = South America.

[3] Percentages for each continent may not sum to 100 within family because some species may be located on multiple continents.

[4] Does not include species that have a limited range in Africa.

Ruminants not only have a wide geographic distribution, but are also found across many climates and habitats. Although the classification system of habitats and climates used in this review (adopted from van Wieren, 1996) is admittedly crude, it still gives a general sense of this distribution. As a whole, ruminant species are evenly spread across open, ecotone, and forested habitats, but they prefer warm to other types of climates (Table 2). The distribution of the Bovidae and Cervidae is generally representative of this overall pattern, whereas other families individually inhabit a more restricted range of habitats and climates (Table 2).

As reported in Table 3 (data from van Wieren, 1996), the median BW of modern ruminants is 45 kg. Body mass ranges greatly, from approximately 2 kg [Salt's dik-dik (*Madoqua saltiana*), royal antelope (*Neotragus pygmaeus*), lesser Malay mouse deer (*Tragulus javanicus*)] to 800 kg [American bison (*Bison bison*), wisent (*Bison bonasus*), gaur (*Bos gaurus*), Asian water buffalo (*Bubalus bubalis*), kouprey (*Bos sauveli*); van Wieren, 1996]. Although not shown in Table 3, some individuals from the largest species achieve BW $\geq$1,000 kg, with the maximum size of a male reticulated giraffe (*Giraffa camelopardalis*) reaching 1,400 kg (Clauss et al., 2003). By family, the Giraffidae are the largest; Antilocapridae, Bovidae, Cervidae are intermediate; and Moschidae and Tragulidae are the smallest (Table 3). The Bovidae and Cervidae have species at or near these BW extremes, whereas the other families display a much more restricted range in BW (Table 3).

Ruminant species display innate dietary preferences, and these differ greatly across species. A concise way of classifying these preferences is with the feeding class system (first proposed by Hofmann and Stewart, 1972), which categorizes species as 1) browsers, which innately prefer browse such as fruits, shoots, and leaves (typically from shrubs, forbs, and trees); 2) grazers, which innately prefer grasses; or 3) intermediate feeders, which switch between browse and grass, usually depending on their seasonal availability. For most of their evolutionary history, ruminant species were predominately or exclusively browsers. Today, a plurality of ruminant species are still classified as browsers (Table 4), and only about a quarter are grazers. The Bovidae and Cervidae have species represented in all 3 feeding classes; the other families are exclusively browsers.

DOMESTICATION OF RUMINANT SPECIES

Details of Domestication

The first livestock species to be domesticated (ruminant or nonruminant) was the goat, at approximately 8,000 BC in the Fertile Crescent of the Near East (Zeder and Hesse, 2000). The goat was initially domesticated to supply meat to burgeoning, congested human populations whose hunting had depleted large prey populations in the wild (Clutton-Brock, 1999; Diamond, 2002). Most of the other 8 domesticated ruminant species (sheep, European and Zebu cattle, water buffaloes, mithans, reindeer, yaks, Bali cattle) were brought under human control by 2,500 BC in either

Table 3. Body mass of wild ruminant species by family[1]

	Body mass, kg		
Family	Median	Minimum	Maximum
Antilocapridae	40	40	40
Bovidae	52.5	2	800
Cervidae	47.5	6	550
Giraffidae	475	250	700
Moschidae	11.5	11	12
Tragulidae	2	2	8
Total	45	2	800

[1] Values computed from species averages reported by van Wieren (1996).

Table 4. Dietary preferences of species (% of total species within family), according to their assignment as browsers (BR), intermediate feeders (IM), or grazers (GR)[1]

Family	Feeding class		
	BR	IM	GR
Antilocapridae	100	0	0
Bovidae	35.3	26.5	39.2
Cervidae	46.7	36.7	16.7
Giraffidae	100	0	0
Moschidae	100	0	0
Tragulidae	100	0	0
Total	41.1	31.9	27.0

[1] Data from van Wieren (1996).

the Near East or southern Asia (Clutton-Brock, 1999). Some of these species, such as the goat, were initially domesticated for meat, but reasons for domestication varied greatly, including for milk, draft, transportation, sacrifice, and barter (Clutton-Brock, 1999).

Molecular approaches (Bruford et al., 2003) have determined that each domestic species is probably derived from several wild species; at least 12 species can claim ancestry to the 9 domesticated species. Of the multitude of available wild species, these 12 were chosen for domestication because they were gregarious, submissive to human captors, unexcitable, and easy to breed (Clutton-Brock, 1999; Diamond, 2002).

Characteristics of Domestic Species

Points in the discussion below are summarized in Table 5. The total population size of domestic species is 3.57 billion, nearly 50-fold larger than that of wild ruminants. As might be anticipated, cattle, sheep, and goats constitute most (about 95%) of the domestic ruminant population. All but reindeer belong to the family Bovidae.

Most species are grazers, with goats and reindeer the notable exceptions. Sheep were classified by Hofmann (1989) as grazers, although others (e.g., Pfister and Malechek, 1986) have argued that they are instead intermediate feeders.

Although BW varies greatly by sex and across breeds, the rough averages in Table 5 demonstrate that the BW of domestic ruminants are large in comparison with many wild ruminants. The smallest species (sheep, goats) are near the median BW of wild ruminants (45 kg) and many species (cattle, mithans, Bali cattle) approach the maximum observed in the wild (800 kg; Table 3).

PERSPECTIVES RELEVANT TO MODERN PRODUCTION SYSTEMS

Wild ruminants, past and present, prove much more diverse (in terms of phylogeny, behavior, diet, and otherwise) than domestic ruminants. Further, the 50-million-year evolutionary history of the ruminant extends far before domestication. Studying ruminant ecology and evolution gives a broad perspective of what ruminants are and how they came to be—much broader than achieved through studying domestic species alone. This broad perspective can augment or even challenge the status quo of livestock research and management, which has been established by using a much narrower perspective. The following discussion presents some

Table 5. Characteristics of domestic species, including population size, mean BW, and feeding class

Species	Population size,[1] millions	BW[2]	Feeding class[3,4]
Goat (*Capra hircus*)	850	35	IM
Sheep (*Ovis aries*)	1,113	50	IM/GR
European and Zebu cattle (*Bos taurus*, *Bos indicus*)[5]	1,390	600	GR
Water buffalo (*Bubalus bubalis*)	202	400	GR
Mithan (*Bos frontalis*)	NA	800	GR
Reindeer (*Rangifer tarandus*)	2	140	IM
Yak (*Bos mutus*)	14	700	GR
Bali cattle (*Bos javanicus*)	4	700	GR
Total	3,574		

[1] Data for goats, sheep, cattle, and water buffaloes from the Food and Agriculture Organization of the United Nations (2008a); for reindeer from Ulvevadet and Klokov (2004); for yaks from Wiener et al. (2003); and for Bali cattle from the Food and Agriculture Organization of the United Nations (2008b).

[2] Data for sheep, cattle, and goats are from typical literature studies (those summarized in Tables 5 and 6 of Hummel et al., 2005); for water buffaloes from Popenoe (1981); for yaks from Wiener et al. (2003); and for all other species from van Wieren (1996), taking BW of wild ancestors.

[3] IM = intermediate feeder; GR = grazer.

[4] Data for goats, cattle, and water buffaloes from Hofmann (1989); for sheep from Hofmann (1989) and Pfister and Malechek (1986); and for all other species from van Wieren (1996), taking feeding class of wild ancestors.

[5] Values for European and Zebu cattle are presented together because separate data are generally not available for these species.

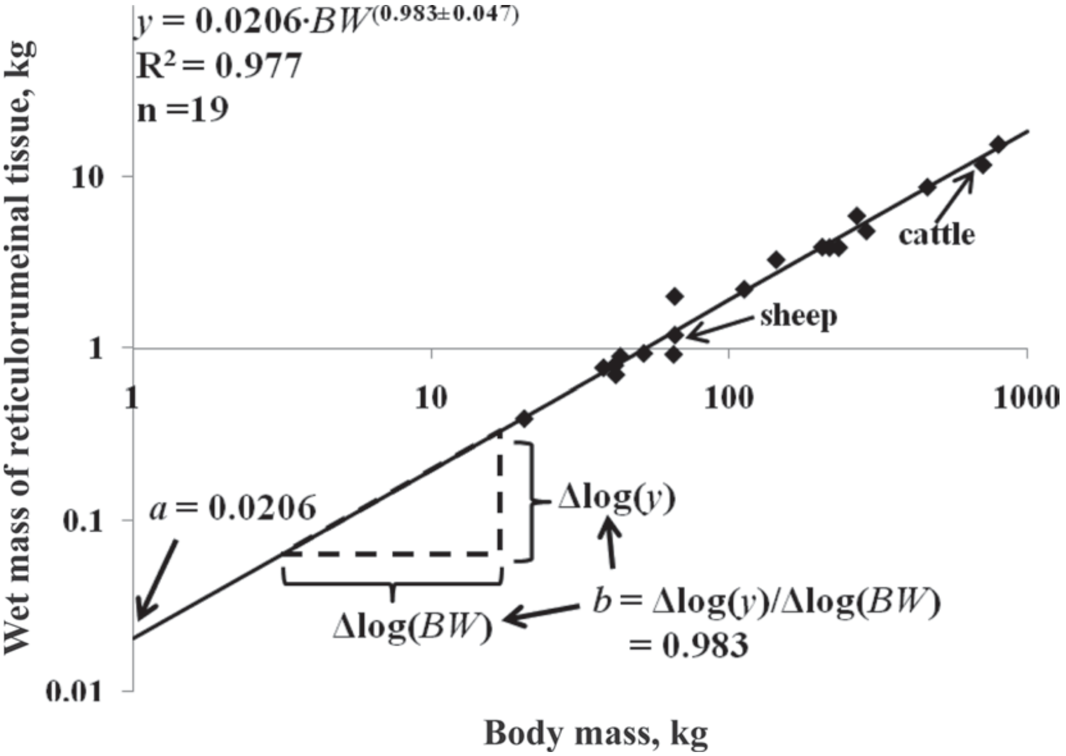

Figure 3. Graph of the allometric relationship between BW (kg) and wet mass of reticulorumen tissue (kg), illustrating the general principles of allometric equations. Tissue mass observations of individual ruminant species are shown with symbols (♦), with observations of sheep and cattle labeled. The solid line indicates the best-fit allometric equation, with the allometric intercept a and scaling parameter b defined graphically. Note that the plot is semilogarithmic. Data are for 18 wild and domestic species from 10 studies (listed in Table 6.1 of Hackmann, 2008).

examples of how principles in ruminant ecology and evolution can offer insight into livestock research and production.

Predicting Values of Physiological Parameters from BW

Body mass has a clear influence on the value of many physiological parameters. For example, the greater feed intake of a cow relative to a goat, intuitively, is largely attributable to the greater BW of the cow. The exact, quantitative relationship between a physiological parameter and BW is often less obvious, however.

Allometric equations (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984) quantitatively express these relationships with the formula

$$y = a \cdot BW^b,$$

where y is the value of a physiological parameter, a is the allometric intercept (value of y at BW = 1), and b is the scaling parameter. Values of a and b are found empirically by regressing BW against y for several species (Figure 3). By using observations from multiple ruminant species (including wild ones), one is provided a widely applicable equation that gives a benchmark prediction for a physiological parameter from BW alone. Some uses of these predictions for livestock research include 1) serving as a first approximation for a physiological value for a species when one has not been measured directly and 2) explaining to what extent observed differences between livestock species are attributable to BW (i.e., act as a control for BW in comparisons).

The allometric equation for metabolic rate (e.g., Blaxter, 1989) is widely known and applied, but many others are much less so. Examples of allometric equations are given in Table 6, including those for predicting anatomical, ingestive and digestive, energetic, reproductive, and other physiological parameters. For illustration, expected values of these parameters for 2 different BW (50 and 500 kg) are shown. Note that many equations have a very high R^2 (>0.95) and thus can be expected to be precise; others have much lower R^2 values (as low as 0.18) and should be applied more cautiously.

The equations listed in Table 6 represent a broad survey of the many available in the literature. For more

Table 6. Some allometric equations useful for predicting physiological parameter values from BW[1,2]

		Equation parameter			Predicted value		
Category	Physiological parameter	*a*	*b*	R^2	BW of 50 kg	BW of 500 kg	Source[3]
Anatomical	Reticulorumen volume, L	0.241	0.925	0.940	8.99	75.61	van Wieren (1996)
	Skull length, cm	6.18	0.337	0.960	23.1	50.2	Janis (1990)
Ingestive and digestive	Voluntary feed intake at maintenance, kg of DM/d	0.0437[4]	0.875	0.967	1.34	10.05	See text
	Maximum intake rate, g of wet matter/min	0.738	0.621	0.754	8.37	34.96	Data from Shipley et al. (1994)
	Chewing rate during rumination, no./s	2.53	−0.141	0.660	1.46	1.05	Data from Langer (1988)
	Reticulorumen DM contents, kg	0.0091	1.15	0.972	0.82	11.56	Illius and Gordon (1991)
Energetic	Basal metabolic rate,[5] Mcal/d	0.0684	0.75	NA[6]	1.29	7.23	Blaxter (1989)
	Peak milk energy yield,[7] Mcal/d	0.088	0.71	0.89	1.41	7.26	Robbins (1993)
Reproductive	Age at sexual maturity, mo	8.86	0.156	0.250	16.3	23.4	van Wieren (1996)
	Reproductive output, young/yr	2.54	−0.167	0.180	1.32	0.90	van Wieren (1996)
	Gestation length, d	129	0.125	0.556	210	280	Data from Peréz-Barbería and Gordon (2005)

[1] Equations are of the form $Y = a \cdot BW^{b}$.

[2] Unit, logarithmic, and other conversions have been applied to equations in original sources to standardize their units and form.

[3] The phrase "data from" preceding a source, where present, indicates that we performed the allometric regression using ruminant data (averaged by species) originally reported by that source.

[4] *a* and predicted values reported in this table are for the 58% NDF, 19% CP mature alfalfa hay of van Wieren (1996); in the original equation, *a* is adjusted by a fixed-effect term for diet, which allows intake to be predicted for other diet types, but this term was omitted here for simplicity.

[5] Equation applies to artiodactyls.

[6] NA = not available.

[7] Equation applies to ungulates with single offspring.

allometric equations, the reader should refer to the sources referenced in the table, as well as Scott (1990) for equations predicting postcranial skeletal dimensions; Clauss et al. (2008) for masseter muscle mass; Hofmann et al. (2008) for salivary gland mass; Robbins et al. (1995) for parotid salivary gland mass and digestive parameters; Illius and Gordon (1991) and Gordon and Illius (1994) for mean retention time, particle breakdown rate, and other digestive parameters; Illius and Gordon (1999) for ingestive parameters related to foraging; Clauss et al. (2002) for fecal particle size; and Mystrud (1998) for activity time.

The equations given in Table 6 have been derived using both wild and domestic ruminant species. Note that one can parameterize allometric equations using other approaches. Domestic species alone can be used because only 2 species observations are technically required to estimate the 2 parameters (3 if error is to be estimated). However, with so few species observations, an outlier from any one species can unduly affect parameter estimates. Wild species should thus be included to increase the number of observations and the robustness of parameter estimates. At the opposite end, nonruminant species (wild or domestic) can be included in addition to ruminants. In this case, phylogenetic differences across the wide range of species, if not controlled for statistically, may make the resultant equation very general, but also very imprecise and potentially biased. For example, adding marsupials to the allometric equation for metabolic rate would make the equation more widely applicable (viz., for marsupials) but would skew the regression because marsupials have characteristically low metabolic rates (Dawson and Hulbert, 1970). A good balance between precision, generality, and robustness is thus found by including domestic and wild ruminant species and these alone.

One must be careful in using allometric equations when a physiological parameter is affected by artificial selection. In such cases, allometric equations often predict poorly—namely, for domestic breeds for which the parameter has been targeted by artificial selection. For example, the equation for peak milk energy yield in Table 6—formulated with wild species and meat-producing domestic breeds fed predominantly forage—predicts a yield of 7.76 Mcal/d for a 550-kg cow. By contrast, observed peak yields for Holstein cows, for which milk production has been intensively selected, are approximately 20 Mcal/d on a similar (predominantly forage) diet (Kolver et al., 2007, applying milk energy equations of NRC, 2001). Although allometric equations have little direct predictive ability in such cases, another valuable purpose emerges: to estimate the impact of artificial selection on a parameter. For peak milk energy yield, assuming that the higher-than-expected yield of the cow is primarily caused by artificial selection, we can infer that artificial selection has increased peak yield in the dairy cow by about 250% (20 Mcal/d observed vs. 7.76 Mcal/d expected).

Role of Physical and Metabolic Factors in Regulating Feed Intake

In addition to the 2 general uses of allometric equations explained above, some allometric equations can be applied to draw deeper, more complex inferences. For example, the allometric equation for voluntary feed intake (**VFI**) demonstrates that forage intake is regulated by physical and metabolic factors simultaneously.

Physiological regulation of feed intake is important to livestock production systems because feed intake affects animal performance and operation costs. Of the many proposed regulation mechanisms (Forbes, 2007), physical (Allen, 1996) and metabolic regulation (Illius and Jessop, 1996) are often suggested to predominate. Generally, these 2 regulation mechanisms (physical, metabolic) are considered to operate on a mutually exclusive basis, with intake of low-energy, bulky diets (usually forages) regulated only physically and high-energy, highly degradable diets regulated only metabolically (Conrad et al., 1964; Baumgardt, 1970).

Theoretical arguments have suggested that these 2 or more regulation mechanisms operate simultaneously (Fisher et al., 1987), as do experiments in which VFA is infused and a physical ballast is placed in the rumen simultaneously (Forbes, 1996). An allometric examination of VFI of wild and domestic ruminants considerably strengthens the case for simultaneous regulation. Because reticulorumen digesta contents and volume are nearly proportional to BW^1 (i.e., proportionally do not change with BW; Table 6), one would also expect VFI to be proportional to BW^1, if physical regulation only were operating. On other hand, because metabolic rate is proportional to $BW^{0.75}$ (Table 6), one would also expect VFI to be proportional to $BW^{0.75}$, if metabolic regulation acted alone. To test which proportionality is observed (if either), we derived an allometric equation for forage intake by using data on 19 wild and domestic species from 5 studies (listed in Table 6.1 of Hackmann, 2008). We performed a regression similar to that shown in Figure 3, except we included an additional, fixed-effect term that adjusts the allometric intercept (a) by diet. The equation we derived (Table 6) indicates that forage intake is proportional to $BW^{0.875\pm0.032}$, with lower and upper 95% confidence limits of $BW^{0.810}$ and $BW^{0.941}$. This agrees with the finding that, for livestock species (cattle, sheep, goats), forage intake scales with $BW^{0.9}$ (Minson, 1990; Reid et al., 1990).

The mean value of the scaling parameter (0.9) and its 95% confidence limits fall in between values expected if intake were regulated only physically (1) and metabolically (0.75). Intuitively, this suggests that physical and metabolic regulation operate simultaneously for forage diets, contrary to the classical suggestion that physical regulation alone should occur; the mechanistic modeling described in Hackmann (2008) confirmed this suggestion. Although a lack of controlled data disallows a similar examination with diets that are not all forage, the wide range in quality of the forage diets (predicted NE_M ranged from 0.71 to 1.77 Mcal/kg of DM; NRC, 2001) suggests the results are not simply constrained to a narrow range of forages. Because this simultaneous regulation is apparent across wild and domestic species alike, it can be inferred that it is highly conserved evolutionarily and is deeply seated.

Conrad et al. (1964), who originally proposed that metabolic and physical regulation are mutually exclusive, also used allometry to support their arguments. They concluded that for high-producing dairy cows, VFI scaled with BW^1 for low digestibility (<66.7 digestible DM) and with $BW^{0.73}$ for high-digestibility (>66.7% digestible DM) diets, consistent with mutually exclusive regulation. However, for high-digestibility diets, scaling parameter values were approximately 0.73 for only 2 of their 5 regressions; all others were lower (≤ 0.62). The upper 95% confidence limits of these 2 favorable regressions (0.962 and 1.03) do not rule out VFI scaling with $BW^{0.9}$ or possibly even BW^1. This fact, and considering that VFI was only poorly related to BW ($R^2 = 0.074$ or lower), indicates that this data set is poor for discriminating intake scaling patterns. Detailed results are not presented for low-digestibility diets, but the above discussion suggests one should remain skeptical of their conclusion that VFI scales with BW^1 for these diets. Although intriguing for their time, the allometric analysis of Conrad et al. (1964) and conclusions based thereon must be rejected in favor of our more discriminating analysis.

Primary Function of the Omasum

Whereas functions of the rumen, reticulum, and abomasum are well delineated, the chief function of the omasum remains somewhat a mystery. It may help retain and separate particles because 1) large particles tend to become trapped between the omasal laminae, whereas small particles and liquids pass through quickly (Bost, 1970; Langer, 1988), and 2) large particles can be ejected from the omasum back into the reticulum (via the reticuloomasal orifice; Ehrlein, 1980). It may more generally serve as a suction pump that regulates the flow of digesta (both liquid and particles) from the reticulum to the abomasum (Stevens et al., 1960), although some have questioned this purported ability (Bost, 1970; Langer, 1988). It may also be an absorptive organ; the omasum absorbs approximately 12.5, 50, 35, 25, 10, and 50% of water, VFA, ammonia, sodium, potassium, and carbon dioxide that enter (Engelhardt and Hauffe, 1975). Some fiber digestion (7 to 9% of total tract; Ahvenjärvi et al., 2000, 2001) also occurs in the omasum. Finally, some claim the omasum reduces particle size (via purported grinding of digesta between laminae), although evidence for this function is at best circumstantial (Bost, 1970).

To establish the primary function of the omasum, we review the omasal form and function of several wild species and suggest how and why the omasum evolved. In tragulids, a true omasum is not present at all; where it should be found, only an isthmus exists instead (Langer, 1988). This isthmus (also called a transition zone) is short, narrow, and with only small, subtle longitudinal folds (Agungpriyono et al., 1992). Although it does not form a distinct compartment like a true omasum, it is still histologically distinct from the reticulum and abomasum (Agungpriyono et al., 1995). Considering this evidence and that the Tragulidae are otherwise primitive (Figure 2), this isthmus probably resembles a very early form of omasum, as concluded by other authors (see Langer, 1988). Because the isthmus lacks structures to retain digesta within it, its contribution to absorption, fiber fermentation, absorption, and particle size reduction must be minimal. Its poor structural development also precludes it from acting as a suction pump to regulate digesta flow. However, the isthmus likely helps retain particles because its small aperture should allow only fine particles to pass into the abomasum and subsequently through the rest of the tract (Langer, 1988).

In small, browsing Pecoran species, which are more advanced than the tragulids, the omasum forms a distinct compartment, but it still tends to be small and has few laminae (Hofmann, 1973, 1989; Langer, 1988, van Wieren, 1996). Hofmann (1989) concluded that its simple structure permits it to serve as little more than a "sieving screen" that prevents large particles from entering the abomasum. In large, grazing ruminants, the omasum is large and with many laminae (Hofmann, 1973, 1989; Langer, 1988; van Wieren, 1996). Whereas the omasum in these species still helps retain particles (Langer, 1988), its large surface area may additionally contribute to absorption (Hofmann, 1973, 1989) and presumably other more advanced functions (e.g., fiber fermentation).

We thus find a progression in omasal form and function from the tragulids to browsing and then grazing Pecoran ruminants. This progression suggests the omasum originally evolved as a simple isthmus that acted as a "floodgate" (Bost, 1970) to retain particles. Compartmentalization, well-developed laminae, and complex motor activity subsequently evolved to support absorption, fiber fermentation, and suction-based digesta flow control. These more derived functions indeed have some adaptive benefit, particularly for grazers, for which they may help process large amounts of refractory fiber (Hofmann, 1973, 1989; Van Soest, 1994). Nevertheless, considering that the particle retention function is pervasive across all species and is the impetus for the evolution of the omasum, this function would seem to be of primary importance.

Dietary Niche Separation and Mixed-Species Grazing

Certain elements of this argument have also been presented by Walker (1994). Studies on the African Serengeti support the use of mixed-species grazing systems—that is, systems in which pastures are stocked with more than one livestock species simultaneously. In their seminal studies, Gwynne and Bell (1968) and Bell (1970, 1971) showed that when an occupied area of the Serengeti plains becomes overgrazed, African buffalo and zebra are the first to migrate into ungrazed regions of long, poor-quality grass. As they remove the top herbage layer (stems and leaves of mature grasses), they expose lower, high-quality layers (stems, leaves, and fruits of immature grass and browse), which wildebeest, topi, and Thompson's gazelle then graze as they move in succession. By occupying different dietary niches, these ruminants and zebras together not only successfully occupy the same habitat, but also use grasslands more efficiently and completely.

Two primary reasons explain why these species occupy different dietary niches and thus can exist sympatrically (i.e., in the same geographic area). First, these species exhibit innately different dietary selectivities (i.e., feeding classes) that would immediately suggest the observed dietary niches; the buffalo and zebra are strict grazers, the wildebeest and topi are more selective grazers, and the Thompson's gazelle is an intermediate feeder (Gwynne and Bell, 1968; Bell 1970, 1971; Hofmann 1973, 1989). Second, these species range greatly in BW; the Thompson's gazelle and buffalo, the smallest and largest of the species, weigh 16 and 447 kg (Gwynne and Bell, 1968; Bell, 1970, 1971). Because VFI scales with $BW^{0.9}$ whereas metabolic requirements scale only with $BW^{0.75}$ (Table 6), nutrient intake increases relative to metabolic requirements with increasing BW. Consequently, large species can adapt to poor-quality material because they can consume relatively large amounts to meet their metabolic requirements, whereas smaller species are constrained to higher quality material because they can eat relatively little (Bell, 1970, 1971; Jarman, 1974; Hackmann, 2008). This principle (the Bell-Jarman principle; Geist, 1974) further reinforces innate selectivity differences to establish different dietary niches.

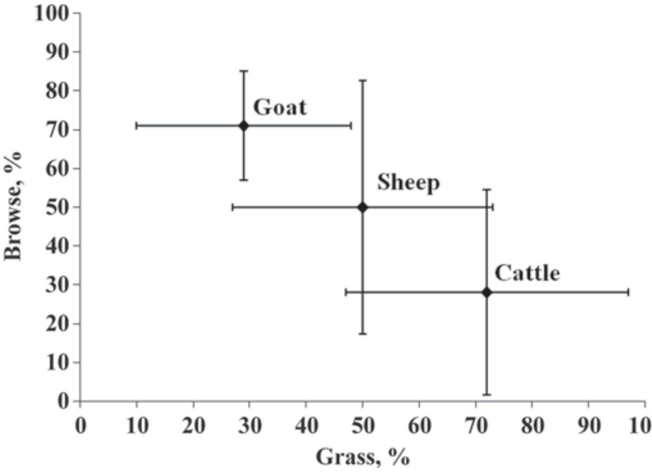

Figure 4. Botanical composition (% of grass and browse) of diets chosen by goats (n = 13), sheep (n = 105), and cattle (n = 121) on pasture. Bars delineate mean ± SD. Data are from Van Dyne et al. (1980).

Significantly, major livestock species (goat, sheep, cattle) differ greatly in feeding class, BW, or both (Table 5). Probably as a combination of these factors, species choose diets that overlap incompletely: as goats choose more browse, cattle choose more grass, and sheep are intermediate (Figure 4). Diets should be even less similar than Figure 4 might suggest because 1) Figure 4 shows ranges that apply to single-species grazing, and cattle shift to poorer quality diets in their range when grazing with sheep (Walker, 1994); 2) sheep eat plant biomass soiled by cattle feces, which cattle themselves avoid (Nolan and Connolly, 1989); and 3) the rough expression of botanical composition shown in Figure 4 ignores other ways diets can differ (e.g., by plant species or part). Livestock species thus have ample opportunity to separate their dietary niches when grazed concurrently.

Given this probable dietary niche separation, one might expect mixed-grazing systems to lead to more complete utilization of pasture and a higher combined level of animal productivity (because more pasture is transformed into animal tissue). In support, Vallentine (1990) observed that the extent of pasture use can be increased by 25% by using multi- vs. single-species grazing, and Walker (1994) found that multispecies grazing increased animal BW gain by 9 and 24% per unit area compared with sheep- and cattle-only systems, respectively.

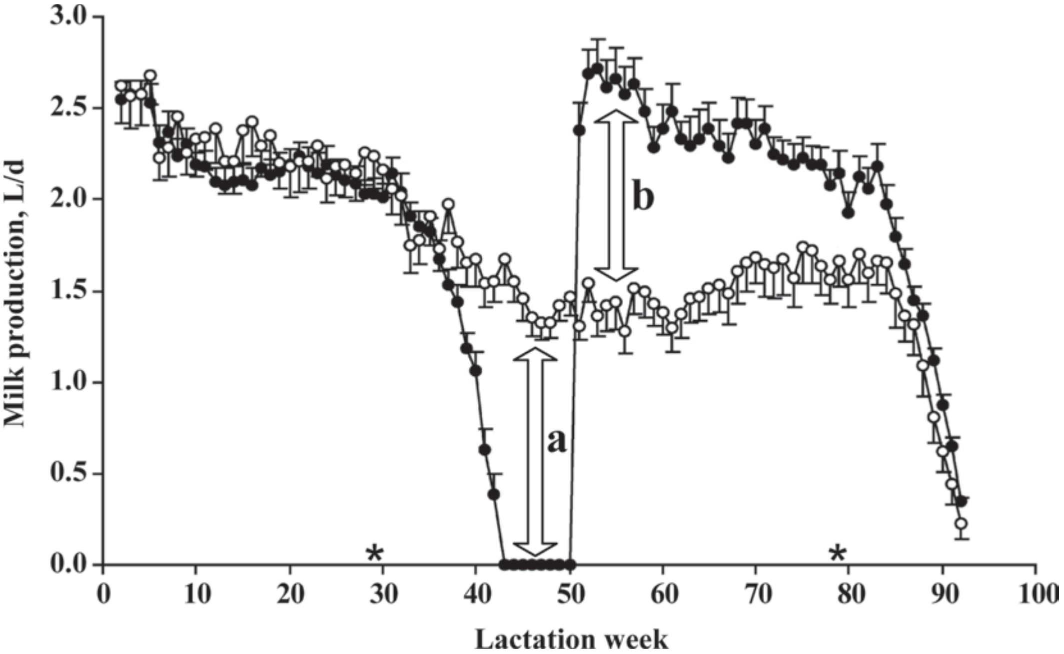

Figure 5. Milk production of extended versus conventional lactations of multiparous Muriciano-Granadina goats milked once daily. Open (○) and closed (●) symbols represent production of goats managed for kidding intervals of 12 mo (K12) and 24 mo (K24), respectively. Arrows labeled a and b highlight where milk production of an extended lactation is greater (during pregnancy and the dry period of K12 goats) and less (during peak lactation of K12 goats) than conventional lactation. The first and second asterisks near the x-axis indicate times that K12 and all goats were rebred, respectively. Figure modified from Salama et al. (2005).

Some legitimate, practical limitations to mixed-species grazing exist, such as elevated facility costs and predation risk of sheep and goats (Vallentine, 1990). However, most barriers are social, based on tradition and prejudice toward species (Walker, 1994). However, the enhanced production and efficiency of the systems compared with conventional ones—as expected from the archetypal mixed-grazing system on the Serengeti—challenge these barriers.

Extended Lactation

Elements of this discussion are derived from Knight (2001). The aim of many dairy cow operations is a 305-d lactation with a 12- to 14-mo calving interval. This requires cattle to be rebred by 100 d after parturition, soon after peak lactation, when they experience a negative energy balance (Bauman and Currie, 1980) and other metabolic stresses that severely reduce fertility (Chagas et al., 2007). With pregnancy rates of US breeds averaging about 25% (Animal Improvement Programs Laboratory, 2008), this management strategy is largely untenable.

One alternative management approach, forwarded by Knight (1984) and others, is to purposely extend lactation as long as possible and thus avoid early rebreeding. This approach, compared with current practice, indeed appears to be better supported by ecological observations. When in severe metabolic stress (poor body condition or nutritional plane) during lactation, many wild species [muskoxen (Adamczewski et al., 1998), red deer (Loudon et al., 1983; Albon et al., 1986), caribou (Gerhart et al., 1997)] will not rebreed or do so only at low rates. Instead of rebreeding, they may extend lactation and thus invest in their current young [caribou (White and Luick, 1984); muskoxen (Knight, 2001)]. In muskoxen, this extended lactation can exceed 1 yr (Adamczewski et al., 1997). As explained by Knight (2001), extending lactation is presumably a maternal strategy to maximize fitness (the most important biological drive of organisms); investing in current offspring by extending lactation is safer and, in the long term, more profitable than producing new offspring when necessary nutritional resources are inadequate.

These observations of wild species suggest that when under metabolic stress, the ruminant animal is evolutionarily entrained to continue lactation rather than rebreed. Attempting to rebreed the high-producing dairy cow soon (60 d) after parturition is a direct fight against this entrained response. If producing replacement heifers is not a major production goal, it might make more sense to rebreed less frequently and exploit the physiological capacity and drive for extended lactation shown in wild ruminants.

Although this argument for extended lactation is largely conceptual, growing experimental evidence suggests practicing extended lactation is viable and profitable. Lactation has been maintained naturally in goats for 4 yr (Linzell, 1973) and in cattle for nearly 2 yr (Auldist et al., 2007); with bST supplementation, it has been maintained for more than 2 yr in cattle (van Amburgh et al., 1997). Milk production far into an extended lactation is less than around peak, but it is more than with production of a rebred animal during late pregnancy and its dry period (Figure 5). All predesigned experiments have demonstrated that, over the long term, extending lactation up to 16 mo (and sometimes longer) does not decrease daily production (van Amburgh et al., 1997; Rehn et al., 2000; Arbel et al., 2001; Österman and Bertilsson, 2003; Salama et al., 2005; Auldist et al., 2007). In some cases, extending lactation has increased either total milk (second lactation of primiparous cows; Arbel et al., 2001) or component (protein and fat of goats; Salama et al., 2005) yields. The economic advantage of extended lactation ranged from \$0.12 to 0.21/(d of calving interval) among treatment groups in Arbel et al. (2001) and \$0.75/(d of productive life) in van Amburgh et al. (1997). [Note that earlier studies claiming no positive economic response (e.g., Holmann et al., 1984) were observational or theoretical, not experimental.] Although more research is clearly needed, these preliminary results suggest that the biological principles of extended lactation, as elucidated by wild ruminants, may be of great service to livestock production systems.

CONCLUSIONS

By offering a comparative vantage point, ruminant ecological and evolutionary research can offer valuable insight into livestock research. This research can reinforce and augment some conventional livestock practices, and if we allow, can challenge and help revise others. With further dialogue and cooperation between animal scientists and ecologists, the insights that ruminant ecology and evolution have to offer should grow in number and usefulness.

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APPENDIX

Global population estimates of wild ruminants were compiled from several sources (Whitehead, 1972; Ohtaishi and Gao, 1990; East, 1999; Nowak, 1999; Wiener et al., 2003; Ulvevadet and Klokov, 2004; Zhou et al., 2004; International Union for Conservation of Nature, 2008), many of which are compilations themselves. We excluded from our estimates domesticated, feral, captive, and nonnatively introduced populations or species. We also excluded species for which estimates were judged very fragmentary (that included only a few isolated or subspecies populations) and were unlikely to approach anything of a global estimate.

In all, we obtained estimates for 150 species (78% of total). This includes 1 species from Antilocapridae (100% of family total), 116 from Bovidae (83% of total), 26 from Cervidae (63% of total), 2 from Giraffidae (100% of total), 4 from Moschidae (80% of total), and 1 from Tragulidae (25% of total). Poor or nonexistent census data account for missing species. In addition, note that estimates for many Asian species include numbers only in China, again because of poor census data.

The population sizes reported here are clear underestimates. In total, they are still more comprehensive and up-to-date than the last apparent global census (McDowell, 1977), which estimated population numbers for only 11 species (excluding feral and currently unrecognized species) in 2 families (Bovidae, Cervidae), for a total of 27 million ruminants overall.