

Evaluation of Techniques for Categorizing Group Membership of White-Tailed Deer

KEVIN L. MONTEITH,¹ *Department of Wildlife and Fisheries Sciences, Box 2140B, South Dakota State University, Brookings, SD 57007, USA*

CHAD L. SEXTON, *National Park Service, Theodore Roosevelt National Park, Box 7, Medora, ND 58645, USA*

JONATHAN A. JENKS, *Department of Wildlife and Fisheries Sciences, Box 2140B, South Dakota State University, Brookings, SD 57007, USA*

R. TERRY BOWYER, *Department of Biological Sciences, 912 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, ID 83209, USA*

ABSTRACT We studied sexual segregation, particularly patterns of group membership for white-tailed deer (*Odocoileus virginianus*), in Lincoln County, Minnesota, USA, to evaluate current techniques used to categorize animals when studying sexual segregation. We categorized group membership according to Hirth (1977) and grouped individuals using our solitary categorization method. Our solitary method was most sensitive to changes in behavior and physiology exhibited by reproductively active females and their association with other deer during sexual segregation. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1712–1716; 2007)

DOI: 10.2193/2005-763

KEY WORDS group membership, Minnesota, *Odocoileus virginianus*, parturition, reproductive behavior, social structure, sexual segregation, techniques, white-tailed deer.

Hypotheses forwarded to explain sexual segregation in sexually dimorphic ruminants have been widely debated (Clutton-Brock et al. 1987, Main et al. 1996, Bleich et al. 1997, Ruckstuhl 1998, Bowyer 2004). Knowledge of the extent and timing of sexual segregation is important for understanding this phenomenon and to address its effect on the ecology and management of ruminants. Sexual segregation frequently peaks near parturition for many sexually dimorphic ruminants and represents the difference in acquisition and need for resources (i.e., resource partitioning), and reproductive strategies between sexes (Bowyer 1984; McCullough et al. 1989; Bowyer et al. 1996; Barboza and Bowyer 2000, 2001), including susceptibility to predation (Bleich et al. 1997). Changes in patterns of group membership are predicted to reflect sexual differences in acquisition of resources and risk of predation.

Hirth (1977) developed a method for categorization of group membership in white-tailed deer (*Odocoileus virginianus*) that is used currently in investigations of sexual segregation. Despite its widespread use (Miquelle et al. 1992, Bleich et al. 1997, Kie and Bowyer 1999, Bowyer et al. 2001b, Bowyer and Kie 2004), the method has not been evaluated thoroughly relative to its ability to accurately reflect life-history strategies, especially for less-social species. In addition, modifications of the Hirth (1977) methodology have been used (e.g., McCullough et al. 1989, Main and Coblenz 1996), which likely represented attempts to improve this technique; however, little rationale associated with physiology, reproductive behavior, or social structure was used to support those modifications. We address whether the categorization of group membership (i.e., the definition of the group in which an individual occurs) effects recording of data related to patterns of group living in white-tailed deer. We hypothesized that the definition for group membership will influence subsequent

descriptions and analyses of group associations related to temporal changes in reproductive physiology and behavior of deer and that this method holds import for delineating periods of sexual segregation in deer and other species.

STUDY AREA

We studied patterns of group membership in white-tailed deer in Lincoln County (44°15'N, 96°17'W) located in southwestern Minnesota in the Northern Great Plains, USA. Lincoln County had a continental climate, consisting of relatively cold and severe winters and warm summers. Average temperature in winter (Dec to Feb) was -8.9° C, and in summer (Jun to Aug) was 21.7° C. Mean annual snowfall in the region was 86.4 cm, and annual precipitation was 62.2 cm, with 78% occurring from April through September (Hokanson et al. 1970).

Common native grasses within Lincoln County included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Canadian wildrye (*Elymus canadensis*), prairie cordgrass (*Spartina pectinata*), Indiangrass (*Sorghastrum nutans*), blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), needle-and-thread grass (*Hesperostipa comata*), porcupine grass (*H. spartea*), and rice-cut grass (*Leersia oryzoides*; Hokanson et al. 1970). Principal crops grown in the region were corn and soybeans, and less important crops included wheat, oats, flax, barley, rye, and alfalfa (Hokanson et al. 1970, Johnson and Larson 1999).

Southwest Minnesota is characterized by flat to rolling topography with elevations ranging from 229 m to 608 m above mean sea level. Major land use and cover types in Lincoln County were composed of 94.3% cultivated lands, 3.9% grassland-shrub, 0.7% water, 0.5% forest, and 0.2% wetland (Minnesota Department of Natural Resources 2000). Of the cultivated land in Lincoln County, 43.8% was planted to corn, 42.0% to soybeans, 7.6% to hay (including alfalfa), 5.2% to wheat, and 1.3% to oats. Crops began to emerge in early June (Minnesota Agricultural

¹ E-mail: KevinLeeMonteith@hotmail.com

Statistics Service 2002), around the time of parturition of white-tailed deer. Less than 20% of the land provided suitable cover for fawning, and habitat available for parturition was composed primarily of small patches of grassland and tree groves (Brinkman 2003). Tree groves were mostly shelterbelts and abandoned farmyards with ground vegetation consisting of smooth brome (*Bromus inermis*). Shelterbelts consisted of spruce (*Picea* spp.), cedar (*Juniperus* spp.), Douglas fir (*Pseudotsuga menziesii*), and silver maple (*Acer saccharinum*; Minnesota Association of Soil and Water Conservation Districts Forestry Committee 1986). In southwest Minnesota, white-tailed deer were the only established free-ranging cervid; however, dispersing mule deer (*O. hemionus*) occasionally were harvested in that region. Coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and dogs were the primary predators on deer (Brinkman et al. 2004).

METHODS

We observed deer approximately 3 days/week for 3–4 hours around sunset when deer were most active (Hirth 1977), by driving an 87-km fixed transect. We drove the transect in alternate directions on each sampling day. Observations began in late April (i.e., before parturition) and continued until mid-July when deer could no longer be observed readily because of increasing heights of crops. This sampling period was selected because sexual segregation in *Odocoileus* is most pronounced near parturition (Bowyer 1984, 1991; McCullough et al. 1989; Stewart et al. 2003), which occurred in late May for deer in Lincoln County (Brinkman 2003, Burris 2005).

We observed deer with the unaided eye, 7× binoculars, or a 12–40× spotting scope from a vehicle; we used spotlights when light was minimal. For each deer within each group observed along the transect, we recorded, sex, age, activity (e.g., standing, walking), habitat, and Universal Transverse Mercator coordinates. We identified sex and age class by size, body conformation, and antler characteristics when present (Bowyer 1986). We took care to make a complete count and accurate classification of sex and age classes of deer. If individuals were obscured by topography or vegetation, we terminated data collection for that group. We recorded sex and age class of each animal in the group: adult male (≥ 2 yr old), yearling male (1 yr old), adult female (≥ 2 yr old), yearling female (1 yr old), and fawn (deer of either sex < 1 yr old), as described by Hirth (1977) and Bowyer (1984). We defined a group as ≥ 1 deer, which included the complete range of sociality in deer (Bowyer et al. 2001b). We considered deer < 50 m apart to be members of the same group. We categorized deer that were ≥ 50 m apart to be members of the same group if their behaviors were associated and if they moved and fed in synchrony (Bowyer et al. 1996).

We categorized social groups with 2 methods; social groups included mixed-sex, adult male, adult female, yearling, or fawn based on the method of Hirth (1977). A mixed-sex group contained ≥ 1 adult female and ≥ 1 adult

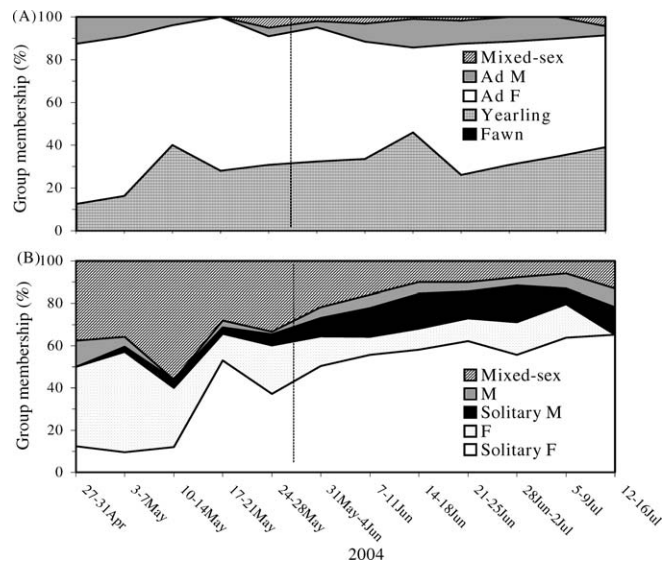


Figure 1. Percentage of social groups of white-tailed deer based on ground sampling in Lincoln County, Minnesota, USA, 2004. Dashed vertical lines represent peak parturition exhibited by deer in the Lincoln County area (Brinkman 2003, Burris 2005). (A) Group membership (e.g., group type) was classified with the categorization method of Hirth (1977). (B) Group membership was defined with our solitary categorization method. No fawn groups were identified as defined by the Hirth (1977) categorization.

male but also could include yearlings and fawns. An adult male group contained ≥ 1 adult male, but also could contain other sex- and age-classes of deer except adult females. Similarly, adult female groups contained ≥ 1 adult female, but could contain other sex- and age-classes except adult males. Yearling groups contained only yearlings of either sex, and fawn groups included only fawns (Hirth 1977).

We also defined social groups using our solitary categorization method. We classified social groups as female, solitary female, male, solitary male, and mixed-sex groups. We defined female groups as those consisting of ≥ 2 adult or yearling females and no males but could contain fawns. Male groups contained ≥ 2 adult or yearling males with no females or fawns. Solitary female groups contained 1 adult or yearling female but could include fawns. Solitary male groups contained 1 adult or yearling male. Mixed-sex groups contained ≥ 1 adult or yearling male and ≥ 1 adult or yearling female and could contain fawns. We used chi-square tests to determine if there were changes in patterns of group membership throughout the sampling period for each method of categorization and used SYSTAT (Wilkinson 1990) to perform all statistical analyses.

RESULTS

We recorded observations during 12 weeks beginning 27 April and continuing to 12 July 2004. Mean (\pm SE) group size was 1.76 ± 0.05 ($n = 746$) and ranged from 1 to 11 deer. Sex ratio (M:F) of observations in 2004 was skewed toward females ($1:2.64 \pm 0.01$).

Each categorization method depicted changes in group associations differently (Fig. 1). The method of Hirth

(1977) revealed a slight decrease in adult female groups and a slight increase in yearling groups over time (Fig. 1). Adult female groups declined from 70% in early May to 50% in July. Yearling groups displayed peaks of 40% in early May and mid-June. Adult male groups declined from 10% to nearly 0% from early May to parturition, and then increased to 10% by mid-June. We observed no fawn groups during the sampling period and adult female and yearling groups composed 60.1% and 30.9% of observations, respectively. Despite these trends, no change ($\chi^2_{4,44} = 47.52, P = 0.33$) in group membership occurred for the method of Hirth (1977).

For the solitary categorization method, solitary male groups increased from 0% in April to 15% of groups observed in July (Fig. 1). Similarly, male groups increased from <1% in early May to >5% of groups observed by June. Female groups declined from 40% in April to 10% of groups observed in July, whereas solitary females increased from 10% in April to >60% of groups observed by July. Moreover, female groups declined from >30% in early May to 10% in late May with a concomitant increase in solitary females from 10% in early May to >50% of observations in late May. Mixed-sex groups declined from 40% in early May to 20% in late May. Changes in group membership through the sampling period were dramatic ($\chi^2_{4,44} = 405.66, P < 0.001$) for the solitary categorization method.

DISCUSSION

Definition of group membership for individuals is often an overlooked issue in behavioral studies (Frid 1997). Sampling design should reflect differences in reproductive behavior, physiology, and social structure of deer because these characteristics can affect interpretation of segregation or aggregation. Such categorizations of mixed-sex groups have been used to define periods of aggregation and segregation (Bowyer 1984, Miquelle et al. 1992, Bleich et al. 1997). Similarly, differential habitat use by sex and changing patterns of sex ratio for animals observed may affect results when evaluating spatial segregation (Bowyer et al. 1996, Stewart et al. 2003) but would not affect the comparison of the 2 categorization methods in our study.

The method of Hirth (1977) and our solitary categorization method for group membership differed based on several characteristics. The Hirth (1977) categorization considered adult animals to be of primary concern because male, female, or mixed-sex groups must contain ≥ 1 adult of the respective sex. The solitary categorization considered yearlings to be similar in reproductive status to adults, indicating that male, female, solitary male, solitary female, and mixed-sex groups require a yearling or adult of the respective sex. Further, the solitary categorization classified lone individuals into a separate category, whereas Hirth (1977) categorized lone and groups of animals into the same category.

Observations of group membership of white-tailed deer indicate the preponderance of solitary individuals (Ozoga

2000) and highlight the importance of studying these individuals to measure and understand their degree of sociality, especially during sexual segregation (Fig. 1). White-tailed deer societies are matriarchal with solitary females representing an important component of the ecology, behavior, and social structure during spring and summer (Ozoga et al. 1982, Ozoga 2000). As date of parturition nears, gestating females seek seclusion, interact aggressively with their offspring from the previous year and other deer, and remain secluded for up to 4 weeks postpartum (Ozoga et al. 1982). The area occupied by reproductively active females near time of parturition ostensibly contains resources needed to enhance reproductive success (Ozoga et al. 1982, Weckerly 1992). This maternal behavior varies markedly from species that aggregate following parturition (Eastland et al. 1989; Bowyer et al. 1998, 1999; Rachlow and Bowyer 1998) and indicates the need for differing methods to study social groups exhibiting varying degrees of sociality. For instance, the method of Conradt (1998) for studying social segregation is not appropriate for solitary ungulates, such as white-tailed deer, because it does not consider lone individuals. Behavioral changes associated with nutrient acquisition and securing of resources and space exhibited by reproductive females with the onset of lactation was accurately reflected in the solitary categorization. An increase in solitary females, a decline in mixed-sexed groups, and slight increases in solitary and male groups occurred near time of parturition (Fig. 1).

Categorizing solitary females in less-social species such as white-tailed deer is necessary to accurately represent their reproductive behavior and degree of sociality. In addition, considering composition of mixed-sex groups as having both sexes of animals ≥ 1 year of age is important because yearling female and male white-tailed deer can achieve sexual maturity, but yearling males rarely mate because of the polygynous mating system (Ozoga 2000). Nonetheless, female yearling white-tailed deer often reproduce in productive populations (McCullough 1979). Yearling female white-tailed deer exhibit 65–70% pregnancy rates in the Midwest where agricultural crops are readily available (Gladfelter 1984). This high pregnancy rate permits yearlings and adults to be classified into one group because they are exhibiting similar reproductive behavior and avoids the bias that may occur with the Hirth (1977) method by misclassifying large yearlings as adult. Moreover, reproductively active females behave differently based on their physiology (Moen 1973, 1978; Jenks et al. 1994; Barboza and Bowyer 2000, 2001) when compared with nonreproductive females. In regions where productivity is lower (Gladfelter 1984, Ozoga 2000), distinguishing between yearlings and adults may be important when categorizing group membership. Thus, different methods of categorizing group membership are appropriate depending upon the reproductive status of yearling females.

Young male white-tailed deer often associate with other males in bachelor groups, join yearling male groups, or

remain solitary at 1 year of age (Ozoga 2000). These behaviors were reflected in the solitary categorization by an increase in solitary males and male groups observed near time of parturition (Fig. 1). Nevertheless, the method of Hirth (1977) may be more appropriate for bighorn sheep (*Ovis canadensis*) and Dall's sheep (*O. dalli*) because subadult males remain in female groups until body size approaches that of adult males (Geist 1971, Rachlow and Bowyer 1994, Ruckstuhl 1998, Ruckstuhl and Neuhaus 2001, Corti and Shackleton 2002).

Although the Hirth (1977) method may be appropriate for some species (e.g., mountain sheep), social structure, reproductive behavior, and productivity of species should be coupled with the mechanistic physiological changes that occur in reproductive animals. Thus, group membership should be carefully defined when evaluating changes in group composition for assessing sexual segregation or other behavioral activities. Our solitary categorization reflected patterns in group membership associated with changes in reproductive behavior, productivity, social structure, and physiology exhibited by white-tailed deer, particularly in agricultural regions of the Midwest. Clearly, the reproductive condition of females, including yearlings, will have important life-history characteristics that are associated with sexual segregation (Barboza and Bowyer 2000, 2001).

MANAGEMENT IMPLICATIONS

Measuring patterns of sexual segregation may be difficult (Bowyer et al. 1996), but is necessary to understand when and why the sexes separate to avoid biased management strategies (Bowyer et al. 2002). Our data indicate that the way in which group membership is defined must be considered to accurately characterize reproductive behavior, patterns of sociality, and habitat use by group in species that sexually segregate. If group membership is not properly defined, habitat modifications or management strategies targeting a specific sex or cohort of animals may result in mismanagement (Bowyer et al. 2001a, Stewart et al. 2003). Hence, appropriate techniques for monitoring patterns of group membership that accurately characterize reproductive behavior and resource requirements are valuable to describe sexual segregation and aid in establishing appropriate management guidelines.

ACKNOWLEDGMENTS

This study was supported, in part, by the South Dakota Agricultural Experiment Station, Federal Aid to Wildlife Restoration administered through the South Dakota Department of Game, Fish and Parks (Study No. 75123), the Griffith Faculty Research Award presented to J. A. Jenks, the Department of Wildlife and Fisheries Sciences at South Dakota State University, and the Department of Biological Sciences at Idaho State University. We thank our technicians, L. A. Dixon and J. A. Delger, who contributed to data collection. J. A. Delger, K. M. Schuler, and L. E. Schmitz reviewed the manuscript and provided many useful comments and suggestions.

LITERATURE CITED

- Barboza, P. S., and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81:473–489.
- Barboza, P. S., and R. T. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275–292.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134.
- Bowyer, R. T. 1984. Sexual segregation in southern mule deer. *Journal of Mammalogy* 65:410–417.
- Bowyer, R. T. 1986. Antler characteristics as related to social status of male southern mule deer. *Southwestern Naturalist* 31:289–298.
- Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72:138–145.
- Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* 85:1039–1052.
- Bowyer, R. T., and J. G. Kie. 2004. Effects of foraging activity on sexual segregation of mule deer. *Journal of Mammalogy* 85:498–504.
- Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1996. Sexual segregation in black-tailed deer: effects of scale. *Journal of Wildlife Management* 60:10–17.
- Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* 79:415–425.
- Bowyer, R. T., D. R. McCullough, and G. E. Belovsky. 2001b. Causes and consequences of sociality in mule deer. *Alces* 37:371–402.
- Bowyer, R. T., B. M. Pierce, L. K. Duffy, and D. A. Haggstrom. 2001a. Sexual segregation in moose: effects of habitat manipulation. *Alces* 37: 109–122.
- Bowyer, R. T., K. M. Stewart, S. A. Wolfe, G. M. Blundell, K. L. Lehmkuhl, P. J. Joy, R. J. McDonough, and J. G. Kie. 2002. Assessing sexual segregation in deer. *Journal of Wildlife Management* 66:536–544.
- Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80:1070–1083.
- Brinkman, T. J. 2003. Movement and mortality of white-tailed deer in southwest Minnesota. Thesis, South Dakota State University, Brookings, USA.
- Brinkman, T. J., J. A. Jenks, C. S. DePerno, B. S. Haroldson, and R. G. Osborn. 2004. Survival of white-tailed deer in an intensively farmed region of Minnesota. *Wildlife Society Bulletin* 32:726–731.
- Burris, B. M. 2005. Seasonal movements of white-tailed deer in eastern South Dakota and southwestern Minnesota relative to traditional ranges and management unit boundaries. Thesis, South Dakota State University, Brookings, USA.
- Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness. 1987. Sexual segregation and density related changes in habitat use in male and female red deer (*Cervus elaphus*). *Journal of Zoology (London)* 211:275–289.
- Conradt, L. 1998. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society London* 265:1359–1363.
- Corti, P., and D. M. Shackleton. 2002. Relationship between predation-risk factors and sexual segregation in Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology* 80:2108–2117.
- Eastland, W. G., R. T. Bowyer, and S. G. Fancy. 1989. Effects of snow cover on selection of calving sites by caribou. *Journal of Mammalogy* 70: 824–828.
- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799–808.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. The University of Chicago Press, Chicago, Illinois, USA.
- Gladfelter, H. L. 1984. Midwest agricultural region. Pages 427–440 in L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.
- Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53.
- Hokanson, H. L., W. W. Anderson, D. W. Calkins, K. W. Hein, F. D. Lorenzen, J. J. Murray, R. O. Paulson, and R. F. Peterson. 1970. Soil Survey of Lincoln County, Minnesota. U.S. Department of Agriculture Soil Conservation Service, Washington, D.C., USA.
- Jenks, J. A., D. M. Leslie, Jr., R. L. Lochmiller, and M. A. Melchior.

1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. *Journal of Mammalogy* 75:1045–1053.
- Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota and the Northern Great Plains. South Dakota State University, College of Agricultural & Biological Sciences, South Dakota Agricultural Experiment Station, Brookings, USA.
- Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80:1004–1020.
- Main, M. B., and B. E. Coblenz. 1996. Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* 60:497–507.
- Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77:449–461.
- McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a k-selected species. University of Michigan Press, Ann Arbor, USA.
- McCullough, D. R., D. H. Hirth, and S. J. Newhouse. 1989. Resource partitioning between sexes in white-tailed deer. *Journal of Wildlife Management* 53:277–283.
- Minnesota Agricultural Statistics Service. 2002. 2002 Minnesota agricultural statistics bulletin. Minnesota Department of Agriculture, St. Paul, USA.
- Minnesota Association of Soil and Water Conservation Districts Forestry Committee. 1986. Minnesota tree handbook. Adventure, Staples, Minnesota, USA.
- Minnesota Department of Natural Resources. 2000. Minnesota land use and cover: 1990's census of the land. Section of Wildlife, Minnesota Department of Natural Resources, St. Paul, USA.
- Miquelle, D. G., J. M. Peek, and V. VanBellenberghe. 1992. Sexual segregation in Alaska moose. *Wildlife Monographs* 122.
- Moen, A. N. 1973. *Wildlife ecology, an analytical approach*. W. H. Freeman, San Francisco, California, USA.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *Journal of Wildlife Management* 42:715–738.
- Ozoga, J. J. 2000. Whitetail intrigue. Krause, Iola, Wisconsin, USA.
- Ozoga, J. J., L. J. Verme, and C. S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. *Journal of Wildlife Management* 46:1–11.
- Rachlow, J. L., and R. T. Bowyer. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *Journal of Mammalogy* 75:328–337.
- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal tradeoffs. *Journal of Zoology* 245:457–465.
- Ruckstuhl, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* 56:99–106.
- Ruckstuhl, K. E., and P. Neuhaus. 2001. Group choice by subadult bighorn rams: trade-offs between foraging efficiency and predator avoidance. *Ethology* 107:161–172.
- Stewart, K. M., T. E. Fulbright, D. L. Drawe, and R. T. Bowyer. 2003. Sexual segregation in white-tailed deer: responses to habitat manipulations. *Wildlife Society Bulletin* 31:1210–1217.
- Weckerly, F. W. 1992. Territoriality in North American deer: a call for a common definition. *Wildlife Society Bulletin* 20:228–231.
- Wilkinson, L. 1990. SYSTAT: The system for statistics. SYSTAT, Evanston, Illinois, USA.

Associate Editor: Hudson.