

SEASONALITY OF SEXUAL SEGREGATION IN DIMORPHIC DEER: EXTENDING THE GASTROCENTRIC MODEL

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ABSTRACT: We extend our gastrocentric model for sexual segregation in dimorphic deer (Cervidae) to include seasonal metabolism of energy and protein in reproductive female, nonreproductive female, and male reindeer and caribou (*Rangifer tarandus*). We define sexual segregation as the differential use of space by the sexes of animals outside the mating season. Minimum density of energy and protein in the diet is predicted to favor sexual segregation in late winter and summer, but not during autumn. Demands for energy during gestation and for energy and protein during lactation increase dietary minima for reproductive females above levels required by nonreproductive females and males. Projections of gross energy and total protein in diets based on estimated metabolizabilities for males and nonreproductive females predicted that males could subsist on the lowest-quality diets during summer. Projections of minimal dietary content of gross energy indicated that reproductive females probably would feed longer than nonreproductive females and males during summer, as suggested by field observations. Differences in feeding activity between the sexes may be a consequence of metabolic demands and, therefore, an outcome of sexual segregation rather than its cause. The gastrocentric model provides an explanation of behavioral ecology of deer with physiological data for 1 species. Further integration of these disciplines may predict the consequences of size and sex on niche partitioning in relation to environmental changes in forage quality and quantity. Nonetheless, simplistic models are only as valid as data upon which they are constructed. Our model indicates the dire need for studies of diet selection and nutritional physiology in the context of both reproductive status and seasonal demands for both sexes of cervids.

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Sexual segregation is the different use of space by male and female ungulates. Mating systems influence size dimorphism in ruminants because males are 20–70% larger than females in polygynous species (Weckerly 1998). Sexually dimorphic ruminants often segregate outside the mating season during winter, spring, and summer (e.g., Berger et al. 2001). Spatial differences between the sexes may result in different dietary selections and niche partitioning between the sexes (Kie and Bowyer 1999). Although sexual differences in diet may be the result of segregation when pre-

ation affects movement of animals (e.g., mountain sheep, *Ovis canadensis*; Bleich et al. 1997, Bleich 1999), sexual segregation persists in populations where predation is low or absent (Clutton-Brock et al. 1987). Metabolic demands for energy and nutrients may cause segregation and niche partitioning between the sexes. Barboza and Bowyer (2000) presented an allometric model of nutrient demands and digestive function to explain differences in diet selection among reproductive females, nonreproductive females, and males across a wide range of body masses. The model

predicted that large males consume abundant foods high in fiber content because high digestive capacity permits prolonged retention and greater digestion of the bulky fiber than in nonreproductive females. Reproductive females are better suited to postruminal digestion than are males, especially during gestation and lactation when food intake may increase with nutrient demands. Diet selection is probably reinforced by ruminal adaptation to high fiber in males, and by increases of hepatic and intestinal tissue in reproductive females (Barboza and Bowyer 2000). This simple model explains sexual segregation and niche partitioning without invoking competitive displacement of males by females (e.g., Clutton-Brock et al. 1987, Main and Coblentz 1996, Pérez-Barberia and Gordon 1999).

The gastrocentric model provides a framework for experimental tests of the hypothesis that sexual segregation is a consequence of the schedule of metabolic demands underlying sexual dimorphism. We now extend the model and address the dietary consequences of metabolic demands in a seasonal context by examining data for caribou and reindeer (*Rangifer tarandus*). Caribou are among the most dimorphic of polygynous ruminants; males are 70% heavier than females at peak mass (Weckerly 1998). Sexual segregation of caribou is apparent from aerial survey of migrating herds during late winter and spring (Cameron and Whitten 1979), and on calving grounds in summer (White et al. 1975). These northern herbivores are well suited to metabolic and digestive comparisons between seasons and between sexes (e.g., White and Fancy 1986). A short period of plant growth in summer emphasizes the ingestive, digestive, and metabolic response of both sexes to grow and establish body tissues for survival through the ensuing winter. Timing of reproductive effort and nu-

trient demands also differ between sexes. Reproducing females incur the greatest costs for gestation, parturition, and lactation from late winter to mid-summer, whereas males incur the greatest costs in autumn during the mating season.

Our extended model uses seasonal changes in body composition of caribou and reindeer with measures of basal metabolism, feeding rates, and feeding times. We estimate costs of antlers, milk, and uterine development, in addition to seasonal changes in basal metabolism to derive the minimum density of metabolizable protein and energy required in the diet during late winter, summer, and autumn. Therefore, we test our general model by applying it to the annual cycle for both sexes of 1 species by using direct measures and conservative estimates of incremental costs derived from other cervids and ruminants (sensu Boertje 1985, Adamczewski et al. 1993, Parker et al. 1999).

METHODS

Body Mass and Composition

We assumed that the seasonal pattern of changes in body composition relative to the maximum body mass were similar among subspecies and locations for *Rangifer*, even though body mass and composition vary greatly within this species (e.g., Ringberg et al. 1981, Tyler 1987, Chan-McLeod et al. 1995). Maximum body mass of both sexes was set at the average for a herd of captive animals held at the University of Alaska Fairbanks (Large Animal Research Station, Fairbanks, Alaska; 65°N 146°W): males 178 kg; females 106 kg. Lipid and protein content of the body without antlers and ingesta were calculated from maximum body mass in September with equations derived for caribou and reindeer by Gerhart et al. (1996). Patterns of body mass, lipid, and protein in females were calculated from those determined for breeding and

nonbreeding caribou in the wild by Chan–McLeod et al. (1999) for March–April (Julian month 3.5), June (Julian month 6), September (Julian month 9), and November–December (Julian month 11.5). The corresponding patterns of mass, lipid, and protein loss in males were calculated from data on captive reindeer during rut and subsequent mass changes from November through June (unpublished data). Daily rates of change in lipid and protein content at March–April, June, and September were calculated from the difference in mass over the subsequent interval (e.g., September–November) and the time elapsed between periods at $30.4 \text{ day}\cdot\text{month}^{-1}$. Equivalents of net energy for changes in protein and lipid in both sexes were 23.7 and 39.3 $\text{MJ}\cdot\text{kg}^{-1}$, respectively (Blaxter 1989).

Gestational costs were estimated for the last trimester (72 days of 216 days; McEwan 1972) and assumed 80% of fetal growth occurred during that period (Barboza and Bowyer 2000). Fetal mass was based on average birth mass of young caribou (6.8 kg) from the captive herd at the University of Alaska Fairbanks during 1999–2000. Fetal composition was estimated from equations for newborn caribou derived by Gerhart et al. (1996). Composition of the uterus was calculated on the basis of 82% fetal tissue in the gravid uterus (Ofstedal 1985). Milk production was estimated at $1,200 \text{ g}\cdot\text{day}^{-1}$ from the midpoint of the lactation curve for caribou at 40 days post partum when milk contained 11% protein and $9 \text{ kJ}\cdot\text{g}^{-1}$ (Parker et al. 1990).

Antler deposition was calculated for the minimum mass of males (115 kg; November) and nonreproductive females (79.5 kg; March–April) as $7.72 \text{ g}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$ based on estimates from male caribou (Geist 1998). Deposition of protein and energy in antlers were calculated for 152 days of growth (April 15 – August 15) with a dry composition of 45% protein and $10.6 \text{ kJ}\cdot\text{g}^{-1}$ (Robbins

1993) based on several species of deer.

Food Intake

Daily intake of dry food ($\text{g}\cdot\text{d}^{-1}$) was calculated as the product of instantaneous rates of intake ($\text{g}\cdot\text{min}^{-1}$) and the time spent consuming food ($\text{min}\cdot\text{d}^{-1}$). Maximum feeding times were held the same for males, nonreproductive females, and reproductive females at the level estimated for lactating female caribou in summer ($821 \text{ min}\cdot\text{day}^{-1}$; White et al. 1975) and for female caribou and reindeer on lichen ranges in March–April ($528 \text{ min}\cdot\text{day}^{-1}$; Holleman et al. 1979). Instantaneous intakes of dry matter were calculated from measures of females with esophageal fistulas that were published on the basis of 80 kg body mass (White et al. 1975, Holleman et al. 1979). Intakes were recalculated on the basis of metabolic body mass ($\text{kg}^{0.71}$; Shipley et al. 1994): $5.49 \text{ g}\cdot 80 \text{ kg}^{-1}\cdot\text{min}^{-1}$ or $0.24 \text{ g}\cdot\text{kg}^{-0.71}\cdot\text{min}^{-1}$ in winter, and $6.0 \text{ g}\cdot 80 \text{ kg}^{-1}\cdot\text{min}^{-1}$ or $0.27 \text{ g}\cdot\text{kg}^{-0.71}\cdot\text{min}^{-1}$ in summer. Feeding times and instantaneous rates of intake in autumn (September) were assumed to be the same as in late winter (March–April), because photoperiod was similar during those periods. Estimates of food intake are maximal because they do not include time spent searching for food and assume that instantaneous intakes are not limited by abundance or distribution of forage and by risk of predation.

Energy Demands

Basal energy expenditure was calculated from the fasting metabolic rate of nonreproductive females in winter ($403 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{day}^{-1}$; Fancy 1986). Basal energy expenditure was increased by 15% ($463 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{day}^{-1}$) in males to account for the greater proportion of lean tissue compared with females among domestic ruminants (National Research Council 1996). Similarly, basal energy expenditure during synthesis of tissues in pregnant females was

assumed to be 45% ($584 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$) higher based on measures of white-tailed deer (*Odocoileus virginianus*) during the third trimester of gestation (Pekins et al. 1998). Estimates of basal energy expenditure were increased by 14.5% in summer and autumn: 461 and 531 $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ in females and males, respectively. This increment is similar to seasonal changes measured in white-tailed deer (Worden and Pekins 1995) and domestic sheep (*Ovis aries*; Blaxter and Boyne 1982, Argo et al. 1999), but is considerably lower than estimates for growing caribou (25%; McEwan and Whitehead 1970) and adult moose (*Alces alces*; 40%; Regelin et al. 1985). The lower value makes the model conservative in predictions of sexual segregation.

The combined cost of activity and thermoregulation was assumed to be equivalent to basal energy expenditure in all groups (Robbins 1993, White 1993) with the concomitant assumption that activity was low when thermal costs were high (e.g., Cuyler and Øritsland 1993). Net energy of tissues was converted to metabolizable equivalents for maintenance and milk production at 80% efficiency (National Research Council 1996). Conversion of dietary metabolizable energy to tissue maintenance or deposition was 67.5%. This value is the average of measures for moose (71.1%) and white-tailed deer (63.9%) consuming browse (Robbins 1993), and is similar to the estimates for domestic cattle consuming a diet of 5 $\text{MJ} \cdot \text{kg}^{-1}$ fresh food (3 $\text{Mcal} \cdot \text{kg}^{-1}$ dry matter; Garrett 1980). Conversion of energy from food to tissue and then to milk was the product of the net energy efficiencies of tissue deposition (67.5%) and tissue use (80%), which was 54%.

Total expenditure of energy was calculated on the basis of metabolizable energy as the sum of basal expenditure, an equal amount for activity and thermoregulation, and equivalents for absolute changes of

tissues (body protein and fat, uterine tissue, milk, and antlers). Dietary demand for energy was the total expenditure minus the equivalent metabolizable energy from catabolism of body protein and lipid.

Protein Demands

Requirements for dietary protein were calculated from nitrogen parameters on the basis of 16 $\text{gN} \cdot 100\text{g}^{-1}$ protein. Digestible protein for maintenance was calculated as 2.89 $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$, based on measures of growing and adult caribou and reindeer in summer and winter (McEwan and Whitehead 1970). Maintenance requirements were increased by 10% in males to include the greater proportion of lean tissue compared with females (Barboza and Bowyer 2000). The maintenance requirement was reduced in all animals by 25% from summer to winter ($2.17 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$), because the annual mean N requirement varied by this proportion for maintenance of male white-tailed deer (Asleson et al. 1996). Metabolic fecal loss of protein was calculated from dry matter intake ($\text{kg} \cdot \text{d}^{-1}$) as 39 $\text{g} \cdot \text{kg}^{-1}$ from an estimate of several studies on reindeer and caribou (Robbins et al. 1987, Robbins 1993). Endogenous loss of urinary N was calculated as the equivalent loss of protein at 0.62 $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$, which was based on the mean for 5 species of cervids (Robbins 1993).

Total protein demand was calculated on the basis of metabolizable protein as the sum of the digestible requirement for maintenance, endogenous losses in feces and urine, and absolute changes in tissue protein (body, uterus, milk, and antlers). Dietary demand for protein was the total expenditure minus the equivalent protein from catabolism of body protein.

Digestive Function

Capacity of the digestive tract was calculated from body mass as 0.1159 $\text{g} \cdot \text{kg}^{-1.032}$

(Demment and Van Soest 1985), and expressed on the basis of dry matter by assuming an average moisture content of 84% in digesta (unpublished data). Rate of metabolizable energy extracted from digesta was the dietary energy demand divided by the capacity of the digestive tract ($\text{MJ}\cdot\text{day}^{-1}\cdot\text{kg}^{-1}$ dry digesta). Mean time (h) for holding digesta in the tract was the minimal dietary content of metabolizable energy ($\text{MJ}\cdot\text{kg}^{-1}$ dry diet) divided by the rate of energy extraction from digesta and expressed on an hourly basis ($\text{MJ}\cdot 24\text{h}^{-1}\cdot\text{kg}^{-1}$ dry digesta). Those calculations do not address physico-chemical attributes of the forage or the functional response of the animal (Barboza and Bowyer 2000). Furthermore, those calculations assume that digestive capacity varies with total body mass even though body composition and food intake differ between seasons and sexes.

Dietary Minima

Minimum dietary contents of metabolizable energy and protein were calculated as the daily dietary demand divided by the daily intake. Minimum gross energy and crude protein content of the diet for females were projected by setting metabolizability of energy at 60%, 70%, and 63% in late winter (Julian month 3.5), summer (Julian month 6), and autumn (Julian month 9), respectively. Those metabolizabilities were based on estimated dry-matter digestibilities of diets consumed by female caribou in the wild (Boertje 1990). Metabolizability of protein was set at 70%, 80%, and 75% to mimic changes in plant phenology at later winter, summer, and autumn, respectively. Corresponding metabolizabilities in males were increased by a factor of 1.2 for energy and by 1.1 for protein to mimic allometric effects of a larger digestive tract on fiber digestion and urea-nitrogen reutilization (Barboza and Bowyer 2000).

RESULTS

Males reached peak body mass and content of protein and lipid at the mating season in September (Fig. 1). Females also achieved peak mass in September, but varied the pattern of lipid and protein mass. Nonreproductive females attained peak protein and lipid mass in November, whereas those body reserves peaked during late winter in March–April for reproductive females (Fig. 1). Small body mass of nonreproductive females resulted in the lowest predictions of maximum dry matter intake during late winter and summer (Fig. 2). Greater body mass of males in September

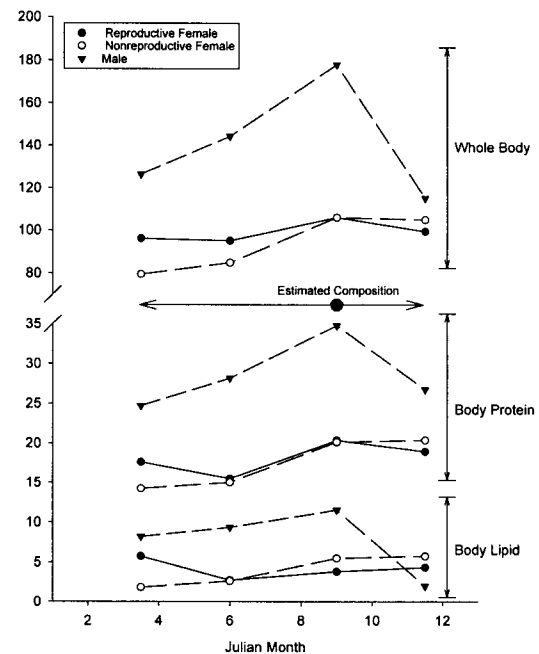


Fig. 1. Estimated mass (kg) of the whole body and its content of lipid and protein for a reproductive female, nonreproductive female, and male caribou. Body composition is calculated for the maximum body mass in September, which is the basis for estimated changes in composition (gray point and arrows). Lipid and protein levels are based on the annual pattern described in wild female caribou (Chan-McLeod et al. 1999) and in captive male reindeer (unpublished data). Maximum mass is 178 kg for males and 106 kg for females.

also resulted in higher intakes of dry matter than for late winter even though feeding times and feeding rates were set at the same level during those periods (Fig. 2).

Energy demands were greatest for basal metabolism and activity plus thermoregulation in both sexes (Fig. 3). Milk production was 40% of total energy expended by reproductive females in summer, whereas uterine development was only 2% of energy expended in late winter, and was exceeded by catabolism of body tissue (6% of expenditure; Fig. 3). Tissue catabolism reduced demands for energy and protein from diets for reproductive females during winter and for males during rut in September (Figs. 3 and 4). Endogenous digestive losses were the principal protein demand in all animals (41–57% of protein expended), whereas endogenous urinary losses were only 4–8% of protein expended (Fig. 4). Catabolism of body protein in reproductive females during winter was 11% of protein expended and greater than the deposition of protein in the uterus (6%; Fig. 4). Protein deposition in milk was considerably more

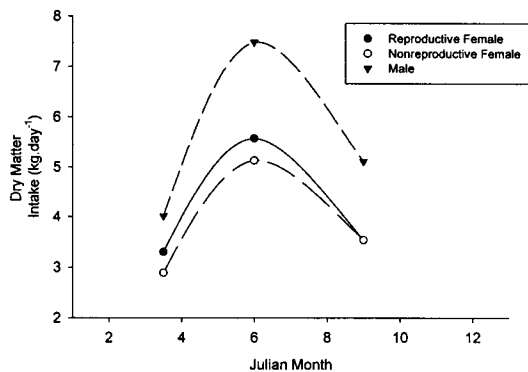


Fig. 2. Dry matter intake ($\text{kg}\cdot\text{day}^{-1}$) for a reproductive female, nonreproductive female, and male caribou. Feeding times and feeding rates are based on females fitted with esophageal fistulae during summer (White et al. 1975) and winter (Holleman et al. 1979). Autumn feeding times and feeding rates in September were assumed to be the same as those for winter.

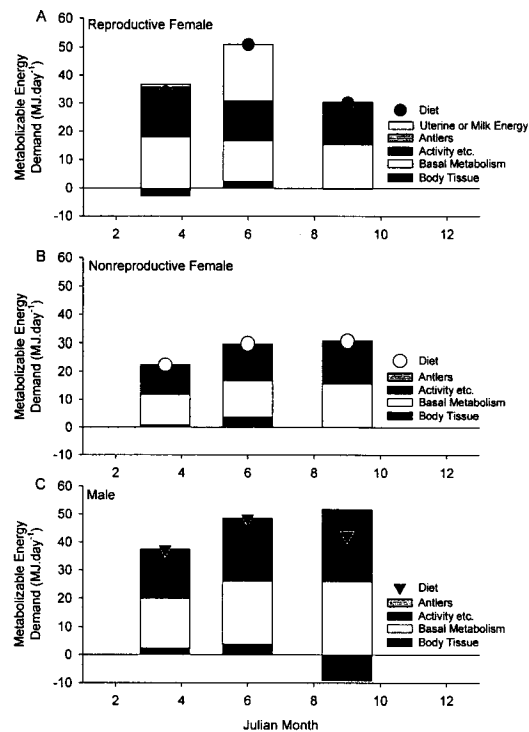


Fig. 3. Demands of metabolizable energy ($\text{MJ}\cdot\text{day}^{-1}$) for a reproductive female (A), nonreproductive female (B), and male caribou (C). Catabolism of body tissues is a negative demand, whereas synthesis of tissues (body protein and lipid, antlers, uterine, and milk constituents), basal metabolism, and activity are positive demands. Net supply from the diet is shown as a single point on each bar as a closed circle (reproductive female), open circle (nonreproductive female), and closed triangle (male).

costly than gestation at 25% of the protein expended in summer by reproductive females. Antler deposition was proportionately more expensive for males than for females, but only accounted for 2.6% and 1% of the respective protein and energy expended by males during summer (Fig. 4).

Minimum energy density of diets followed changes in intake of dry matter and body mass. Low intakes in winter increased the predicted minimum content of energy in the diet for nonreproductive females, even though absolute demands were

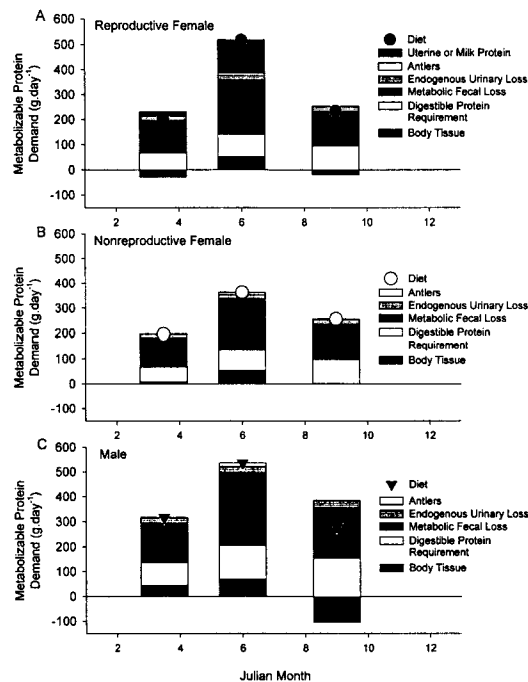


Fig. 4. Demands of metabolizable protein ($\text{g}\cdot\text{day}^{-1}$) for a reproductive female (A), nonreproductive female (B), and male caribou (C). Catabolism of body tissues is a negative demand, whereas synthesis of tissues (body protein, antlers, uterine, and milk protein), digestible requirement, and endogenous fecal and urinary losses are positive demands. The net supply from the diet is shown as a single point on each bar as a closed circle (reproductive female), open circle (nonreproductive female), and closed triangle (male).

greater in summer when intakes also were high (Figs. 3 and 5A). Food intakes of males were low in relation to energy demands in winter and resulted in a greater estimate of minimum content of dietary energy when compared with nonreproductive females. That is, winter energy demands for males were 167%, while intakes were only 139% those of nonreproductive females (Figs. 2 and 5A). For reproductive females, high demands for energy during gestation and lactation resulted in the greatest density of dietary energy in late winter and summer (Fig. 5A). Mean retention

times of digesta also reflected seasonal changes in intake and body mass (Fig. 5B). Predictions of greater retention times in reproductive females during gestation and lactation were the result of small differences in body mass when compared with nonreproductive females (Figs. 1 and 5B). Mean retention times of males were 16–19% greater than those for nonreproductive females during each period (Fig. 5B).

Protein demands of nonreproductive females were accompanied by changes in intake and resulted in predictions of minimum density of dietary protein that were similar among periods (Fig. 6). Minimum density of dietary protein was offset by tissue

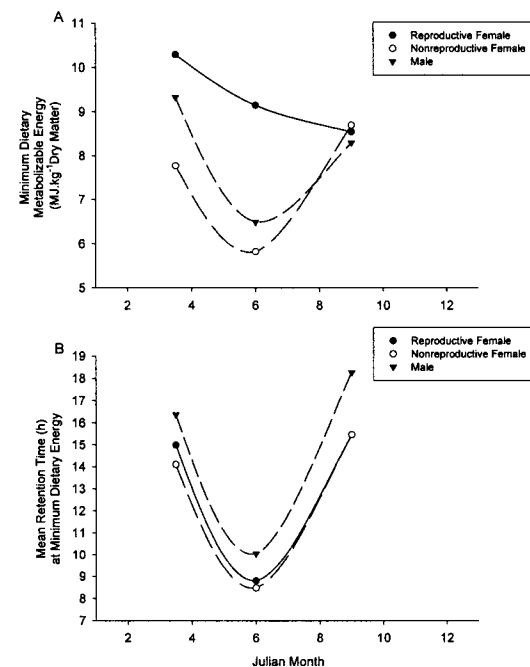


Fig. 5. Minimum dietary contents of metabolizable energy ($\text{MJ}\cdot\text{kg}^{-1}$ dry matter) needed to meet energy demands for a reproductive female, nonreproductive female, and male caribou (A). Estimates are based on dry matter intake and dietary demands (net tissue catabolism). Mean retention time for digesta at the corresponding minimal dietary energy content is based on digestive capacity (B; Demment and Van Soest 1985).

mobilization in reproductive females during winter and autumn, and by males during autumn (Figs. 4 and 6). Low intakes by males increased the predicted density of dietary protein during winter when compared with smaller nonreproductive females (Fig. 6).

When dietary minima were combined with projected metabolizabilities, reproductive females required diets with 32% and 57% more gross energy than nonreproductive females during winter gestation and summer lactation, respectively (Fig. 7B). Protein required by lactating females also was 32% greater than the projection for nonreproductive females but loss of body protein offset the dietary contribution of protein for reproductive females to below the level required for nonreproductive animals during winter and autumn (Fig. 7C). When metabolizabilities of energy and protein were increased for males (energy 12–14% and protein 7–8%), projected diet quality was similar between males and nonreproductive females during winter, and lowest for males in summer and autumn (Fig. 5).

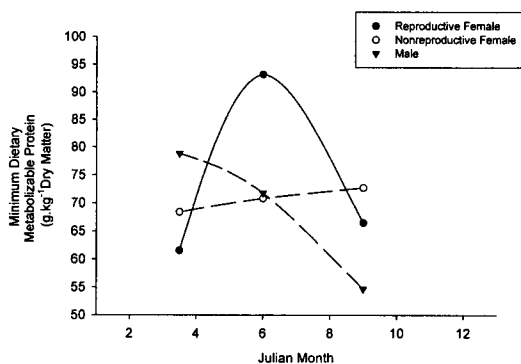


Fig. 6. Minimum dietary contents of metabolizable protein (g.kg^{-1} dry matter) for a reproductive female, nonreproductive female, and male caribou. Estimates are based on dry matter intake and dietary demands (net tissue catabolism).

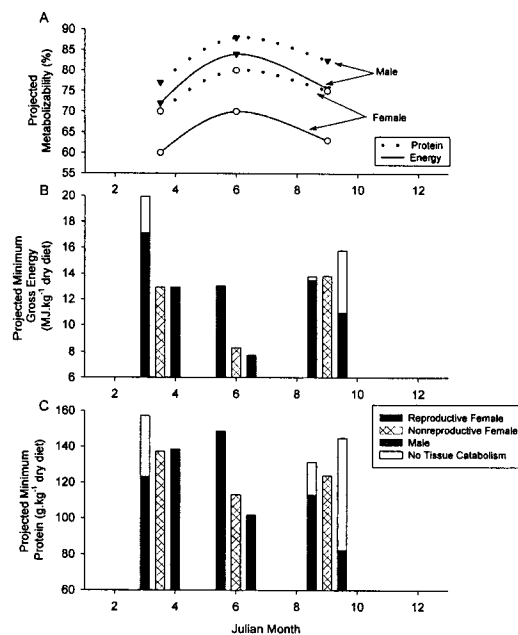


Fig. 7. Projected metabolizability of protein and energy in diets of male and female caribou (A). Corresponding projections are for minimum dietary gross energy content (B) and protein content (C) for a reproductive female, nonreproductive female, and male caribou. Stippled and shaded bars are estimated dietary minima with extended open bars for estimates when body tissues are not used.

DISCUSSION

Demands for energy during gestation and for energy and protein during lactation increase dietary minima (Fig. 5A and 6) for reproductive females above levels required by nonreproductive females and males. Projections of gross energy and total protein in diets that are based on estimated metabolizabilities of males and nonreproductive females predicted that males could subsist on the lowest quality of diet during summer. Therefore, sexual segregation is favored by minimum dietary predictions in both late winter and summer. Conversely, dietary minima for energy (Fig. 5A) are similar between sexes in autumn suggesting that segregation is not favored by dietary differences when animals enter the mating

season.

This extended model confirms the predictions of the general model described by Barboza and Bowyer (2000) by including several details of seasonal metabolism with data for *Rangifer* or with close approximations for cervids to provide realistic estimates of diet quality for wild ruminants. Calculated expenditures of metabolizable energy were 0.84 and 1.06 MJ.kg^{-0.75}.day⁻¹ for nonreproductive animals in March–April and June, respectively, whereas corresponding estimates for reproductive females were 53–56% greater at 1.29 and 1.67 MJ.kg^{-0.75}.day⁻¹. Proportional differences in expenditures of metabolizable energy between females were less than those for net energy required for maintenance of body mass in captive caribou and reindeer, which are twice as large in reproductive females as nonreproductive animals in June (0.46 vs. 0.23 MJ.kg^{-0.75}.d⁻¹; Chan–McLeod et al. 1994). Estimates of net energy expenditure are lower for wild caribou during pregnancy, and only 0.57 and 0.67 MJ.kg^{-0.75}.d⁻¹ in April and June, respectively (Adamczewski et al. 1993). Differences between metabolizable and net energy estimates reflect the heat increment of feeding and corrections for efficiency of conversion to maintenance and production included in the metabolizable value. We also included the combined costs of activity and thermoregulation as equivalent to basal metabolism, which accounted for 47% of total expenditure in late winter. That estimate is considerably greater than the cost of activity alone that was derived from observations of wild caribou during late winter (27–30% of total expenditure; Adamczewski et al. 1993). Our estimates of metabolizable energy expenditure also include increments to basal metabolism during the last trimester of gestation and increments for summer. Therefore, our estimates of metabolizable energy expenditures are also greater than those estimated

for reproductive caribou in the wild during late gestation (0.64 MJ.kg^{-0.75}.day⁻¹) and lactation (0.93 MJ.kg^{-0.75}.day⁻¹; Boertje 1985).

Inclusion of basal increments and net energy efficiencies in our model provide generous estimates for energy demands in males and females. We also used the highest feeding times and feeding rates in each period to solve for minimum dietary quality. Although feeding rates used in our model are only 54–59% of the maximum instantaneous rate for several mammals (0.45 g.kg^{-0.71}; Shipley et al. 1994), feeding rates of caribou may be further reduced by structure and distribution of forage species and the available biomass in each habitat (White et al. 1975, Trudell and White 1981), thereby increasing minimum dietary quality. Differences in total activity and energy expenditure also may alter minimum dietary quality. For example, minimum diet quality may decline with activity in winter (Adamczewski et al. 1993, Cuyler and Øritsland 1993) or increase with insect harassment in summer (White et al. 1975, Boertje 1985). Insect harassment also reduces sexual segregation in caribou from 59% to 39% of all groups during July (White et al. 1975). Thus, sexual differences in the use of habitats may alter actual intake rates and total activity costs. For example, uplands with an abundant biomass of dead plants that are high in fiber content also may have low insect abundance because of less substrate moisture and higher wind speed. Consequently, upland areas may allow males to sustain high rates of intake at low diet quality. Conversely, wetter areas with a greater abundance of live plant biomass would provide adequate energy and protein densities for reproductive females even though insect harassment may reduce time spent feeding.

Densities of gross energy do not vary greatly among forages (Boertje 1990,

Robbins 1993). Therefore, differences in projected density of gross energy in diets between reproductive females and nonreproductive females probably would result in different times spent feeding. That is, reproductive females would probably feed 32% and 57% longer than nonreproductive females consuming the same diets in winter and summer, respectively. That outcome is consistent with eating times that were greater in lactating females (821 min.d⁻¹) compared with nonbreeding caribou (706 min.d⁻¹) and males (662 min.d⁻¹) during summer (White et al. 1975). Our result indicates that differences in feeding and searching activity between males and females in summer may be a consequence of metabolic demands.

Barboza and Bowyer (2000) noted that resolving why the sexes of dimorphic ruminants sexually segregate has been hampered by the lack of an operational definition. Most research designed to test hypotheses concerning sexual segregation have defined the phenomenon to require a differential use of space by the sexes outside the mating season (Bowyer 1984, Miquelle et al. 1992, Bowyer et al. 1996, Main and Coblenz 1996, Bleich et al. 1997, Kie and Bowyer 1999). Recently, however, several studies have indicated differences in activities of the genders as the cause of sexual segregation. One study dealing with activity patterns of the sexes (Conradt 1998) clearly restricted implications of that hypothesis to "social segregation", or the manner in which sexes associate. Kie and Bowyer (1999) demonstrated that marked differences in spatial segregation of the sexes occurred with few differences in social segregation. Factors responsible for spatial segregation and sociality may differ and investigating them as if they were a single process is counter productive. A second study on foraging behavior (Ruckstuhl 1998), however, implicated differential movement patterns and time bud-

gets as the cause of sexual segregation. Nonetheless, Ruckstuhl (1998) did not demonstrate a difference in use of space by the sexes. Hypotheses founded in movement or activity cannot explain why genders use space differently because nothing in those explanations prevents the use of the same space by the sexes at different times. Indeed, that differential use of space is a characteristic (not just a definition) of sexual segregation (Bowyer 1984, Miquelle et al. 1992, Bleich et al. 1997, Bowyer et al. 2001). Moreover, our extended gastrocentric model indicates that differences in feeding and searching activity between sexes of ruminants likely is a consequence of metabolic demands and allometry rather than a cause of sexual segregation.

If differences in total activity and sociality do not offer an explanation for spatial segregation of the sexes, what are the physiological mechanisms involved in this process? Differences between the sexes in retention of digesta (Fig. 5B) would have increased ruminal digestion and the metabolizability of energy in males compared with females. If ruminal retention is 75% of total retention in the digestive tract, ruminal dry matter digestibility of browse stems (e.g., blueberry, *Vaccinium* spp.) would be 60% and 54%, and 71% and 65% for browse leaves (e.g., maple, *Acer* spp.) in males and nonreproductive females, respectively. Those estimates subtend a sexual difference of 10–12% for ruminal degradation based on studies of mule deer (Spalinger et al. 1986), with further postruminal digestion in the small intestine and the colon. This difference is consistent with diet projections in Figure 7, which used a proportional increase of 20% in energy metabolizability for males over females. Differences in retention time and degradation rate also would depend on the physical characteristics of forage and the reduction of particle size through chewing and rumination. For

example, grass hay fed to Nubian ibex (*Capra ibex*) was digested equally well by large males, lactating females, and nonreproductive females, probably as a result of greater rumination in females than in males (Gross et al. 1996). Rates of food intake ($\text{g}\cdot\text{min}^{-1}$) of manipulated grass swards also were similar between sexes of Soay sheep because small females achieved faster cropping rates than large males (Pérez-Barberia and Gordon 1999). Gross et al. (1996) fed the same diet of grass hay to both sexes of Nubian ibex (*Capra ibex*) and observed longer ruminal retention and greater fill (per metabolic body weight) of the digestive tract in males compared with much smaller, nonreproductive females. Conversely, Jenks et al. (1994) reported greater ruminal fill in female than in male white-tailed deer, but those authors did not measure the density (mass/volume) and concentration of fiber (g/g) in the contents of the rumen. Consequently, the rumen may have contained more fibrous digesta of lower density in males than in females, if dietary selection and ruminal flow differed between sexes. Effects of body size and seasonal metabolism on digestive function in male and female cervids await confirmation from direct experimentation.

Long retention times and digesta volumes in males also were projected to increase protein metabolizability by 10% in males compared with females. This increment would offset digestible protein required for maintenance, which was set at 110% of the female requirement to account for a proportionately larger muscle mass in males (Barboza and Bowyer 2000). Reduced requirements for males may be the result of proportionately smaller endogenous losses in urine or feces. Recycling urea to the digestive tract could minimize urinary losses of urea. Urea recycling varies with season from 45% in summer to 58% in winter for male caribou (Wales et al. 1975).

Low intake of protein also causes similar conservation of urea in female and yearling reindeer during winter (Hove and Jacobsen 1975, Jacobsen et al. 1981). Although digesta passage and fermentation affect urea degradation (Barboza et al. 1997; Annison and Bryden 1998), protein intake and metabolic demand also affect urea reutilization (Sarraseca et al. 1998, Waterlow 1999). Urea recycling and reutilization probably are greater in males than females during summer, when ruminal passage and minimum levels of dietary protein are lower in males. Slow passage rates also may permit greater recovery of dietary, endogenous, and microbial protein from ruminal digesta in males during winter and summer. Defining effects of body size, seasonal metabolism, food intake, and digestive function on protein conservation requires direct confirmation from experiments with male and female deer.

Large changes in metabolism associated with mass gain for rut or gestation also affect food intake. Intakes may be suppressed by hormonal influences on females during late gestation (Forbes 1986, Gedir and Hudson 2000) and on males during rut (Miquelle 1990, Miquelle et al. 1992). Reductions in intake would require corresponding increases in dietary quality and, thereby, increase densities of dietary protein for gestating females to the same levels for nonreproductive females and males during late winter (Fig. 6 and 7). These predictions are supported by food-choice experiments in domestic sheep, which select rations of greater protein content when metabolic demands are increased by growth, pregnancy, or parasitic infection, even when food intake is depressed (Kyriazakis and Oldham 1993, Cooper et al. 1994, Kyriazakis et al. 1994). Availability of foods with higher densities of protein and energy than required at maximum intake would allow animals to minimize feeding times if abun-

dance does not limit feeding rate. Increases in intestinal and hepatic tissue (Fell 1972) may allow reproductive females to maximize their gains from those high quality diets, whereas large males may be adversely affected (Barboza and Bowyer 2000). Although high-quality diets would be most advantageous to reproductive females in late winter and summer, those same diets may preclude males from switching to lower quality foods. Readily fermentable diets of high metabolizable energy decrease ruminal pH, alter ruminal microbial populations, decrease cellulolytic activity, and change mucosal structure and absorption (Franzolin and Dehority 1996, Russell and Wilson 1996, Owens et al. 1998). Similarly, diets with high contents of metabolizable protein may result in excess production of ammonia in rumen and blood (Van Soest 1994). Consequently, food intake and dietary choice are affected directly by the carbohydrate and protein composition of the diet and are associated with changes in ruminal conditions of domestic sheep (Cooper et al. 1995, Kyriazakis and Oldham 1997, Villaba et al. 1999). Nonetheless, food intake and selection are more complex than the simple avoidance of toxic limits, and involve both systemic physiological controls as well as associative effects of learning (Day et al. 1998, Kyriazakis and Day 1998, Provenza et al. 1998). The combined response for domestic ruminants is to select diets that meet the metabolic demand for nutrients, that is, to avoid accumulations of excess metabolites within the digestive tract or in circulation (Illius and Jessop 1996). Similar studies of dietary selection in relation to metabolic requirements are required for male and female deer.

Nonreproductive females and males may have greater temporal flexibility in their nutrient demands than reproductive females, which must continue to support fetal devel-

opment if parturition is to coincide with plant production in the spring. Maternal body mass and condition influence pregnancy rates in caribou (Cameron et al. 1993) and other cervids (Keech et al. 2000). Maternal nutrition and condition also affect timing of parturition in moose, and mass and survivorship of young moose, caribou, and white-tailed deer (Chan-McLeod et al. 1994, Sams et al. 1995, Keech et al. 2000). Therefore, mass changes in nonreproductive females probably reflect gains for successful reproduction in autumn (Chan-McLeod et al. 1999), whereas low fat contents in the previous winter may be a cause rather than the consequence of not carrying a fetus through to parturition in spring. Gains of fat and protein in nonreproductive females and males during late winter may be adventitious and dependent upon environmental conditions. Lipid and protein gains during summer combine phenotypic responses to the environment with genotypic storage for reproduction in both males and females (King and Murphy 1985). Body fat content and body size vary greatly between populations of caribou with the smallest body size and largest proportional fat contents in the high Arctic reflecting longer winters, shorter growing seasons, and lower forage abundance than more southerly ranges. Thus, body size and patterns of fat and protein deposition in each sex may vary with the environmental conditions of their range (Klein 1999). These differences may alter the relative demands of males and females and the nutritional basis for segregation of the sexes in each population.

Body size also affects the costs of antler development in each sex, with even smaller costs for less massive and complex antlers of females compared with the elaborate antlers of male caribou. Because size of male antlers changes with age in red deer (*Cervus elaphus*) and moose (Hyvärinen et al. 1977, Stewart et al. 2000), differences

between the sexes may be greatest when comparing young males with older females. Comparisons of antlers between sexes are also influenced by differences in the antler cycle between males, reproductive females, and nonreproductive females (Bubenik 1975). Antler development probably is not constrained by specific nutrient limitations (Grasman and Hellgren 1993, Asleson et al. 1996), but antler size may be limited by poor diet quality because of high density of animals (Hyvärinen et al. 1977), or by tradeoffs between tissues during summer mass gain and growth of males (Stewart et al. 2000).

The gastrocentric model provides an explanation for behavioral ecology and life-history strategies of ruminants with physiological data for a species. This integration can predict consequences of size and sex on niche partitioning in relation to environmental changes in forage quality and quantity. Nevertheless, simplistic models are only as valid as data upon which they are constructed. Our model indicates an urgent need for studies of diet selection and nutritional physiology in the context of both reproductive status and seasonal demands for both sexes of cervids to further understand sexual segregation of dimorphic ruminants.

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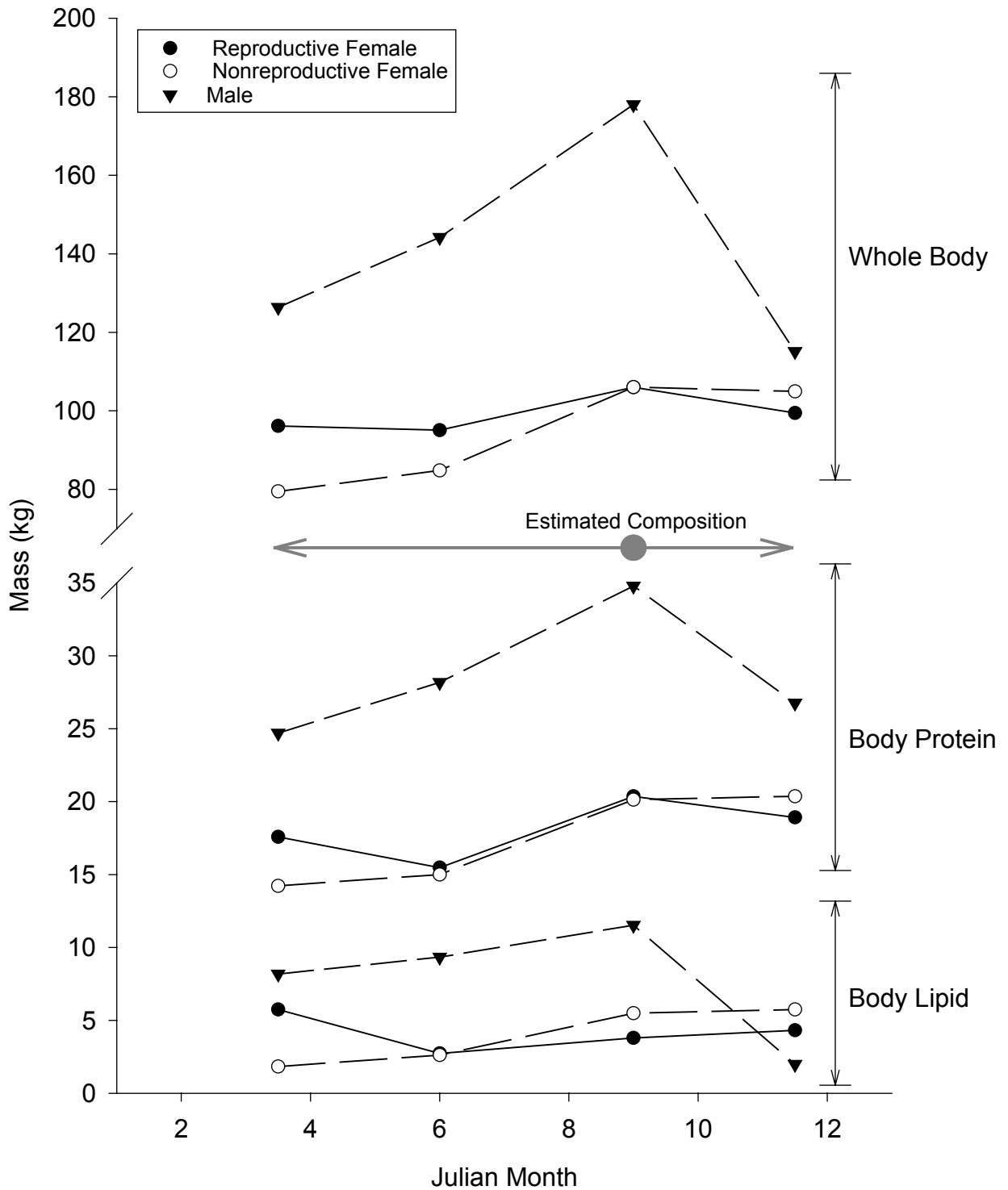


Figure 1.

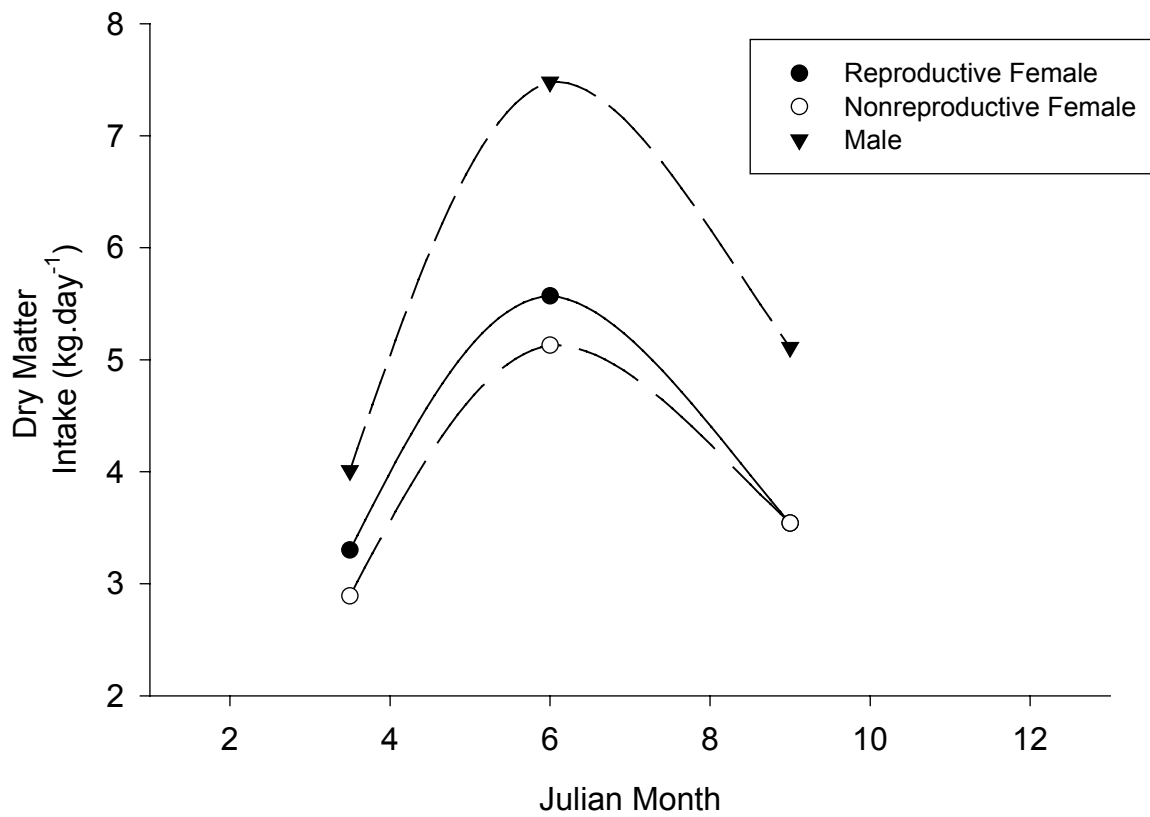


Figure 2.

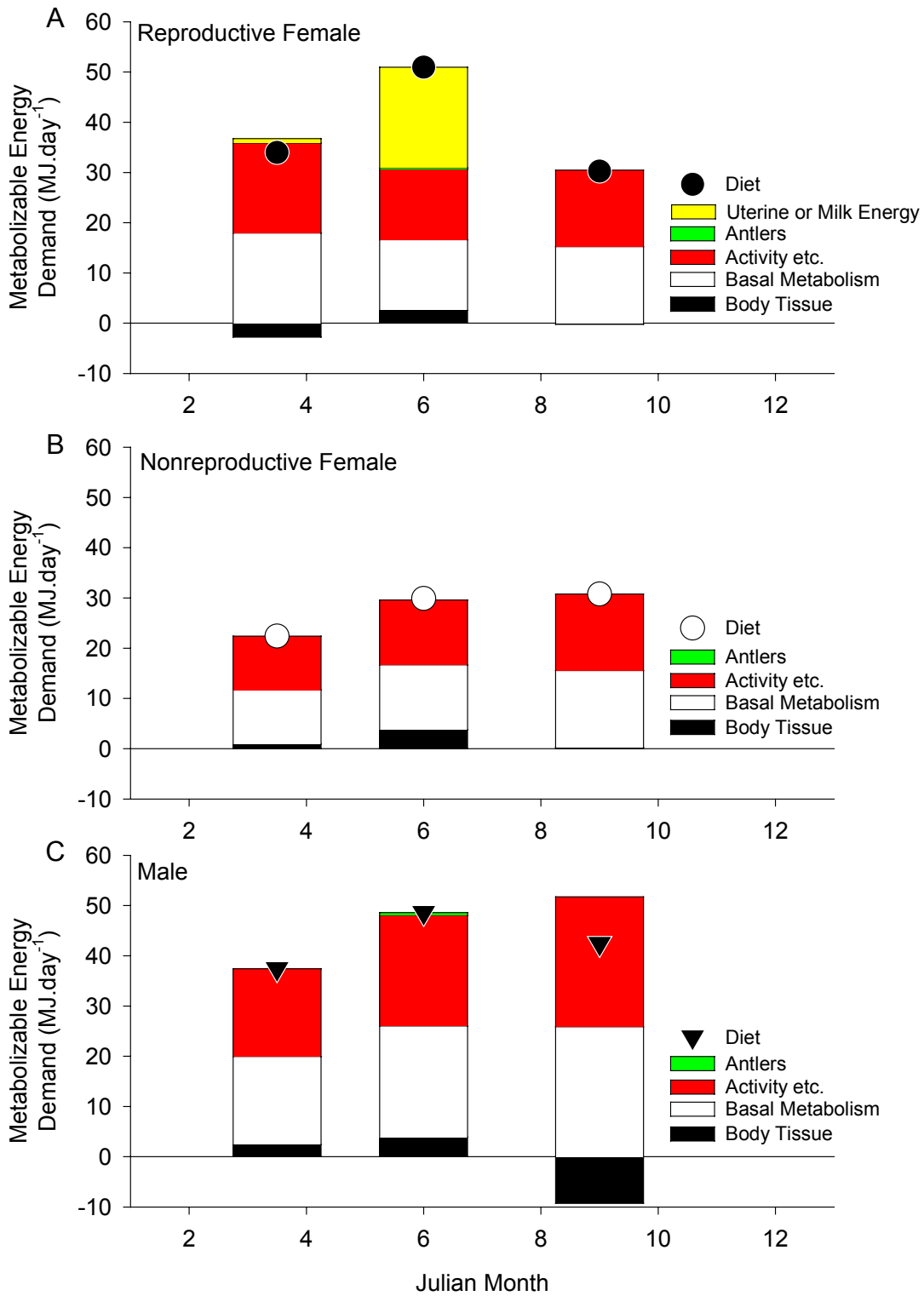


Figure 3.

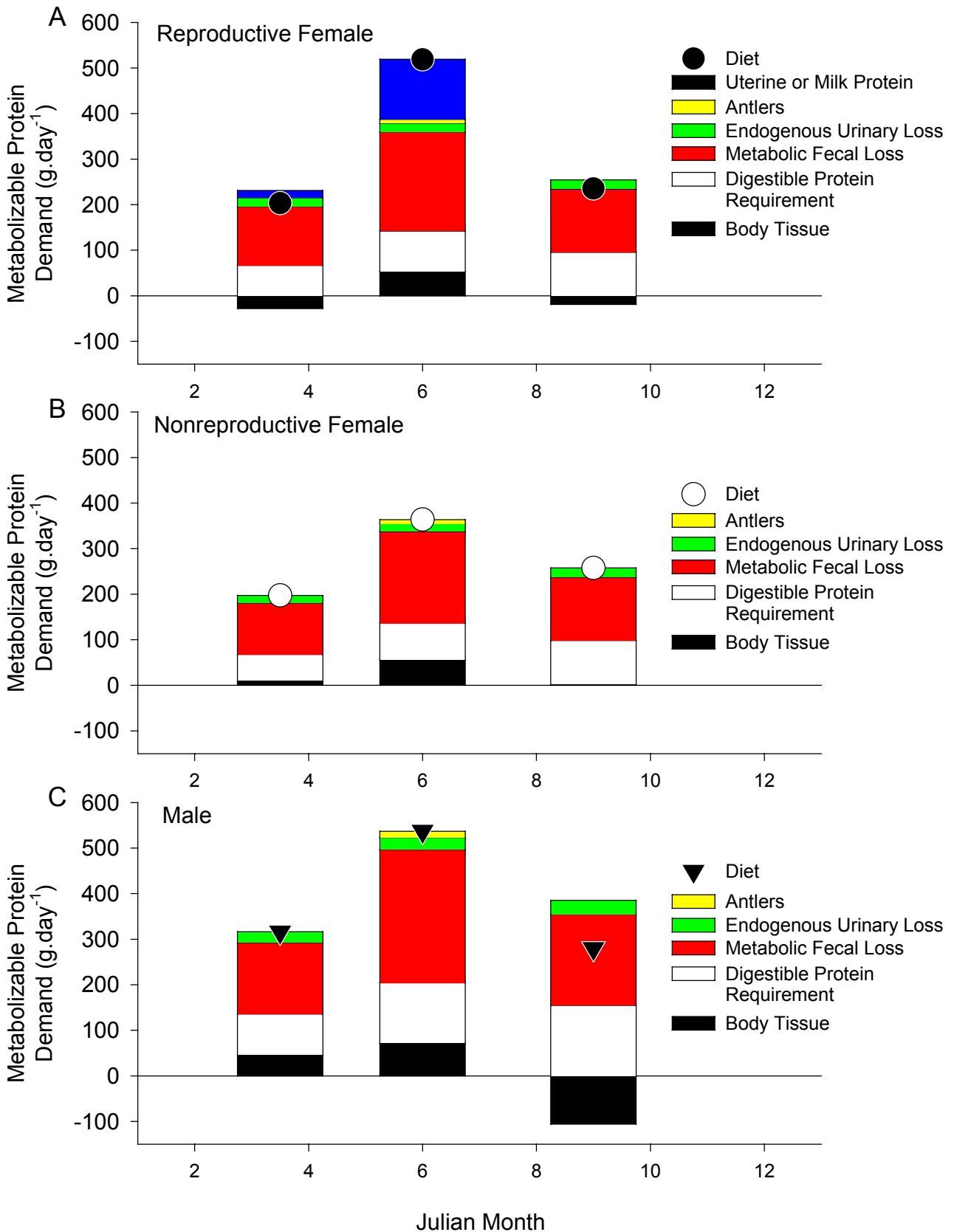


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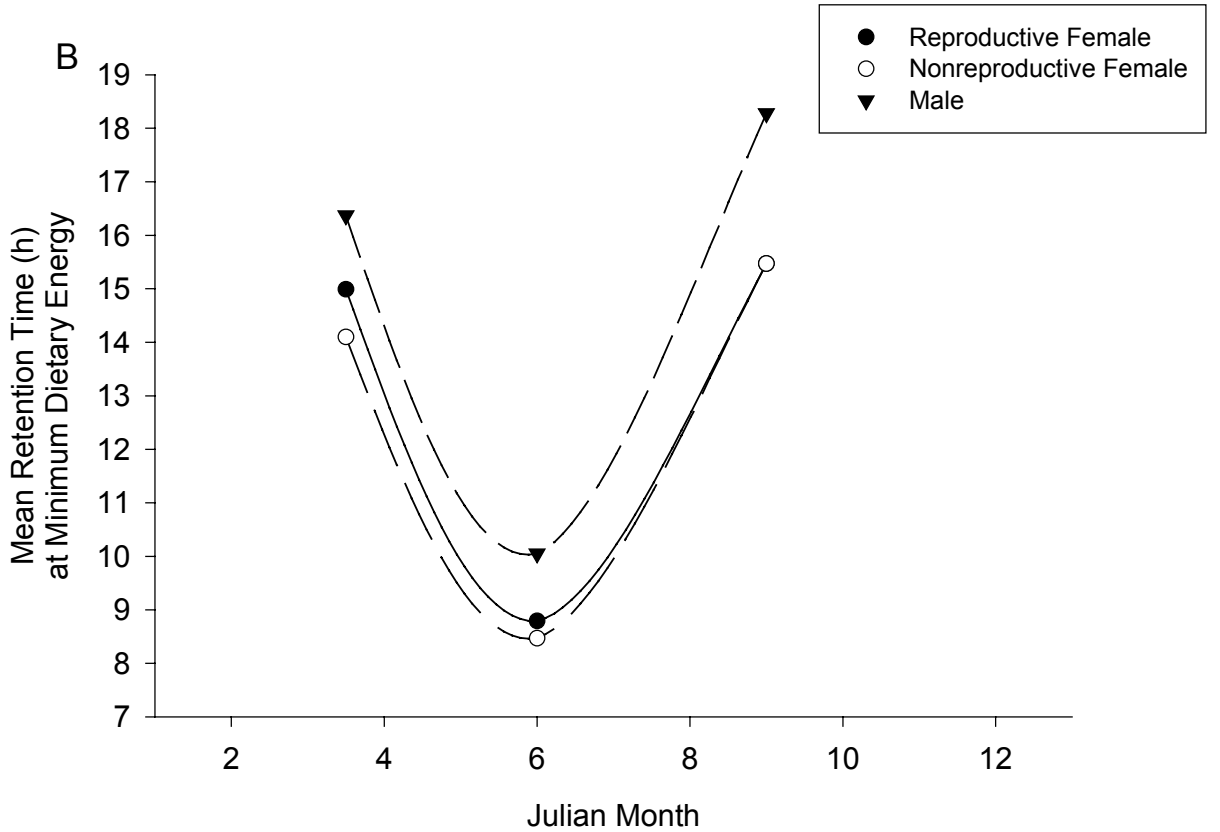
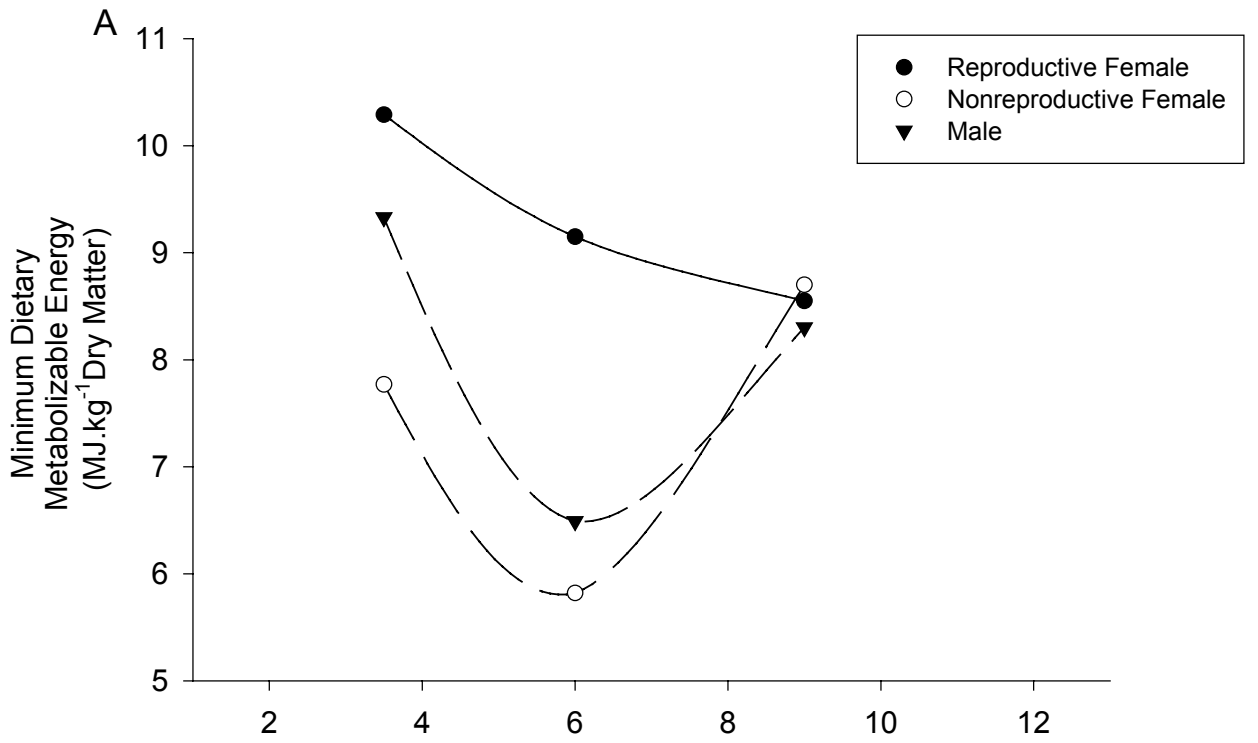


Figure 5.

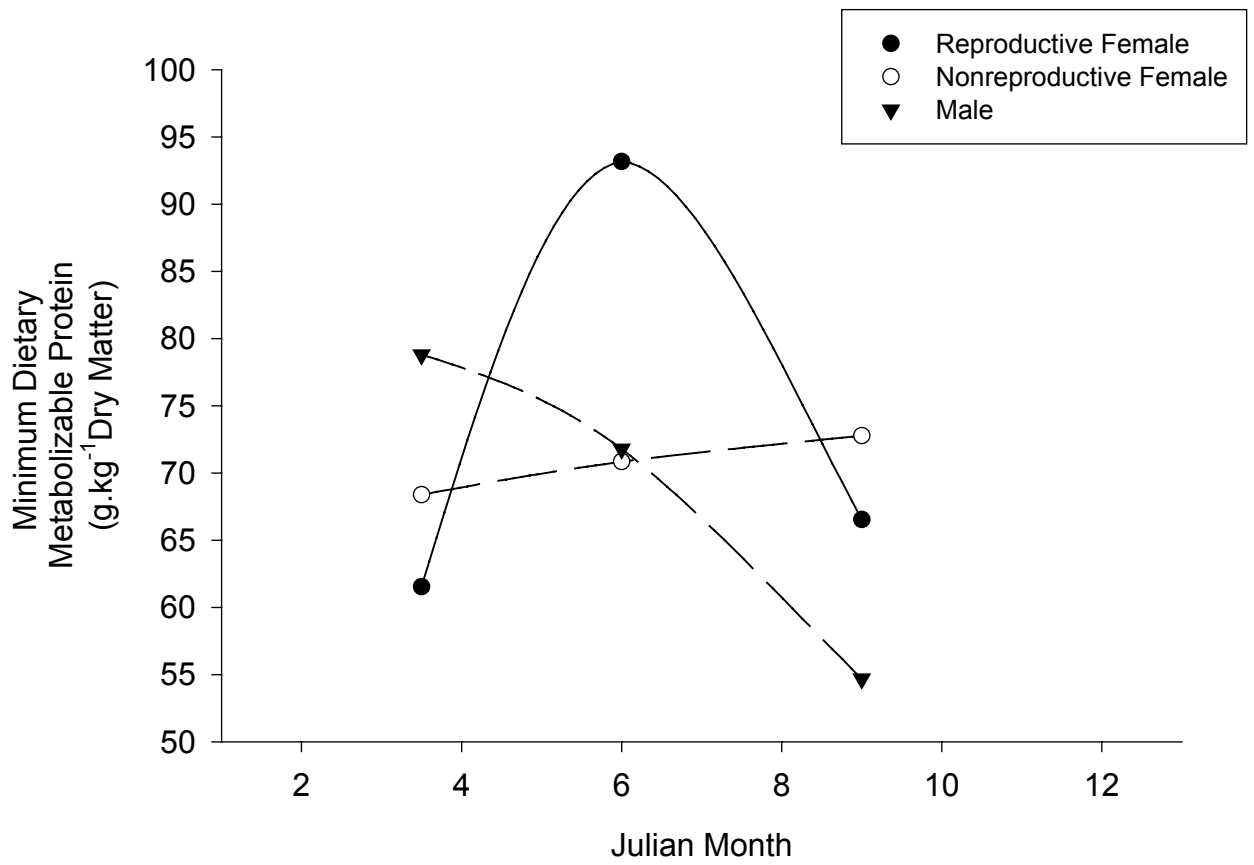


Figure 6.

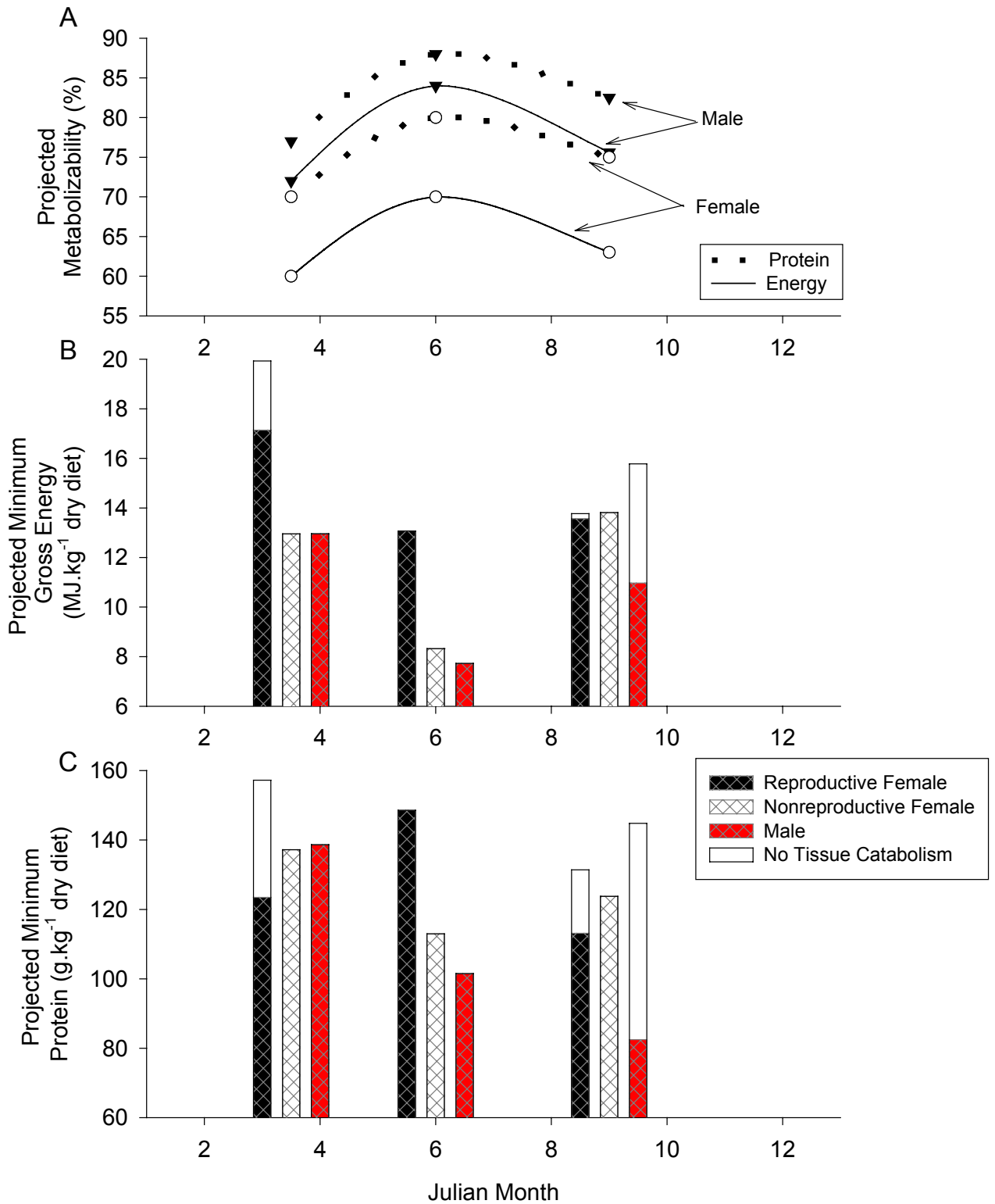


Figure 7.