

WINTER FAWN SURVIVAL IN BLACK-TAILED DEER POPULATIONS AFFECTED BY HAIR LOSS SYNDROME

Authors: Bender, Louis C., and Hall, P. Briggs

Source: Journal of Wildlife Diseases, 40(3): 444-451

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-40.3.444

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

WINTER FAWN SURVIVAL IN BLACK-TAILED DEER POPULATIONS AFFECTED BY HAIR LOSS SYNDROME

Louis C. Bender^{1,3,4} and P. Briggs Hall²

- ¹ Washington Department of Fish and Wildlife, 2950 Ley Road, Cle Elum, Washington 98922, USA
- ² Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, Washington 98012, USA
- ³ Current address: US Geological Survey, New Mexico Cooperative Fisheries and Wildlife Research Unit, PO Box 30003 MSC 4901, Las Cruces, New Mexico 88003, USA
- ⁴ Corresponding author (email: lbender@nmsu.edu)

ABSTRACT: Overwinter fawn mortality associated with hair loss syndrome (HLS) is anecdotally thought to be important in declines of Columbian black-tailed deer (Odocoileus hemionus columbianus) populations in Washington and Oregon (USA). We determined prevalence of HLS in black-tailed deer, September and April fawn:doe ratios, and minimum overwinter survival rates of fawns for selected game management units (GMUs) in western Washington from 1999 to 2001. Prevalence of HLS ranged from 6% to 74% in fawns and 4% to 33% in does. Minimum fawn survival ranged from 0.56 to 0.83 and was unrelated to prevalence of HLS in either does (r=0.005, P=0.991) or fawns (r=-0.215, P=0.608). The prevalence of HLS in either does or fawns was also unrelated to either fall fawn: doe ratios (HLS does: r = -0.132, P = 0.779; HLS fawns: r = 0.130, P=0.760) or spring fawn:doe ratios (HLS does: r=-0.173, P=0.711; HLS fawns: r=-0.020, P=0.963). However, the prevalence of HLS in does and fawns was strongly related (r=0.942, P=0.002), and GMUs with high prevalence of HLS had lower deer population densities (fawns: r=-0.752, P=0.031; does: r=-0.813, P=0.026). Increased overwinter mortality of fawns because of HLS was not supported by our data. Decreased production of fawns, increased summer mortality of fawns, or both were seen in six of eight study GMU-year combinations. Observed rates of productivity and minimum fawn survival were inadequate to maintain population size in five of eight study GMU-year combinations, assuming an annual doe survival rate of 0.75. The influence of deer condition and population health on adult survival, fawn production, preweaning fawn survival, parasitism, and prevalence of HLS in both fawns and adults need to be clarified to identify what factors are limiting black-tailed deer productivity.

Key words: Black-tailed deer, fawns, hair loss syndrome, HLS, Odocoileus hemionus columbianus, productivity, survival.

INTRODUCTION

Hair loss syndrome (HLS) has been observed in western Washington (USA) since 1996. During subsequent years, the extent and frequency of occurrence have spread throughout western Washington and Oregon (USA); by 1999, deer in virtually all lower elevation sites (<610 m) in Washington west of the Cascade Mountain crest were affected (Fig. 1), although HLS is infrequently observed above about 610 m. Prior to observations in Washington in 1996, HLS apparently had not been described in black-tailed deer (Odocoileus hemionus columbianus). However, hair loss because of heavy winter tick (Dermacentor albipictus) infestations frequently has been observed in moose (Alces alces) populations (McLaughlin and Addison, 1986; Samuel, 1991).

Deer affected with HLS typically manifest clinical signs of hair loss, emaciation, and lethargy beginning in late fall or early winter (November-December). Prevalence of HLS has ranged as high as 74% in fawns and 33% in does in western Washington (Table 1). Clinical signs are most common in fawns; 68% of reports of HLS from 1996 to 2000 were fawns (L. Bender, unpubl. data). Causes of HLS are unknown. However, affected fawns had heavy infestation of lung parasites (likely Dictyocaulus spp. and larval-Parelaphostrongylus odocoilei, the latter previously unreported in Washington) combined with heavy infestations of biting lice (Foreyt et al., 2004). Significant licking and biting of lice-infested areas by affected deer likely results in hair loss by self-mutilation with secondary hyperpigmentation and hyperkeratosis of the skin. Hair loss

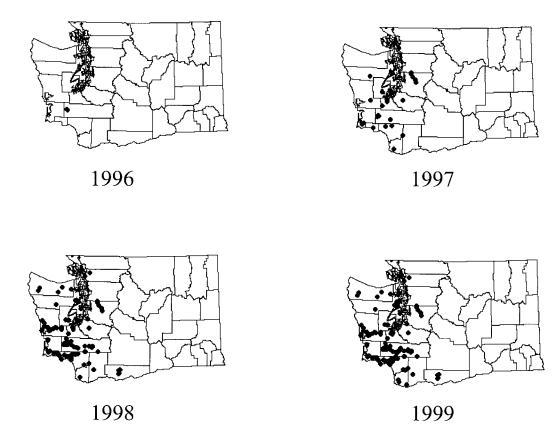


FIGURE 1. Apparent spread of hair loss syndrome (HLS) through western Washington, 1996–99. After 1999, HLS was ubiquitous throughout low-elevation (<610 m) habitats in western Washington. Points represent one or more observation of a deer with HLS; the lines represent county boundaries.

from self-mutilation by excessive grooming has also been reported in moose with winter tick infestations (Samuel, 1991; Mooring and Samuel, 1999). In Washington, almost all mortality associated with HLS has been among fawns, with hypothermia and malnutrition the common causes of death (B. Hall, unpubl. data). Similarly, emaciation and death from hypothermia and malnutrition were seen in moose suffering

TABLE 1. Fall (September) and spring (May) fawn: doe ratios, prevalence of hair loss syndrome (HLS) in fawns and does in early May, and minimum September–May fawn survival for western Washington game management units (SD).

		September	May	Prevale	_ Minimum	
Unit	Year			Fawns	Does	fawn survival
160	1999	65(9)	39(6)	55(4)	unknown	0.60(0.13)
160	2000	66(9)	37(6)	74(3)	33(4)	0.56(0.13)
160	2001	49(7)	36(6)	46(4)	28(3)	0.73(0.17)
530a	2000	66(7)	39(4)	9(2)	4(1)	0.59(0.09)
550	2001	48(5)	30(3)	6(1)	11(2)	0.63(0.10)
551	2001	53(8)	44(7)	17(3)	10(2)	0.83(0.19)
667	2000	88(9)	52(5)	11(2)	5(1)	0.59(0.09)
667	2001	94(9)	57(6)	48(3)	20(2)	0.61(0.09)

 $^{^{\}rm a}$ Extrapolated from ground surveys; all other data from helicopter surveys.

hair loss because of winter tick infestation (McLaughlin and Addison, 1986; Del Giudice et al., 1997). In early summer, affected deer molt into summer pelage and lose signs of HLS.

On the basis of anecdotal observations, local mortality from HLS or the factors that predispose deer to HLS can be very high—up to 100% fawn mortality on certain Puget Sound islands. However, the effects of other variables influencing productivity (i.e., population density) on these island populations are unknown. Thus, the effects of HLS on the population are unknown. Since the onset of HLS in 1996, black-tailed deer harvest in some game management units (GMUs), anecdotally viewed as heavily affected, has declined (L. Bender, unpubl. data). Biologists and the general public subjectively view HLS as having a significant effect on blacktailed deer populations, primarily through overwinter fawn mortality (Stouder, 2003).

Black-tailed deer populations in coastal forests are characterized by lower rates of productivity than mule deer (Odocoileus hemionus) or white-tailed deer (Odocoileus virginianus) in adjacent ecoregions (Heffelfinger et al., 2003). Low productivity makes black-tailed deer populations more susceptible to population declines instigated by factors that further depress production or survival of fawns. To stem apparent declines in black-tailed deer populations throughout the Pacific Northwest, it is important that population-level effects of factors potentially limiting productivity, such as HLS, be identified to develop effective management actions to maintain populations. Thus, we investigated the extent and effect of HLS on black-tailed deer in western Washington. Our goals were to: 1) determine prevalence of HLS in fawn and adult black-tailed deer in areas with high and low prevalence, 2) determine population productivity (late September fawn:doe ratios) and recruitment (May fawn:doe ratios) in these areas, 3) determine minimum overwinter fawn survival rates in these areas, and 4) model the potential effect of HLS on black-tailed deer populations in these areas.

MATERIALS AND METHODS

Study areas

We surveyed portions of five western Washington GMUs: GMU 460 (47.37°N, 121.30°W; 1999–2001), GMU 530 (46.17°N, 123.07°W; 2000), GMU 550 (46.09°N, 122.40°W; 2001), GMU 651 (47.08°N, 123.19°W; 2001), and GMU 667 (46.42°N, 122.27°W; 2000-01). These units were chosen on the basis of historical black-tailed deer productivity and harvest (GMUs 530 and 667 high, GMUs 550 and 651 medium, GMU 460 low) and a subjective evaluation of the level of HLS present (GMU 460 high; GMUs 530, 550, and 651 medium; GMU 667 low). Minimum mean deer densities were 3.8 ± 1.6 , 14.5 ± 2.6 , 16.9 ± 1.9 , 16.6 ± 4.9 , and 18.4±1.5 deer/2.6 km² for GMUs 460, 530, 550, 651, and 667, respectively (L. Bender, unpubl. data). Land ownership in each area was predominately private industrial timberland managed for Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) production.

Surveys

We conducted composition surveys in late September and paired these with follow-up surveys the following late April or early May. We classified all deer observed by sex and age (fawn, adult). Furthermore, each deer was classified as affected or unaffected by HLS on the basis of visual observations of the pelage. Because the obvious signs of HLS (hair loss, hyperpigmentation of skin) do not appear until November-December but persist through early June, we used observations from spring surveys to assign prevalence levels to study GMUs. We conducted all spring and fall surveys (except for GMU 530 in 2000) in a Bell JetRanger or LongRanger (L4) helicopter flown by a pilot highly experienced in wildlife surveys. Study GMUs were surveyed by flying low over open forest structure types and flushing or observing deer, which were then classified. All areas surveyed were less than 610 m in elevation; more than 95% were less than 457 m.

We extrapolated the fall survey in GMU 530 from region-wide ground surveys conducted by Washington Department of Fish and Wildlife (WDFW) staff. Comparison of helicopter and ground composition counts for deer and elk (*Cervus elaphus*) indicated that no differences existed between methods for fawn:doe ratios (Bender et al., 2003).

Data analysis

We determined prevalence of HLS for fawns and does in each GMU annually as prevalence = number of fawns with HLS/total number of fawns and = number of does with HLS/total number of does. We determined variance around proportions of fawns or does with HLS by the binomial approximation (Zar, 1996). We used correlations (Zar, 1996) to explore relations among fall and spring fawn:doe ratios, prevalence of HLS, and fawn survival. We also used correlations to explore relations between fawn survival and prevalence of HLS with mean deer population densities.

We used survey data to calculate fawn:doe ratios for September (productivity) and April/ May (recruitment). We determined minimum fawn survival rates, S_{m} , from composition data as $S_{\rm m} = F_{\rm R}/F_{\rm P}$, where $F_{\rm P}$ is fawns per 100 does in September and F_R is fawns per 100 does in April/May (Bender et al., 2002b). $S_{\rm m}$ is a minimum fawn survival estimate because adult doe mortality also occurs during the September-April/May period; thus, the number of fawns per 100 does observed in April/May corresponds with some number of does less than 100 relative to the number of fawns per 100 does in September. We determined variances around fawn:doe ratios following Czaplewski et al. (1983). We determined the variance around estimates of fawn survival by parametric bootstrapping (Bender et al., 2002b).

We determined trends in deer populations for each GMU by calculating the finite rate of population increase, λ, which is less than 1 if a population is declining, 1 if stable, and more than 1 if increasing (White and Bartmann, 1998). For populations in which recruitment is estimated (e.g., the fawn:doe ratio for May), λ = $F:D_{\text{May}}/2$ + S_{doe} , where $F:D_{\text{May}}$ is the observed fawn:doe ratio in May and S_{doe} is the annual survival rate of does (White and Bartmann, 1998). Because annual doe survival was unknown, we calculated λ with the use of doe survival rates of 0.75 and 0.80 to cover the range of values seen in black-tailed deer in the Pacific Northwest (see Results). We determined 90% confidence intervals for each estimate of λ with the use of parametric bootstrapping at N=10,000 iterations (Bender et al., 2002b). We further determined the probability of $\lambda < 1.00$ (i.e., the probability that the population was declining) by determining the proportion of the N=10,000 bootstrap iterations of λ that were less than 1.00. We used an α level of 0.05 to test for significance in each of the above.

RESULTS

Prevalence of HLS observed in fawns in April/May ranged from 6% to 74% (Table 1). Prevalence in adult does ranged from 4% to 33%. Minimum fawn survival rates were 0.56-0.83 (Table 1). Prevalence of HLS in either does (r=0.005, P=0.991) or fawns (r=-0.215, P=0.608) was unrelated to fawn survival. The prevalence of HLS in either does or fawns was also unrelated to either fall fawn:doe ratios (HLS does: r=-0.132, P=0.779; HLS fawns: r=0.130, P=0.760) or spring fawn:doe ratios (HLS does: r = -0.173, P = 0.711; HLS fawns: r=-0.020, P=0.963). Prevalence of HLS in does and fawns was strongly related (r=0.942, P=0.002).

Deer density was unrelated to fawn survival (r=0.098, P=0.817), fall fawn:doe ratio (r=0.386, P=0.346), and spring fawn: doe ratio (r=0.507, P=0.200). Population density was negatively related to prevalence of HLS in both fawns (r=-0.752, P=0.031) and does (r=-0.813, P=0.026).

Assuming annual doe survival of 0.75, annual λs ranged from 0.900 to 1.035, and deer populations were declining in five of eight cases (all P > 0.975; Table 2). Assuming annual doe survival of 0.80, annual λs ranged from 0.950 to 1.085, and deer populations were declining in only one of eight cases (Table 2).

DISCUSSION

Hair loss syndrome is hypothesized to affect black-tailed deer populations primarily through increased overwinter fawn mortality and therefore reduced population productivity. It is also anecdotally believed that HLS, or factors that predispose deer to HLS, could result in lowered body condition of does, which is directly tied to individual productivity; survival; viability and survival of fawns; and, consequently, population productivity (Wakeling and Bender, 2003). Our data spanned a range of 6–74% prevalence of HLS in fawns and 4–33% in does (Table 1). Despite this range in prevalence, HLS was unrelated to fawn production (September fawn:doe ra-

Table 2. Calculated annual finite rate of population increase (λ), 90% confidence interval (CI), and probability that λ <1.000 (i.e., probability that the population is declining) for each study area \times year combination, assuming adult doe survival rates ($S_{\rm d}$) of 0.75 or 0.80.

Unit	Year	$S_{ m d} {=} 0.75$			$S_{\rm d} = 0.80$		
		λ	90% CI	$P_{\lambda < 1.00}$	λ	90% CI	$P_{\lambda < 1.00}$
160	1999	0.945	0.895-0.993	0.975^{a}	0.995	0.945-1.043	0.591
160	2000	0.935	0.887 - 0.981	0.985^{a}	0.985	0.959 - 1.029	0.715
160	2001	0.930	0.883 - 0.974	0.992^{a}	0.980	0.921 - 0.978	0.771
530	2000	0.945	0.909 - 0.979	0.997^{a}	0.995	1.015 - 1.103	0.615
550	2001	0.900	0.871 - 0.928	1.000^{a}	0.950	0.965 - 1.072	0.998^{a}
651	2001	0.970	0.915 - 1.022	0.824	1.020	0.965 - 1.072	0.280
367	2000	1.010	0.965 - 1.053	0.362	1.060	0.933 - 1.024	0.013
367	2001	1.035	0.987 - 1.081	0.114	1.085	1.037 - 1.131	0.002

^a Values with superscript are significant α≤0.05.

tios), recruitment (April–May fawn:doe ratios), or overwinter fawn survival. Moreover, our observed minimum overwinter fawn survival (0.56–0.83) was comparable to other black-tailed deer fawn survival studies (Gilbert, 1992; Bender et al., 2002a) and was higher than regional mule deer fawn overwinter survival (0.44; Unsworth et al., 1999). Therefore, unless adult mortality differed markedly among study GMUs, there is little evidence to suggest an effect on overwinter fawn survival from HLS across the range of prevalence studied.

Population productivity is low for blacktailed deer in the Coastal Forest ecoregion, likely because of poor nutrition and the subsequent effects of nutrition on individual condition and reproductive parameters (Heffelfinger et al., 2003; Wakeling and Bender, 2003). Levels of productivity needed to maintain population size depend on the interaction of fawn production, fawn survival, and doe survival. Survival rates of black-tailed deer have been poorly documented. McNay and Voller (1995) found adult doe survival rates of 0.86-0.90 for the December-June period on Vancouver Island (British Columbia, Canada), and 0.73 annually. Blacktailed deer does living in urban habitats of greater Vancouver, Washington, had annual survival rates of 0.70 and 0.73 (Bender et al., 2002a). Migratory black-tailed deer in the Klickitat River Basin of southcentral Washington had annual survival rates of 0.80 for adult females (Mc-Corquodale, 1999). Estimates based on age structure of harvested black-tailed deer in western Washington were 0.78 for southwestern Washington inclusively (L. Bender, unpubl. data), 0.75 for the central Cascade foothills of Washington (estimated from Gilbert, 1992, Table 2), and 0.81 for the southern Cascade foothills of Washington (L. Bender, unpubl. data).

Trends in populations determined by calculating the finite rate of population increase (White and Bartmann, 1998) showed that of the study GMUs, fawn production or recruitment, or both, was consistently high enough to maintain population size on the basis of annual doe survival of 0.75 in GMU 667 only (Table 2). If a higher doe survival rate of 0.80 is substituted, then only three of eight GMUyear combinations observed in western Washington had at least a 50% probability of growing, and one had a more than 90% probability of declining (Table 2). Regardless of the ultimate cause(s), black-tailed deer populations had a high likelihood of declining throughout most of western Washington given observed levels of fawn recruitment and representative levels of adult doe survival. Moreover, if HLS or factors that predispose deer to HLS decrease adult survival, as winter tick-associated hair loss does in moose (Del Giudice et al., 1997), then our results are conservative, and black-tailed deer populations might be more likely to decline than indicated by use of historic adult doe survival rates (0.75 or 0.80).

On the basis of our data, population demographics of black-tailed deer from October to May were similar in each study area, regardless of the degree of HLS. This indicates that concern for increased overwinter fawn mortality from HLS is unfounded. Thus, if HLS is affecting population productivity in heavily affected areas, it is doing so by decreasing doe condition (and consequently pregnancy rates), fawn viability, or both or by directly affecting fawn survival before September. Poor body condition has been shown to decrease rates of pregnancy in elk (Cook, 2000). Poor doe condition has been related to decreased numbers of fetuses, decreased rates of twinning, increased prenatal fawn mortality, decreased fawn viability, decreased fawn birth mass, later fawn birth dates, decreased postnatal care, increased fawn abandonment, and lowered rates of mass gain (Langenau and Lerg, 1976; Carroll and Brown, 1977; Verme and Ullrey, 1984; Sams et al., 1996; Swihart et al., 1998; Wakeling and Bender, 2003). In turn, these effects are strongly related to lowered preweaning fawn survival (Clutton-Brock et al., 1982; Verme and Ullrey, 1984; Sams et al., 1996; Swihart et al., 1998). Moose affected with hair loss from tick infestations had lower body fat levels in late spring than did unaffected moose because of inadequate nutrition (McLaughlin and Addison, 1986; Del Giudice et al., 1997). Negative effects of HLS on doe condition could thus affect numbers of fawns born and September productivity ratios, and thereby deer populations, without decreasing overwinter fawn survival.

Strong negative correlations between deer population density and prevalence of HLS warrant further investigation into the possibility that HLS might be contributing to declines in deer populations through effects on fawn production and preweaning survival. However, in the most heavily af-

fected GMU (460; Table 1), declines in deer numbers began well before detection of HLS in Washington. Furthermore, prevalence of HLS was not related to fall fawn:doe ratios in our study GMUs. Together, these results suggest that HLS is unlikely to be solely responsible for the low productivity or apparent declines in black-tailed deer populations. However, although little mortality has been observed among adult deer in Washington, it is possible that HLS or predisposing factors might affect deer populations through decreased adult (rather than fawn) survival, as seen with moose suffering hair loss (Del Giudice et al., 1997). Del Giudice et al. (1997) observed no differences in moose recruitment during a winter tick epizootic on Isle Royale (Michigan, USA), despite declines in moose population size.

Management implications

Preliminary data suggest that HLS or factors that predispose deer to HLS were not affecting black-tailed deer populations through increased overwinter fawn mortality following the onset of clinical signs of HLS in November or December. However, productivity of deer in most GMUs was low and either inadequate or barely adequate to maintain population size. Furthermore, because overwinter survival of fawns was high, productivity problems were associated with either fawn production or survival before late September. Numbers of fawns produced, degree of maternal care, and preweaning survival are largely products of nutrition and its effects on doe body condition (Langenau and Lerg, 1976; Carroll and Brown, 1977; Verme and Ullrey, 1984; Sams et al., 1996; Swihart et al., 1998), although density-independent factors (i.e., predation, inclement weather) can also act to limit summer survival of fawns. Nutrition is known to be a strong limiting factor on deer (Parker et al., 1999; Heffelfinger et al., 2003) and elk (Cook et al., 2002) in coastal forests of the Pacific Northwest, and poor body condition because of inadequate nutrition could

also predispose deer to parasite infestation (Van Volkenberg and Nicholson, 1943; Demarais et al., 1983). Because of the effects of nutrition on condition, productivity, and survival and because heavy internal and external parasite infestation is hypothesized to be a causal mechanism for HLS (Foreyt et al., 2004), further work is needed to clarify the interactions of doe condition, doe survival, production and survival of fawns, degree of internal and external parasitism, and prevalence of HLS and thus to clarify the role of HLS in declines of black-tailed deer in the Pacific Northwest.

ACKNOWLEDGMENTS

We thank Weyerhaeuser Company, Plum Creek Timberlands, and the US Navy for external support of this project. The WDFW Wildlife Management Program provided internal support through Pittman-Robertson Act funds. We thank P. Miller, G. Schirato, and R. Spencer (WDFW) for assistance on composition surveys.

LITERATURE CITED

- Bender, L. C., D. P. Anderson, and J. C. Lewis. 2002a. Ecology of black-tailed deer in urban Vancouver, Washington. Washington Department of Fish and Wildlife, Vancouver, Washington, 58 pp.
- , E. Carlson, S. M. Schmitt, and J. B. Haufler. 2002b. Production and survival of elk (*Cervus elaphus*) calves in Michigan. American Midland Naturalist 148: 163–171.
- —, W. L. MYERS, AND W. R. GOULD. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. Wildlife Biology 9: 199–205.
- CARROLL, B. K., AND D. L. BROWN. 1977. Factors affecting neonatal fawn survival in south-central Texas. Journal of Wildlife Management 41: 63– 69.
- COOK, R. C. 2000. Studies of body condition and reproductive physiology in Rocky Mountain elk. MS Thesis, University of Idaho, Moscow, Idaho, 117 pp.
- COOK, J. G., R. C. COOK, L. C. BENDER, P. B. HALL, AND L. L. IRWIN. 2002. Nutritional influences on Northwestern elk herds: Wild elk capture and nutritional condition assessment. Progress report, National Council for Air and Stream Improvement, LaGrande, Oregon, 15 pp.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D.

- ALBON. 1982. Red deer: Behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, 378 pp.
- CZAPLEWSKI, R. L., D. M. CROWE, AND L. L. MCDONALD. 1983. Sample sizes and confidence intervals for wildlife population ratios. Wildlife Society Bulletin 11: 121–128.
- DEL GIUDICE, G. D., R. O. PETERSON, AND W. M. SAMUEL. 1997. Trends of winter nutritional restriction, ticks, and numbers of moose on Isle Royale. Journal of Wildlife Management 61: 895–903.
- Demarais, S., H. A. Jacobsen, and D. C. Guynn. 1983. Abomasal parasite counts as a health index for white-tailed deer in Mississippi. Journal of Wildlife Management 47: 247–251.
- Foreyt, W. J., B. Hall, and L. C. Bender. 2004. Evaluation of ivermectin for treatment of hair loss syndrome in black-tailed deer. Journal of Wildlife Diseases 40: 434–443.
- GILBERT, B. 1992. Long term population dynamics of a black-tailed deer herd on commercial forestland in western Washington. MS Thesis, University of Washington, Seattle, Washington, 125 pp.
- HEFFELFINGER, J. R., L. H. CARPENTER, L. C. BENDER, G. ERICKSON, M. D. KIRCHOFF, E. R. LOFT, AND W. M. GLASGOW. 2003. Ecoregional differences in population dynamics. *In* Mule deer conservation: Issues and management strategies, J. C. de Vos, Jr., M. R. Conover, and N. E. Headrick (eds.). Jack H. Berryman Institute Press, Logan, Utah, pp. 63–91.
- LANGENAU, E. E., JR., AND J. M. LERG. 1976. The effects of winter nutritional stress on maternal and neonatal behavior on penned white-tailed deer. Applied Animal Ethology 2: 207–223.
- McNay, R. S., and J. M. Voller. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. Journal of Wildlife Management 59: 138–146.
- MCCORQUODALE, S. M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63: 861–871.
- McLaughlin, R. F., and E. M. Addison. 1986. Tick (*Dermacentor albipictus*)-induced winter hair-loss in captive moose (*Alces alces*). Journal of Wildlife Diseases 22: 502–510.
- MOORING, M. S., AND W. M. SAMUEL. 1999. Premature loss of winter hair in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with grooming rate. Canadian Journal of Zoology 77: 148–156.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monograph
- SAMS, M. G., R. L. LOCHMILLER, C. W. QUALLS, JR.,

- D. M. LESLIE, JR., AND M. E. PAYTON. 1996. Physiological correlates on neonatal fawn mortality in an overpopulated herd of white-tailed deer. Journal of Mammalogy 77: 179–190.
- SAMUEL, W. M. 1991. Grooming by moose (Alces alces) infested with the winter tick, Dermacentor albipictus (Acari): A mechanism for premature loss of winter hair. Canadian Journal of Zoology 69: 1255–1260.
- STOUDER, S. 2003. Hairloss syndrome—Coastal conundrum. Mule Deer 8: 10–13.
- SWIHART, R. K., H. P. WEEKS, JR., A. L. EASTER-PILCHER, AND A. J. DENICOLA. 1998. Nutritional condition and fertility of white-tailed deer (Odocoileus virginianus) from areas with contrasting histories of hunting. Canadian Journal of Zoology 76: 1932–1941.
- UNSWORTH, J. W., D. F. PAC, G. C. WHITE, AND R. M. BARTMANN. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63: 315–326.
- VAN VOLKENBERG, H. L., AND A. J. NICHOLSON.

- 1943. Parasitism and malnutrition of deer in Texas. Journal of Wildlife Management 7: 220–223.
- VERME, L. J., AND D. E. ULLREY. 1984. Physiology and nutrition. *In* White-tailed deer: Ecology and management, L. K. Halls (ed.). Stackpole Books, Harrisburg, Pennsylvania, pp. 91–118.
- Wakeling, B. F., and L. C. Bender. 2003. Influence of nutrition on mule deer demographics. *In* Mule deer conservation: Issues and management strategies, J. C. de Vos, Jr., M. R. Conover, and N. E. Headrick (eds.). Jack H. Berryman Institute Press, Logan, Utah, pp. 93–118.
- WHITE, G. C., AND R. M. BARTMANN. 1998. Mule deer management—What should be monitored? In Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona, J. C. DeVos, Jr. (ed.). Arizona Game and Fish Department, Phoenix, Arizona, pp. 104–118.
- ZAR, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, 662 pp.

Received for publication 8 November 2002.