Oecologia (2000) 124:40–54

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The relationship between ecological segregation and sexual body size dimorphism in large herbivores

Received: 18 August 1999 / Accepted: 31 January 2000

Abstract Ecological segregation (sexual differences in diet or habitat use) in large herbivores has been intimately linked to sexual body size dimorphism, and may affect both performance and survival of the sexes. However, no one has tested comparatively whether segregation occurs at a higher frequency among more dimorphic species. To test this comparatively, data on sex-specific diet, habitat use and body size of 40 species of large herbivores were extracted from the literature. The frequency of ecological segregation was higher among more dimorphic herbivores; however, this was only significant for browsers. This provides the first evidence that segregation is more common among more dimorphic species. The comparative evidence supported the nutritional-needs hypothesis over the incisor breadth hypothesis, as there was no difference in frequency of segregation between seasons with high and low resource levels, and since segregation was also evident among browsers. Whether the absence of a correlation between ecological segregation and level of sexual body size dimorphism for intermediate feeders and grazers is due to biological differences relative to browsers or to the fact that the monomorphic species included in the analysis were all browsers is discussed.

Key words Body size · Ecological segregation · Ruminants · Sexual body size dimorphism · Sexual segregation

Introduction

The mechanisms behind sexual segregation among large herbivores have been extensively debated in the last decade (Main and Coblentz 1990; Miquelle et al. 1992; Bon and Campan 1996; Main et al. 1996; Bleich et al. 1997; Gross 1998; Main 1998). A recent advance has been to separate sexual segregation into social segregation (grouping with their own sex), spatial segregation (sexual differences in space use), diet segregation (sexual differences in diet use) and habitat segregation (sexual differences in habitat use) (Conradt 1998a). Conradt (1998b, 1999) and Ruckstuhl (1998) have convincingly demonstrated that size-related differences in foraging behaviour between males and females (see also Grubb and Jewell 1974; Pellew 1984; Seip and Bunnell 1985; Holmes 1988; Komers et al. 1993; Frid 1994; Ginnett and Demment 1997; Pérez-Barbería et al. 1997; but see Melton et al. 1990; Roberts and Dunbar 1991; Oakes et al. 1992) may lead to social segregation. However, ecological segregation (diet and habitat segregation combined) occur independently of social segregation (Conradt 1998b), and is especially important since it may affect both performance and survival of the sexes (Clutton-Brock et al. 1982; Owen-Smith 1993; Forsyth 1999).

Body size is regarded as a major factor in the nutritional ecology of large herbivores (Bell 1971; Jarman 1974; Demment and Van Soest 1985). Since the relative energy requirements decrease with increasing body size ($\text{weight}^{0.75}$), while rumen volume is isometric with size, large herbivores can survive on a lower-quality diet than smaller ones (the Jarman-Bell principle; Bell 1971; Geist 1974; Jarman 1974). Two proposed mechanisms for ecological segregation among herbivores incorporate this principle; the nutritional-needs hypothesis (NNH; Demment and Van Soest 1985) and the incisor breadth hypothesis (IBH; Clutton-Brock and Harvey 1983; Clutton-Brock et al. 1987; Illius and Gordon 1987; Gordon and Illius 1988). The NNH predicts that males should accept lower diet and habitat quality than females only when they are larger, since high-quality items are rare (i.e. there is a negative relationship between abundance and quality) and larger herbivores can subsist on a lower-quality diet than smaller herbivores (Demment and Van Soest 1985).

The basis of the IBH is that intake is partially limited by the incisor arcade breadth (which scales to $\text{weight}^{0.33}$) in periods of limited food supply, i.e. when grass swards

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are grazed to short levels, whereas intake is about isometric ($\text{weight}^{0.9}$) to body size in periods with no food restriction, i.e. when grass swards are tall (Clutton-Brock and Harvey 1983; Illius and Gordon 1987; Gordon and Illius 1988). Whenever the scaling coefficient of intake is lower than requirements ($\text{weight}^{0.75}$), small herbivores have a competitive advantage since each bite will represent a larger fraction of the daily metabolic requirements. The IBH therefore predicts that in periods of low resource levels, females outcompete males from mutually preferred swards only when males are larger. The IBH thus predicts, in contrast to the NNH, sexual segregation only in periods of limited food supply (winter in temperate areas/dry season in tropical areas), and this mechanism may only be applicable to grazing herbivores (Gordon and Illius 1988; du Toit 1995).

Apart from body size dimorphism, there is also much evidence supporting the reproductive-strategy hypothesis (RSH) as an important mechanism of ecological segregation (Main and Coblentz 1990; Miquelle et al. 1992; Main et al. 1996; Bleich et al. 1997), while social factors (Bon and Campan 1996) are more important for social segregation (Clutton-Brock et al. 1987). The RSH states that males should seek high-quality forage in order to improve body condition and growth, since fighting ability, which is correlated with body size, greatly influences their reproductive success. Females should select habitats that maximize their ability to raise young since this limits their reproductive success. Among ungulates, there are often extremely high (and highly variable) levels of mortality among newborn and young (Linnell et al. 1995; Gaillard et al. 1998). Since females take care of young, they should find areas with few predators, even at the expense of forage quality. The RSH predicts no comparative pattern of ecological segregation with regard to sexual body size dimorphism.

Even though sexual body size dimorphism is an integral part of the theory of sexual segregation (above), no one has presented comparative evidence that sexual segregation is more common in more dimorphic species. This is best tested using ecological segregation, since (1) social segregation can only be observed among gregarious herbivores (Conradt 1998b), and group size is closely correlated with levels of sexual body size dimorphism (Weckerly 1998; Loison et al. 1999) and (2) spatial segregation is very dependent on the spatiotemporal scale of observation (Bowyer et al. 1996). Here, I analyse whether ecological segregation is more common among more dimorphic species by comparing data on sex-specific diet and habitat use from 40 species of large herbivores with different feeding styles from both seasons when resource levels are high (summer/wet season) and low (winter/dry season).

Materials and methods

Data on diet and habitat use by both sexes of 40 temperate and tropical large herbivores were retrieved from the literature by searching in Zoological Records (volume 115–133) in WebSPIRS including the words “diet” or “habitat” and by looking in the reference lists of these papers (Appendix 1). Only studies published in English were included. Data were organized into four seasons (January–March, April–May, June–August, September–December), but if there was overlap with two categories, the study was included in only one category if the overlap was less than a month. Studies where data did not come from a specific season (Langlands 1969; Sinclair 1977; Hart 1992; Clemente et al. 1995) were excluded. For territorial species, only comparisons between territorial males and adult females were included, while non-territorial individuals were excluded. A broad definition of habitat was used (e.g. Wiens et al. 1993), including forage quantity, quality, risk/security factors (e.g. cover and number of predators), altitude and availability of water and minerals (salt). Data on feeding type were extracted from Hofmann (1989) and Loison et al. (1999), while data on body weights were extracted from various sources (Appendix 1).

Statistical analysis

Since information regarding ecological segregation was extracted from a variety of sources using very different indices of segregation, only the presence or absence of segregation was recorded. For each species, the number of habitat/food indices showing segregation (S_i, i=1, 2, ... , N) and the total number of indeces (n) were counted (Appendix 1). Under the assumption of independence of S_i, the number of indices showing segregation can be assumed to have a binomial distribution Bin(S_i, $p_{(Si)}$), where $\mathrm{p}_{(Si)}$ is the probability of species i being segregated (which can be estimated as $\hat{p}=S_i/n$ and $n=n_{(Si)}+n_{(1-(Si))}$); subsequently, logistic regression was used (Hosmer and Lemeshow 1989). Any violation of the assumption of independence will lead to unaccounted heterogeneity (overdispersion). This is usually assessed by statistical significance of the residual deviance (i.e. the goodness-of-fit statistic) of the fitted model. However, due to low sample size for many species, I used a quasi-likelihood test that need not correspond to any particular distribution, and which can be used to combine any available link and variance function (Venables and Ripley 1994). The level of sexual body size dimorphism was calculated as the proportional size difference between the heaviest (H) and lightest sex (L) $\{\log[(H-L)/L]\}$. I included season as a factor (high/low) in the model, based on assumed resource levels. For temperate-region herbivores, low and high resource levels were regarded as winter and summer, respectively. For tropical-region herbivores, low and high resource levels were regarded as summer (dry season) and winter (wet season), respectively. Although timing of the seasons, especially the wet season, may vary regionally in tropical regions and introduce more variation, this should not produce any bias. Climatic region (tropical/temperate) and feeding type (browser/intermediate feeder/grazer/non-ruminant) were included into the model since the IBH may only apply to grazers. Unfortunately, although the literature on the statistical treatment of phylogenetic data is considerable (Harvey and Pagel 1991; Martins and Hansen 1996), no method is available to treat data used in logistic regression (Martins and Hansen 1996). To at least partly account for phylogeny, I used as a factor in the analysis whether the herbivore was a cervid, bovid or came from another phylogenetic family (data from Loison et al. 1999). Mountain bighorn sheep (*Ovis canadensis canadensis*) and desert bighorn sheep (*O. c. mexicana* and *O. c. nelsoni*) were treated as different species due to large differences in body size and in sexual body size dimorphism. The omnivorous wild boar (*Sus scrofa*) was included since it is predominantly a herbivore (Jedrzejewska and Jedrzejewski 1998).

Results

The frequency of ecological segregation among large herbivores increased with increasing levels of sexual body size dimorphism (logistic regression, n=69, df=1, χ^2=101.120, P=0.024). The frequency of ecological seg-

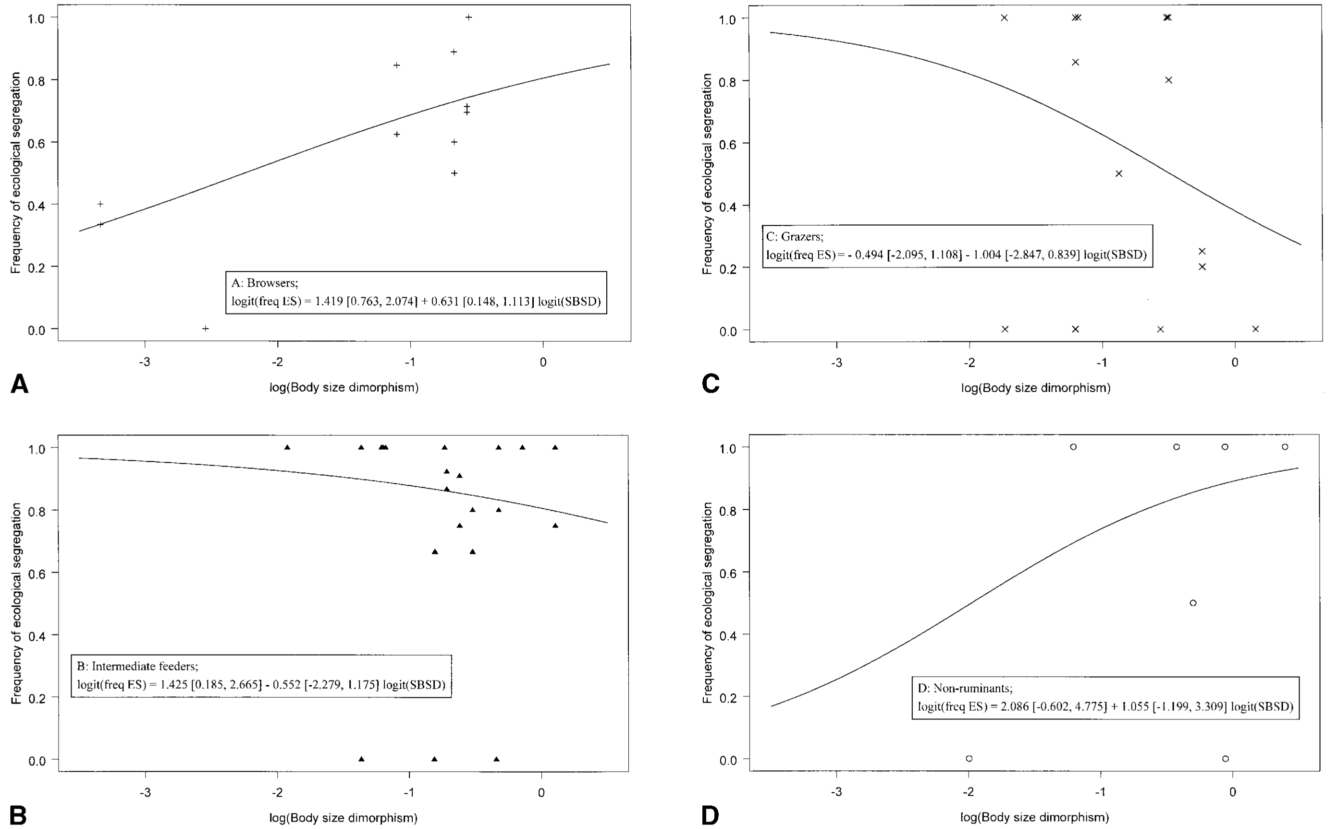

Fig. 1 The relationship between frequency of ecological segregation (*freq ES*) and sexual body size dimorphism (*SBSD*; log transformed) among large herbivores of different feeding types; browsers (**A**), intermediate feeders (**B**), grazers (**C**) and non-ruminants (**D**). Note that the relationship between frequency of ecological segregation and sexual body size dimorphism was only significant for browsers when conducting separate analyses for each feeding type. Note also that data points were weighted by the (square root) number of food/habitat indices in the analysis

regation was also variable among herbivores of different morphological feeding types (df=3, χ^2=88.361, P=0.006). Furthermore, feeding type and level of sexual body size dimorphism interacted significantly (Fig. 1; df=3; χ^2=80.058; P=0.040). When conducting separate analyses for each feeding type, there was only a significant effect of level of sexual body size dimorphism on frequency of ecological segregation among browsers (n=12, df=1, χ^2=9.782, P=0.021). There was no significant negative or positive effect in intermediate feeders (n=27, df=1, χ^2=28.320, P=0.463), grazers (n=17, df=1, χ^2=32.291, P=0.148) or among non-ruminants (n=9, df=1, χ^2=14.408, P=0.169), but note that variation in the level of sexual body size dimorphism was low for these feeding types. For the full model, levels of ecological segregation did not vary significantly with phylogenetic affiliation (df=2, χ^2=106.188, P=0.080), among seasons with different resource levels (df=1, χ^2=100.904, P=0.642) or among climatic regions (df=1, χ^2=100.649, P=0.613). No other interactions were significant when incorporated into the model (all P>0.15). There was no evidence of overdispersion in the model (χ^2=74.877, df=57, P>0.05), thus supporting the assumption of independence in S_i.

Discussion

This study provides the first comparative evidence that frequency of ecological segregation increases with increasing levels of sexual body size dimorphism. However, this relationship was dependent on morphological feeding type (sensu Hofmann 1989), as frequency of ecological segregation only increased significantly with increasing levels of sexual body size dimorphism for browsers. This was thus contrary to the predictions of the IBH, since it is unlikely that incisor arcade breadth limits intake in browsers (du Toit 1995), and frequency of segregation was expected to be higher at low seasonal resource levels if the IBH applies (Clutton-Brock et al. 1982; Illius and Gordon 1987), which was not the case. Further, Conradt et al. (1999) have provided experimental evidence that habitat segregation in red deer (*Cervus elaphus*) on the Isle of Rhum, Scotland, was not caused by indirect competition. With the current knowledge, the NNH is thus a more likely mechanism behind ecological segregation than the IBH.

Feeding type is considered an important axis of niche differentiation in ruminants (Hofmann 1973, 1989), although recent empirical testing has demonstrated that body size is more important than feeding type for ruminant ecology (Gordon and Illius 1994, 1996; Robbins et al. 1995; Mysterud 1998; Pérez-Barbería and Gordon 1999; but see Iason and Van Wieren 1999). There was also evidence that segregation did occur among virtually monomorphic species, although less frequently (Fig. 1, Appendix 1). There is substantial support for predictions from the RSH regarding spatial, temporal and intra-sexual patterns of segregation (Main and Coblentz 1990; Miquelle et al. 1992; Kohlmann et al. 1996; Main et al. 1996; Bleich et al. 1997; Appendix 1). One may speculate that different nursing strategies of young along the hider-follower continuum (Lent 1974) in different habitats may in part explain the effect of feeding type.

The lack of and tendency for a reversed relationship between frequency of ecological segregation and increasing levels of sexual body size dimorphism in intermediate feeders and grazers (Fig. 1) should be interpreted with caution. There were no data on sex-specific diet and habitat use from monomorphic species among intermediate feeders and grazers. This may reflect the fact that few such species exist (Weckerly 1998; Loison et al. 1999), but also, possibly, that segregation is not always sought in species with low levels of dimorphism. Illius and Gordon (1987) suggested that, based on their model, segregation should occur when males are about 20% larger than females. If there is a threshold difference in sexual body size dimorphism above which segregation occurs, this may not be possible to detect with the current data set with no grazers below this threshold.

There are some further problems with the current analysis. Phylogenetic affiliation was only partly accounted for by including family into the model, since, unfortunately, no phylogenetic method is available to treat data in logistic regression (Martins and Hansen 1996). Although phylogeny may pose a problem to any comparative analysis (Harvey and Pagel 1991; Martins and Hansen 1996), body size and sexual body size dimorphism are not a conservative trait among large herbivores (Weckerly 1998; Loison et al. 1999), and for other taxonomic groups, sexual body size dimorphism may actually be population specific (Bondrup-Nielsen and Ims 1990; Yoccoz and Mesnager 1998). In ungulates, the effect of body size on activity was not affected when incorporating phylogeny into the analysis, whereas the effect of feeding type was lowered (Pérez-Barbería and Gordon 1999). Therefore, phylogeny may not be an important problem with regard to the effect of sexual body size dimorphism.

Since information regarding ecological segregation was extracted from a variety of sources using very different indices of segregation, only the presence or absence of segregation was recorded, and thus some information was lost. Conradt (1998a) provides a new index of social, spatial and habitat segregation that is stochastically unrelated to sex ratio, population density or group size, which have plagued other indices. This is a major step forward in the study of sexual segregation (Pérez-Barbería and Gordon 1998), and will make future comparative work easier. However, it may take decades before enough studies on ecological segregation using this index have been published to provide enough data for a new comprehensive comparative analysis.

Acknowledgements I thank Norman Owen-Smith, Jerry Thomas Warren, Nigel G. Yoccoz and two anonymous referees for valuable comments on the manuscript. Iain J. Gordon stimulated my interest in sexual segregation by suggesting this as a topic for my trial lecture for my doctoral defence. I also thank Joseph Fox and Rich B. Harris for information regarding Tibetan ungulates, and Nils Chr. Stenseth for information about Africa. Special thanks to Nigel G. Yoccoz for very valuable help with the statistical analysis. Discussions with Thomas F. Hansen and Rolf A. Ims regarding the statistical treatment of the data are also appreciated.

Appendix 1 Data on diet (*F*; *Ql* quality, *Qn* quantity, *Com* composition) and habitat (*H*; *S* security e.g. steep/rugged terrain or cover, *P* number of predators, *A* altitude, *W* water, *M* mineral/salt) use of male (*m*) and female (*f*) large herbivores from different regions (*Reg*; *Tr* tropical; *Te* temperate) obtained by various methods (*Met*; *DO* direct observation, *RT* radio-telemetry, *Rum* rumen/stomach content analyses, *Fec* faecal content analyses, *OF* oesophageal fistulae). The number in species name rows under the different seasons indicates the proportion of indices showing segregation over the total number of indices. Reference on line of species name indicates from where data on body weights were extracted; for references of feeding type (*FT*; *CS* concentrate selector, *IF* intermediate feeder, *GR* grass roughage eaters, *NR* non-ruminant herbivore), see Materials and methods

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
Aepyceros melampus	Tr	IF	57,216	43,970		2/2		2/2			Loison et al. 1999
					FCom: m≠f					Rum	Stewart 1971
					HS: m<f					DO	Jarman and Sinclair 1979
					FCom: m=f FQl: m<f					Rum, Fec	Dunham 1980
						FCom: m≠f FQl: m<f		FCom: m≠f FQl: m<f	FCom: m≠f FQl: m<f	Rum	Van Rooyen and Skinner 1989
Alces alces	Te	CS	440,000	330,500		5/8		11/13			Loison et al. 1999
								HS: m<f		DO	Peterson 1955
						H: m=f	H: m=f	H: m=f	H: m≠f	DO	Hauge and Keith 1981
						H: m≠f		H: m≠f	H: m≠f	RT	Mytton and Keith 1981
							HP: m>f FCom: m≠f FQl: m>f	HP: m>f FCom: m≠f FQl: m>f		DO	Edwards 1983
								HS: m<f		DO	Stephens and Peterson 1984
						HA: m=f HM: m=f		HA: m>f HM: m<f	HA: m>f HM: m<f	RT	Miller and Litvaitis 1992
					FCom: m≠f FQl: m<f	H: m≠f HFQn: m>f HS: m>f		H: m≠f HS: m<f HFQn: m>f		RT	Miquelle et al. 1992
						H: m≠f	H: m=f	H: m=f	H: m=f	RT	Kufeld and Bowden 1996
					H: m≠f					RT	MacCracken et al.1997
Antidorcas marsupialis	Te	IF	30,600	26,700				1/1			Loison et al. 1999
								FCom: m≠f		Rum	Davies et al. 1986
Axis axis	Tr	GR	88,000	55,000		1/1		1/1			Loison et al. 1999
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	RT	Moe and Wegge 1994
Bison bison	Te	IF	469,900	274,750		0/1		0/1			Loison et al. 1999
						H: m=f		H: m=f		DO	Larter and Gates 1991
Bos taurus	Te	GR	500,000	425,000		0/1		1/1			Lazo and Soriguer 1993
						H: m=f	H: m≠f	H: m≠f	H: m=f	DO	Hall 1988
Capra hircus	Te	IF	67,143	46,429		2/3		2/3			Mason 1981
						H: m≠f		H: m=f		DO	Riney and Caughley 1959
						H: m=f	H: m≠f	H: m≠f	H: m=f	DO	Gordon 1989
						H: m≠f		H: m≠f		DO	Gordon and Illius 1989
Capra ibex	Te	IF	95,000	45,000		3/4		4/4			Loison et al. 1999
						HFQl: m<f				DO	Nievergelt 1981
						HA: m<f	HA: m<f		HA: m=f	DO	Francisci et al. 1985

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
						H: m≠f HA: m=f	H: m≠f HA: m>f HS: m>f HFQl: m<f	H: m≠f HA: m>f HS: m<f HFQl: m>f	H: m=f HA: m>f	DO	Villaret et al. 1997
Capra pyrenaica	Te	IF	70,000	37,500		2/2		1/1			Loison et al. 1999
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Alados 1985
						FCom: m≠f				DO	Alados and Escos1987
Capreolus capreolus	Te	CS	27,680	26,730		1/3		2/5			Loison et al. 1999
								HFQn: m<f		RT	Thor 1990
								H: m=f		RT	Selås et al. 1991
								HS: m=f HFQn: m<f		RT	Mysterud 1996
						H: m=f		H: m=f		RT	Mysterud et al. 1999a
						HS: m<f HFQnQl: m=f				RT	Mysterud et al. 1999b
Cervus canadensis	Te	IF	312,000	238,667		1/1		1/1			Loison et al. 1999
						FCom: m≠f	FCom: m≠f	FCom: m≠f	FCom: m=f	DO	Harper et al. 1967
Cervus elaphus	Te	IF	160,000	107,500		13/15		12/13			Loison et al. 1999
							HFQn: m<f	HFQn: m<f	HFQn: m<f	DO	Charles et al. 1977
						FQl: m<f	FQl: m<f	FQl: m<f	FQl: m<f	Rum	Staines and Crisp 1978
						HFQl: m<f HA: m<f				DO	Watson and Staines 1978
					HA: m=f	HA: m<f H: m≠f HFQn: m>f	HA: m<f H: m≠f	HA: m<f H: m≠f HFQn: m>f	HA: m<f H: m≠f	DO	Clutton-Brock et al.1982, 1987
						FCom: m≠f FQl: m<f HFQl: m<f	FCom: m≠f FQl: m<f HFQl: m<f		FCom: m≠f FQl: m<f HFQl: m<f	Rum, DO	Staines et al. 1982
						HA: m>f H: m≠f		HA: m>f H: m≠f		DO	Osborne 1984
					H: m≠f					RT	Catt and Staines 1987
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Gordon 1989
						H: m≠f		H: m≠f		DO	Gordon and Illius 1989
								FCom: m≠f FQl: m<f	FCom: m≠f FQl: m<f	Fec	Kerridge and Bullock 1991
						H: m=f	H: m=f	HFQl: m<f	HFQl: m<f	DO	Lazo et al. 1994
						FCom: m=f	FCom: m=f	FCom: m=f	FCom: m=f	Rum	Groot Bruinderink and Hazebroek 1995
Cervus nippon	Te	IF	79,867	50,133		4/5		2/3			Loison et al. 1999
						FCom:,m≠f	FCom:,m≠f		FCom:,m≠f	Fec	Takatsuki 1980
						HFQl: m>f	HFQl: m>f	HFQl: m=f	HFQl: m=f	DO	Koga and Ono 1994
						FCom: m≠f	FCom: m≠f	FCom: m≠f	FCom: m≠f	Fec	Padmalal and

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
						FQl: m>f	FQl: m>f	FQl: m>f	FQl: m>f		Takatsuki 1994
						FQl: m=f			FQl: m>f	Rum	Asada and Ochiai 1996
Dama dama	Te	IF	71,000	41,200		3/4		4/5			Loison et al. 1999
						FCom: m≠f FQl: m>f	FCom: m≠f FQl: m<f	FCom: m≠f FQl: m<f	FCom: m≠f FQl: m=f	Fec	Putman et al. 1993
								FCom: m=f FQl: m>f	FCom: m=f FQl: m>f	Fec	Kerridge and Bullock 1991
					H: m=f					DO	Thirgood 1995
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Apollonio et al. 1998
Elaphus maximus	Tr	NR	390,000	300,000		3/3		3/3			Weckerly 1998
					FCom: m≠f					DO?	Owen-Smith 1988
						FQl: m>f HFQlQn: m>f HS: m<f	FQl: m>f HFQlQn: m>f HS: m<f	FQl: m>f HFQlQn: m>f HS: m<f	FQl: m>f HFQlQn: m>f HS: m<f	DO	Sukumar and Gadgil 1988
Equus caballus	Tr	NR	407,000	358,333		0/1		0/1			f: Wolfe et al. 1989; m: Feh 1990
						FCom: m=f	FCom: m=f	FCom: m=f	FCom: m=f	Fec	Lenarz 1985
Gazella granti	Tr	IF	65,000	45,000		0/1					Loison et al. 1999
						FCom: m=f				Rum	Spinage et al. 1980
Giraffa camelopardalis	Tr	CS	110,000	70,000				3/3			Weckerly 1998
					H: m≠f					DO	Foster 1966
					H: m≠f					DO	Foster and Dagg 1972
					H: m≠f HFQn: m<f FQl: m<f					DO	Pellew 1984
								H: m≠f HS: m<f F: m≠f		DO	Young and Isbell 1991
Kobus ellipsiprimnus	Tr	GR	238,000	183,000		0/2		0/2			Loison et al. 1999
						FQl: m=f H: m=f	FQl: m=f H: m=f	FQl: m=f H: m=f	FQl: m=f H: m=f	DO, Fec	Tomlinson 1979
					H: m≠f					DO	Wirtz and Kaiser 1988
Kobus leche	Tr	GR	104,000	79,500		1/1		1/1			Loison et al. 1999
					HFQl: m<f	H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Williamson 1990
Macropus fuliginosus	Tr	NR	53,500	27,500		0/1		1/1			Weckerly 1998
						H: m=f		H: m≠f		DO	Johnson and Bayliss 1981

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
Macropus	Tr	NR	66,000	26,500		2/2		2/2			Weckerly 1998
						F: m≠f		F: m≠f		Rum	Newsome 1980
						H: m≠f		H: m≠f		DO	Johnson and Bayliss 1981
Madoqua kirkii	Tr	CS	5,100	5,500		0/1		0/1			Loison et al. 1999
						FCom: m=f		FCom: m=f	FCom: m=f	DO	Manser and Brotherton 1995
Odocoileus hemionus	Te	CS	87,500	56,000		5/7		16/23			Loison et al. 1999
							HS: m<f	HS: m>f	HS: m>f	DO	Dasmann and Taber 1956
								HA: m>f HFQn: m<f HS: m<f		DO	King and Smith 1980
					HFQl: m<f		H: m≠f HW: m<f HFQn: m=f	H: m≠f HW: m<f HFQn: m=f	H: m≠f HW: m<f HFQn: m=f	DO	Bowyer 1984
						HA: m=f	HA: m=f	HA: m=f	HA: m=f	RT	Schoen and Kirchhoff 1985
					H: m=f HS: m<f					DO	Bowyer 1986
					H: m≠f HW: m=f	HA: m<f HW: m=f	H: m=f HA: m<f HW: m=f	H: m=f HA: m<f HW: m=f	H: m=f HA: m<f HW: m=f	RT	Ordway and Krausman 1986
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	RT	Ragotzkie and Bailey 1991
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	RT	Weckerly 1993
								H: m=f		DO	Bowyer et al. 1996
								H: m≠f HS: m<f HP: m>f HW: m<f HFQn: m>f HFQl:m=f FQl: m>f	FQl: m=f	DO, Fec	Main and Coblentz 1996
						H: m≠f HW: m>f		H: m≠f HW: m<f		RT	Nicholson et al. 1997
Odocoileus virginianus	Te	CS	68,000	45,000		6/10		8/9			Loison et al. 1999
					FCom: m=f					Rum	McCullough 1979
							FCom: m≠f	FCom: m≠f		Rum	Korschgen et al. 1980
									FCom: m≠f FQl: m<f	Rum	Warren and Krysl 1983
						FCom: m=f			FCom: m=f	Rum	McCullough 1985
								H: m≠f		RT	Tierson et al. 1985
					FQl: m<f	FCom: m≠f FQl: m<f				Fec, Rum	Beier 1987, 1988
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Scarbrough and Krausman 1988
						H: m≠f	H: m=f	H: m=f	H: m=f	DO	McCullough et al. 1989
						H: m≠f	H: m≠f	H: m≠=f	H: m≠f	RT	Beier and McCullough 1990

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
						FCom: m=f FQl: m=f			FCom: m≠f FQl: m≠f	Rum	Weckerly and Nelson 1990
								H: m≠f HFQlQn: m>f	FCom: m=f H: m≠f HFQlQn: m>f	DO, Rum	LaGory et al. 1991
						H: m=f	H: m=f	H: m≠f	H: m=f	RT	Nixon et al. 1991
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	DO	Kie and Bowyer 1999
Oreamnos americanus	Te	IF	69,000	53,000				1/1			Loison et al. 1999
								HS: m<f		DO	Chadwick 1983
					H: m=f					RT	Singer and Doherty 1985
Ovibos moschatus	Te	IF	334,000	266,000		0/1		2/2			Loison et al. 1999
							FCom: m≠f	FCom: m≠f		Fec	Oakes et al. 1992
						H: m=f		H: m≠f	H: m≠f	DO	Forchhammer 1995
Ovis ammon	Te	GR	130,000	60,000				0/1			Geist 1971
								H: m=f		DO	Harris and Miller 1995
Ovis canadensis candensis	Te	GR	93,875	72,107		6/7		3/3			Loison et al. 1999
						H: m≠f	H: m≠f		H: m≠f	DO	Geist and Petocz 1977
						HS: m>f HA: m=f	HS: m=f HA: m>f			DO	Morgantini and Hudson 1981
						HF: m≠f FCom: m≠f	FCom: m=f		FCom: m=f	DO, Fec	Shank 1982
						HA: m>f HS: m>f				DO	Tilton and Willard 1982
							HA: m<f HFQn: m>f HP: m>f FQl: m>f	HA: m<f HFQn: m>f FQl: m>f		DO, Fec	Festa-Bianchet 1988
							HS: m<f			DO	Berger 1991
Ovis canadensis nelsoni/mexicana	Te	GR	70,746	43,989		3/3		4/5			Loison et al. 1999
					H: m≠f					RT	Bates and Workman 1983
								HA: m>f H: m≠f		RT	Gionfriddo and Krausman 1986
					HA: m>f HF: m>f HFQl: m=f	H: m≠f FCom: m≠f	H: m≠f FCom: m=f	H: m≠f FCom: m=f	H: m≠f FCom: m=f	RT, Fec	Krausman et al. 1989
						FCom: m≠f	FCom: m≠f	FCom: m≠f	FCom: m≠f	Fec	Miller and Gaud 1989
					H: m≠f HFQn: m>f HS: m<f HW: m<f HP: m>f FQnQl: m>f FCom: m≠f					RT, Fec	Bleich et al. 1997

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
Ovis dalli	Te	GR	76,600	48,800				0/2			Weckerly 1998
								FCom: m=f FQl: m=f		Fec	Seip and Bunnell 1985
Ovis gmelini	Te	GR	36,500	20,500		1/5		1/4			Cransac et al. 1998[a]
							H: m≠f HA: m>f HS: m<f HFQn: m>f			DO	Bon et al. 1995
						H: m=f HS: m=f	H: m≠f HS: m<f	H: m=f HS: m=f	H: m≠f HS: m<f	DO	Cransac and Hewison 1997
						FCom: m=f			FCom: m=f	Rum	Cransac et al. 1997
						H: m≠f HS: m=f	H: m=f HS: m<f	H: m≠f HS: m=f	H: m≠f HS: m=f	DO	Cransac et al. 1998
Pantholops hodgsoni	Tr	IF	45,500	27,500				2/2			Schaller and Junrang 1988
								H: m≠f HA: m>f		DO	Harris and Miller 1995
Procapra picticaudata	Tr							2/2			
								H: m≠f HA: m<f		DO	Harris and Miller 1995
Rangifer tarandus	Te	IF	136,667	88,867		3/4		20/22			Loison et al. 1999
								H: m≠f HS: m<f FCom: m≠f		Fec	Helle 1980
								H: m≠f HF: m>f HS: m<f	H: m=f HF: m=f HS: m=f	DO	Van Wieren and de Bie 1980
						HA: m≠f	HA: m=f	HA: m=f	HA: m=f	RT	Fuller and Keith 1981
						FCom: m≠f	FCom: m=f	FCom: m=f	FCom: m=f	Rum	Leader-Williams et al. 1981
								HA: m<f HP: m>f HFQn: m>f		DO	Bergerud et al. 1984
								H: m≠f HS: m<f HFQl: m>f		DO	Curatolo 1985
								HA: m<f HS: m<f HFQn: m>f		RT	Simpson et al. 1985
						H: m≠f				DO	Carruthers et al. 1986
							HP: m>f HFQnQl: m>f FQl: m>f	HP: m>f HFQnQl: m>f FQl: m≥f		DO, Fec	Heard et al. 1996
						H: m=f	H: m≠f HP: m>f HFQnQl: m>f	H: m≠f	H: m=f	DO	Jakimchuk et al.1987

Appendix 1 (continued)

Species	Reg	FT	Male weight (g)	Female weight (g)	Year	January–March	April–May	June–August	September–December	Met	Reference
								H: m≠f		DO	Chetkiewicz et al. 1992
Redunca arundinum	Tr	GR	68,000	48,000		1/2		1/2			Loison et al. 1999
						H: m≠f HS: m=f		H: m≠f HS: m=f		DO	Howard 1986
Rupicapra pyrenaica	Te	IF	30,500	23,500		4/4		4/4			Couturier 1938 cited in Pepin et al. 1996
						H: m≠f		H: m≠f		DO	Lovari and Cosentino 1986
						H: m≠f FQl: m<f FCom: m≠f	H: m≠f FQl: m<f FCom: m≠f	H: m≠f FQl: m<f FCom: m≠f	H: m≠f FQl: m<f FCom: m≠f	DO, Fec	Pérez-Barbería et al. 1997
Rupicapra rupicapra	Te	IF	38,500	26,000				2/2			Loison et al. 1999
								HFQlQn: m<f HA: m>f		DO	Shank 1985
Sus scrofa	Te	NR	90,000	51,700				1/2			Gallo Orsi et al. 1992
					FCom: m=f					Rum	Groot Bruinderink et al. 1994
							HS: m<f HFQn: m=f	HS: m<f HFQn: m=f	HS: m<f HFQn: m=f	RT	Spitz and Janeau 1995
Tragelaphus strepticeros	Tr	CS	257,000	170,000		1/2		1/2			Loison et al. 1999
						H: m=f	H: m=f	H: m=f	H: m=f	DO	Simpson and Cowie 1967 reanalysed in du Toit 1995
						H: m≠f	H: m≠f	H: m≠f	H: m≠f	RT	du Toit 1995

[a] Larder weight

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