Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates

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REVIEW Because of its applied character, wildlife science needs opportunities to summarise existing knowledge by reviewing, either by presenting leading ideas and results of study teams, or summarising advanced knowledge of selected scientific or management problems. Reviews should be concise.

Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates

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A total of 111 papers and reports, coming from 79 major studies and 19 other studies, on neonatal (first summer) mortality of 10 species of northern, temperate ungulates were reviewed. To avoid biases from indirect techniques only studies on radio-collared neonates and/or their dams were included, apart from a few notable exceptions. Neonatal mortality rates observed for different studies averaged 47% (68 studies) in environments where predators occurred, with predation accounting for an average of 67% (53 studies) of this mortality. No other single cause of mortality exceeded that of predation, which accounted for 0-100% of the mortality recorded in various studies. In contrast, mortality averaged 19% for studies in environments lacking predators. Other prominent causes of mortality were hypothermia/starvation and accidents. Disease was found to play a small role only. The predator species involved varied greatly between study areas, with both medium sized (bobcat *Lynx rufus*, Canada lynx *Lynx canadensis*, coyote *Canis latrans* and red fox *Vulpes vulpes*) and large (wolf *Canis lupus*, mountain lion *Felis concolor*, black bear *Ursus americana* and brown bear *Ursus arctos*) terrestrial predators preying upon the neonates. Despite the prominent role of predation, little is known about its long-term compensatory or additive nature, and therefore its impact on population dynamics is unclear. Factors influencing predation rates are poorly understood, although a few studies found significant sex-biased predation, and effects of weather or juvenile/maternal body condition. Timing of mortality within the first summer varied with the predators involved and the neonatal security strategy of the species, but was not confined to the immediate post-partum period.

Key words: Ungulate, neonatal mortality, mother-young relationships, predation, population dynamics

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Ungulate mortality is usually attributed to two main causes, predation and food limitation (Sinclair 1985, Skogland 1991), although these interact with a plethora of other stochastic and predictable factors. Each cause of mortality can be affected differently by ecological factors and environmental conditions, and therefore it is important to know the exact causes of mortality and their relative magnitude before their role in population dynamics, behaviour and life history evolution can be fully ascertained (Promislow & Harvey 1991, Roff 1992).

Ungulate populations generally show a classic U-shaped pattern of age-specific mortality, with high mortality associated with the juvenile period, low mortality during prime adulthood, and increasing mortality associated with senescence (Caughley 1966, Millar & Zammuto 1983, Fowler 1987). The relative magnitude of mortality in each of the three periods is a vital consideration in the development of population dynamic models for age-structured populations (Gaillard et al. 1993).

Many problems exist with the methodology of mortality estimation. Studies based on carcass collection provide data on the relative age and sex structure of dead individuals (Nelson & Mech 1986, Jedrzejewski et al. 1992, Huggard 1993) and can be used to construct life tables (Spinage 1972, Millar & Zammuto 1983). Estimates of mortality based on population counts and determination of the female/young ratio provide only coarse estimates of the processes involved within the population. These methods generally fail to identify the causes and the detailed chronology of mortality (e.g. Bergerud 1971, Salwasser et al. 1978, Picton 1984). Far better estimates of mortality make use of individually marked animals, either with ear tags or radio collars (e.g. Smith 1986, Hamlin et al. 1984, Gaillard et al. 1993). These techniques provide both accurate details of cause and timing of mortality, and reduce many of the problems of sampling error that affect the other techniques.

While many studies make use of radio-collared yearlings and adults, most do not use radio-collared neonates (e.g. Bartmann et al. 1992) and, therefore, lack data on first summer mortality. As this is often the period of most concentrated mortality (Caughley 1966), failure to quantify first summer (neonatal) mortality and the factors influencing it weakens the results. A few studies of neonatal mortality based on radio-marked fawns (Cook et al. 1971, Beale & Smith 1973, Hamlin et al. 1984) are widely cited and together with anecdotal, visual observations on neonatal mortality (White 1973, Truett 1979, Hamlin 1979, Fox & Streveler 1986, Miller et al. 1988) are used to generalise about the importance of predation. It is not widely appreciated that many studies have been made on radio-marked and tagged ungulate neonates of temperate and arctic species, since the first radio-marking of neonates in 1965 (Cook et al. 1967). Only two attempts have been made to summarise certain components of the literature, for moose *Alces alces* and caribou *Rangifer tarandus* by Ballard (1992, 1994).

As the populations of large carnivores in Europe are generally increasing it is desirable to determine what effects predators will have on ungulate populations, once they have returned to an area. It is widely believed that large predators will prey heavily on ungulate neonates and as a result cause a reduction in the ungulate populations. As predators exist in greater numbers in North America, more studies on the effects of predation are available from that part of the world. It is our intention to review as many of these studies as possible, to bring to a wider audience the existing data, and to pinpoint what needs to be obtained. More specifically we ask the following questions: 1) What is the level of neonatal mortality, and 2) what is the relative role of predation in neonatal mortality? Furthermore, we discuss some of the ecological and evolutionary impacts of neonatal mortality.

Literature sources and data presentation

Literature was collected from many diverse sources, mainly by screening the literature cited sections of published and unpublished mortality studies, or reading through the contents pages of journal back issues. Researchers working with the species involved were also contacted directly. Database searches generally failed to find many studies, especially those that were never published. In general, the availability of reports was poor, with many large and definitive studies never cited or abstracted, and once identified they were nearly unobtainable. In total, 111 papers or reports resulting from 79 major studies on 10 species of northern ungulates were identified and obtained. Incidental observations from various other studies were also included as supporting data.

We tried to consistently categorise data from the different studies, and used the following conventions: All neonates suspected of being abandoned as a result of marking were removed from the tables; all probable causes of death were presumed to be correctly identified, therefore all deaths reported as probable predation were registered as predation; disease includes the animals dying from infectious agents, congenital deformity, parasite infestation as well as stillborn animals; starvation includes those dying from starvation, hypothermia and natural abandonment (but not marking-induced abandonment). Hunting or poaching deaths and marked neonates whose transmitter's failed during the first summer have been totally removed from the analysis. Based on the published data, we accordingly recalculated all mortality rates whenever possible.

Three indexes were calculated: 1) percentage of mortality was calculated from the total number of included deaths and the total number of fawns initially marked; 2) percentage of predation was calculated from the number of predator related deaths and the total number of fawns initially marked; and 3) percentage of mortality caused by predation was calculated from the number of predator related deaths and the total number of fawn deaths. Even though study periods varied, we exclusively analysed mortality during the first summer after birth, and in a few cases early autumn. Only in a few cases did the period analysed here exceed six months.

Detailed data were available for nine wild ungulate species, moose, pronghorn *Antilocapra americana*, white-tailed deer *Odocoileus virginianus*, black-tailed/mule deer *O. hemionus*, caribou/reindeer, wapiti/red deer *Cervus elaphus*, bighorn sheep *Ovis canadensis*, Rocky mountain goat *Oreamnos americanus* and roe deer *Capreolus capreolus*, and one feral population of domestic Soay sheep *Ovis aries*. Observations on bison *Bison bison* and musk ox *Ovibos moschatus* were also included. Most studies were on North American species or populations. Only six studies were on European species, and of these only three on roe deer involved radio-collared neonates.

Possible biases from handling neonates

The reliability, life span and range of miniature radio transmitters has greatly improved during the last twenty years (Kenward 1987) and several designs for expandable collars are available (Kolz & Johnson 1980, Steigers & Flinders 1980a, Schulz & Ludwig 1985, Keister et al 1988, Bon & Cugnasse 1992). Therefore, there are no technical problems with radio-collaring neonates.

Handling and radio-collaring neonates could theoretically produce biases (Wenger & Springer 1981). Mortality could be overestimated if marking-induced abandonment was not identified or if collars and ear tags predisposed neonates to predation. Abandonment can be reduced to a minimum through correct handling techniques and is easy to identify if neonate/dam behaviour is monitored after marking (Wenger & Springer 1981, Trainer et al. 1983, Garner et al. 1985, Livezey 1990). No studies have shown an effect of marking on survival, although intuitively large and brightly coloured markers should be avoided (Ballard et al. 1981, Garrot et al. 1985, Keister et al 1988, Ozoga & Clute 1988, Larsen & Gauthier 1989). Total mortality can be underestimated if the capture process fails to identify perinatal and stillbirth deaths, or if the post-capture monitoring scares predators away. Perinatal mortality can only be controlled for by closely monitoring parturient females and locating birth sites (Huegel et al. 1985a, Andersen et al. 1995), and is likely to be the greatest bias included in the present review (O'Pezio 1978, Whitten et al. 1992, Roffe 1993). Observer effect can be minimised by using 'mortality-sensors' in collars and monitoring neonates from a distance.

Generally, biases resulting from the careful marking and radio-collaring of neonates do not seem to pose large problems in wildlife mortality studies, and with correct techniques adequate sample sizes can be readily obtained (e.g. Downing & McGinnes 1969, Carrol & Brown 1977, Beale 1978, Trainer et al. 1983, Garner et al. 1985, Andersen et al. 1995).

The level of neonatal mortality and the role of predation

From the studies it is clear that neonatal mortality can often reach high levels (mean ± SD, 45% ± 25, N = 74), yet there is a large variation between individual studies (Table 1). Eight separate studies showed mortality levels of more than 80% while five other studies showed mortality rates below 10%. While many factors such as disease, starvation, parasites and accidents are involved, predation is by far the most important single factor operating in environments where predators exist. Predation rates averaged 37% ± 24 (N = 50) and caused an average of 67% ± 33 (N = 53) of the neonatal mortality in areas with predators. This role of predation is illustrated by the fact that while mortality rates (all causes) averaged 47% ± 24 in predator areas (N = 68), the average in areas lacking predators was 19% ± 8 (N = 6). Although based on a small sample size, the latter value is very similar to the value of 14% neonatal mortality for 12 ungulate species in captivity (Loudon 1985, English & Mulley 1992). From these results it is relatively clear that where they occur, predators are the major proximate cause of neonatal mortality, and that populations preyed upon suffer higher rates of neonatal mortality than populations not preyed upon (Table 2).

Variation also appeared to exist between species (see Table 2) although the intra-specific variation (high standard deviations) masked out any significant inter-specific trends (Kruskal-Wallis ANOVA; χ^2 = 13.4, df = 7, P = 0.06).

However, the published data must be interpreted with caution. In her bighorn study Hass (1989) found neonatal mortality rates of 89%, mainly resulting from coyote *Canis latrans* predation. The bighorn population had been transplanted from a mountain habitat to a prairie habitat. As bighorns are dependent on the presence of steep escape terrain as part of their neonatal security strategy (Berger 1991), the observed predation rates could be an artefact of the artificial location of the population.

The role of different predator species

At least part of the inter-study variation in mortality rates apparent in Table 1 must be due to variation in the predator fauna present in the various study areas (Table 3). This variation is both a result of natural variation in predator distribution patterns and an artefact of human activity. For example, alligators *Alligator mississippiensis* have only been involved in white-tailed deer neonate predation in one study (Epstein et al. 1983, 1985), the only study

Table 1. The number of neonates marked, the number of deaths due to predation, disease or parasites, starvation, accidents or unknown causes, with total percentage of mortality (% Mortality), the percentage of marked fawns killed by predators (% Predation) and the percentage of the total mortality due to predation (% Mortality to predation) in each of the known studies (Reference numbers). Studies carried out in large enclosures or environments without primary neonate predators are indicated with an asterisk (*).

Species	Study type[1]	No of marked neonates	Numbers of deaths due to: Predation	Disease	Starvation	Accidents	Unknown	% Mortality	% Predation	% Mortality to predation	Reference number
Moose	1	47	23	0	0	2	2	57	47	81	1, 2
	1	198	101	0	0	15	5	61	51	83	4, 5
	1	74	33	0	3	1	1	51	46	89	6, 7, 54
	1	11	1	0	0	0	0	9	9	100	8
	1	117	77	0	0	7	11	81	66	82	9
	1	33	23	0	0	0	4	79	67	85	10
	2*	229						11			11
	1	12	6	0	0	0	0	50	50	100	34
	1	88	26	0	0	0	0	30	30	100	35
	2							39			3
Pronghorn	1	200	97				30	64	49	76	12, 94
	1	30	15	0	0	0	9	80	50	63	13
	1	62	27	0	12	1	0	65	44	68	14, 15
	1	15	9	0	0	0	0	60	60	100	16
	1	131	83	3	3	0	2	69	64	91	17, 93
	4	53					36	68			18
	1	7	0	0	0	0	0	0	0	0	19
	4,2	58					36	63			20
	1	36	15	6	0	1	1	64	42	65	91
	1	47	25	0	4[3]	0	0	62	53	80	92
	1	102	60				12	71	59	83	95
	1	32	19				8	84	59	70	96
	1	29	16				1	59	55	94	97, 98
	1	34	19				3	65	56	86	99
	1	65	15	0	8[3]	0	0	37	23	63	100
White-tailed deer	1	7	0	4	0	0	0	57	0	0	21
	1	81	48	4	5	1	0	72	59	83	22
	1	32	28	0	0	0	0	85	85	100	23
	1	120	28	6	4	0	11	41	23	57	24
	1	46	38	0	0	1	2	85	79	93	25
	1	40	0	0	3	0	0	8	0	0	26
	1	44	25	0	0	1	12	86	57	66	27, 28
	1	55	10	1	0	2	0	24	18	77	29
	1	54	11	2	1	0	2	30	20	69	30
	1	40						41			31
	1	40						18			33
	4*	226						19			33
	4*	459						12			32
	2,4	17						0	0	0	58
	1	2					6	27			59
	1	2					11	41			60
	1	31	0	10	0	2	2	45	0	0	65
	1	39						33			66
	1	65						37			67
	1	23						100			68
	1	21	9	0	0	0	0	44	44	100	104
Mule deer	1	12	5	0	0	0	4	75	42	56	36
	1	26	10	1	0	3	0	54	38	71	37
	1	167	48	0	2	1	3	32	29	89	38, 39
	1	38	20	0	0	0	1	55	53	95	69
	1	25	12	2	0	1	0	60	48	80	87, 88
	1	21	0		0	0	0	10	0	0	89
	1	11	3	0	0	0	0	27	27	100	90
	1	278	36	10	6	6	5	23	13	57	102, 103
Black-tailed deer	1	16	4	0	1	1	1	44	25	57	40
Caribou	3	57	18	15	16	3	5			32	41
	2	6						50			42
	3	287	174	69	14	0	30			61	43, 63

Species	Study type[1]	No of marked neonates	Numbers of deaths due to					% Mortality	% Predation	% Mortality to predation	Reference number
			Predation	Disease	Starvation	Accidents	Unknown				
Caribou cont.	1	221	40	1	0	2	0	20	18	93	44
	1	182	13	1	0	1	4	10	7	68	45
	2	87						30			45
	3	60	8	15	29	3	5			13	46
	1	104					14	14			62
	2	224					56	25			62
	1,2	226	92	0	1	2	8	46	41	89	64
Wapiti	1	53	34	1	0	0	0	66	64	96	47
	1	15	0	0	0	0	0	0	0	0	57
	1	70	3	2	6	1	1	19	4	23	48
Red deer	4,2*	285						18			49
Bighorns	2	209					65	31			50
	2	49					41	84[2]			51
	2	46					18	39			52
	2	28					22	79			105
	2	10					6	60			106
Soay sheep	2,4*	559					183	33			54
Mt. goat	1,2,4	43					7	16	0	0	101
Roe deer	1	45	21	0	0	2	0	51	47	91	53
	1,2*	148	0	0	19	8	0	18	0	0	56
	1,2	95	23	1	2	2	3	33	24	74	55

[1] Study types: 1 = radio-collared neonates; 2 = radio-collared or marked dam; 3 = carcass collection; 4 = ear-tagged neonates.
[2] This population has been transplanted and occupies habitat without escape terrain (see text).
[3] Hypothermia involved.

References:

1. Franzmann et al. 1980
2. Franzmann & Peterson 1978
3. Hauge & Keith 1981
4. Ballard et al. 1981
5. Ballard et al. 1991
6. Franzmann & Schwartz 1986
7. Schwartz 1991
8. Boer 1988
9. Larsen et al. 1989
10. Gasaway et al. 1992
11. Sæther et al. 1992
12. Beale & Smith 1973
13. von Gunten 1978
14. Barrett 1978
15. Barrett 1984
16. Tucker & Garner 1980
17. Keister et al. 1988
18. Byers & Moodie 1990
19. Alldredge et al. 1991
20. Fairbanks 1993
21. Bolte et al. 1970
22. Cook et al. 1971
23. Garner et al. 1976
24. Carroll & Brown 1977
25. Bartush & Lewis 1981
26. Schulz et al. 1983
27. Epstein et al. 1983
28. Epstein et al. 1985
29. Huegel et al. 1985b
30. Nelson & Woolf 1987
31. Smith 1987
32. McGinnes & Downing 1977
33. Ozaga & Verme 1986
34. Beaulieu 1984 in Stewart et al. 1985
35. Mercer in Ballard 1992
36. Dickinson et al. 1980
37. Steigers & Flinders 1980b
38. Hamlin et al. 1984
39. Hamlin & Mackie 1989
40. Welker 1986
41. Miller & Broughton 1974
42. Fuller & Keith 1981
43. Miller et al. 1988
44. Mahoney et al. 1990
45. Whitten et al. 1992
46. Roffe 1993
47. Schlegel 1976
48. Bear 1989
49. Guinness et al. 1978
50. Festa-Bianchet 1988
51. Hass 1989
52. Hass 1990
53. Aanes & Andersen in prep.
54. Grubb 1974
55. Liberg et al. 1993
56. Andersen et al. 1995
57. Wallace & Krausman 1992
58. Nixon et al. 1991
59. Schwede et al. 1992
60. Jackson et al. 1972
61. Bergerud & Page 1987
62. Fancy & Whitten 1991
63. Millar & Zammuto 1983
64. Adams et al. 1995
65. Logan 1973
66. Bryan 1980 in Porath 1980
67. Veteto & Hart 1976 in Porath 1980
68. Cartwright & Rogers 1977 in Porath 1980
69. Nellis 1977 in Connolly 1981
70. Stewart et al. 1985
71. Wilton 1983
72. Wilton et al. 1984
73. LeResche 1968
74. Messier & Crête 1985
75. Nelson & Mech 1986
76. Litvaitis & Bartush 1980
77. Mathews & Porter 1988
78. White 1973
79. Salwasser et al. 1978
80. Truett 1979
81. Seip 1992
82. Bergerud et al. 1984
83. Bergerud 1971
84. Miller et al. 1985
85. Ashcroft 1986
86. Reynolds & Garner 1987
87. Anderson 1975
88. Andersen 1976
89. Zwank 1977
90. Wenger & Springer 1981
91. Bodie 1979
92. Autenrieth 1986
93. Trainer et al. 1983
94. Beale 1978
95. Beale 1986
96. Firchow 1980
97. McNay 1980 in Trainer et al. 1983
98. O'Gara et al. 1986
99. Corneli et al. 1984
100. Autenrieth 1984
101. Festa-Bianchet et al. 1994
102. Trainer et al. 1981
103. Trainer 1975
104. Kunkel & Mech 1994
105. Krausman et al. 1989
106. Harper 1984
107. Carbyn & Trottier 1987
108. Gray 1983
109. Clarkson & Liepins 1993
110. Mech 1988
111. Ozoga & Verme 1982
112. Ratcliffe & Rowe 1979

Table 2. Mean percentages (± SD) of neonatal mortality, neonates killed by predators and mortality due to predation for nine species of northern temperate ungulates in populations subject to predation, and the percentage of mortality in populations not subject to predation. The means (± SD) are rounded to nearest whole numbers. The numbers in parentheses refer to the references listed in Table 1.

Ungulate species	% Neonate mortality		% Killed by predators		% Mortality due to predation		% Mortality without predation
Moose	51 ± 23	(9)	46 ± 19	(8)	90 ± 9	(8)	11 (1)
Pronghorn	61 ± 20	(15)	47 ± 18	(13)	72 ± 25	(13)	
White-tailed deer	46 ± 28	(19)	32 ± 32	(12)	54 ± 42	(12)	16 (2)
Mule/black-tailed deer	42 ± 21	(9)	31 ± 17	(9)	67 ± 30	(9)	
Caribou	28 ± 15	(7)	22 ± 17	(3)	59 ± 32	(6)	
Wapiti/red deer	28 ± 34	(3)	23 ± 34	(3)	40 ± 50	(3)	18 (1)
Roe deer	42 ± 13	(2)	36 ± 16	(2)	83 ± 12	(2)	18 (1)
Bighorn sheep	52 ± 22	(4)					
Mountain goa	16	(1)	0	(1)	0	(1)	

which occurred inside alligator habitat. Wolves *Canis lupus* were only reported as a predator in one white-tailed deer study (Nelson & Mech 1986, Kunkel & Mech 1994) because this was the only white-tail study in an area with wolves. The absence of wolves from other white-tailed deer study sites is almost completely due to the human mediated extinction of wolves from most of the southern part of their range (Peterson 1988). In areas without wolves, white-tailed deer were mainly preyed on by coyotes (Steigers & Flinders 1980b, Huegel et al. 1985b, Nelson & Woolf 1987) which have filled the ecological niche vacated by wolves (Peterson 1988). While brown bears *Ursus arctos* and black bears *Ursus americana* are documented to be the most important predators of moose calves (with which they are sympatric, Ballard et al. 1981), it is clear that the lack of habitat overlap (historic and present) with pronghorn explains the absence of bear predation in this species.

Such complications make it difficult to explain why some predator species are more important in some areas than in others, or to some ungulate species than to others. There did appear to be a weight threshold as no predators smaller than 5 kg were mentioned. The red fox *Vulpes vulpes* is the smallest predator to be mentioned as a major neonate predator. While they prey on roe deer fawns in Europe (Borg 1991, Liberg et al. 1993, Lindström et al. 1994, Aanes & Andersen in prep., Andersen et al. 1995), their role in North America seems mainly to be that of a scavenger (Ozoga et al. 1982). Once over this weight threshold, body size appears to play a minor role,

Table 3. Number of studies or observations for 10 ungulate species subject to predation on neonates giving the total number of individual studies or independent observations in which a particular predator has been involved including the number of studies (in parenthesis) in which this particular predator was the main predator of neonates.

Ungulates/ predators	Brown Bear	Black Bear	Wolf	Coyote	Bobcat	Lynx	Mt. Lion	Fox	Eagle	Miscellaneous[1]	References[2]
Moose	6(3)	10(5)	7	2							1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 71, 72, 73, 74
Pronghorn				15(10)	10(2)				10(2)	Bd./Pf.	12, 13, 14, 15, 16, 17, 18, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100
White-tailed deer		6	2(1)	11(7)	8(3)			1		Al./Dg.	22, 23, 24, 25, 27, 28, 29, 30, 59, 60, 66, 67, 68, 71, 72, 75, 76, 77, 78, 104, 111
Mule/Black-tailed deer		1		8(6)	1		4(3)		3		36, 37, 38, 39, 40, 63, 69, 71, 79, 80, 87, 88, 89, 90, 102, 103
Caribou	5	1(1)	8(3)	1		2(2)		1	2(1)	Wl.	41, 43, 44, 45, 61, 64, 81, 82, 83, 84, 86
Wapiti		2(1)		2(1)	1		2(1)		1		47, 48, 71
Red deer									1(1)		49
Roe deer								2(2)	1	Wc.	53, 55, 112
Bison			1								107
Musk ox	1		3								108, 109, 110

[1] Al. = alligator, Dg. = domestic dog, Bd. = badger, Wl. = wolverine, Pf. = Prairie falcon, Wc. = wildcat
[2] Numbers refer to the list in Table 1

as indicated by the wide range of predator species involved in predation on even the large calves of moose and wapiti.

In temperate areas, neonates are only seasonally available (Rutberg 1987), making it impossible for a predator to be a year-round neonate specialist. It is therefore not surprising that the most important predators appear to be the generalist canids (coyotes) and ursids (brown and black bears), with the more specialised felids having a lesser, but not insignificant, role. Mountain lions *Felis concolor* are ungulate specialists and prey on all age classes of mule deer and wapiti (Hornocker 1970), so neonates of these species are expected to appear in their diet. The Canada lynx *Lynx canadensis* is almost exclusively a lagomorph hunter, and has only been observed to prey on neonatal caribou (Mahoney et al. 1990) within the simple Newfoundland ecosystem, possibly as a response to lows in the hare cycle (Bergerud 1971). The bobcat *Lynx rufus* is the most generalist of all the North American felids and is the felid most involved in predation on neonates (see Table 3). In most cases the major predator of neonates is also a predator of older age classes.

The only avian predator to commonly kill neonates is the golden eagle *Aquila chrysaetos*, and only in relatively few studies has this been observed (Whitten et al. 1992, Ratcliffe & Rowe 1979, see Table 3). Golden eagles appear to be the only predator capable of regularly killing Rocky mountain goat neonates in their steep cliff habitats (Rideout 1978, Chadwick 1983, Festa-Bianchet et al. 1994). Corvids and other scavengers were not implicated in any predation on the ungulate species reviewed here. Isolated incidents of neonate predation by smaller carnivores such as American badger *Taxidea taxus*, prairie falcon *Falco mexicanus*, and European wild cat *Felis sylvestris* have been reported, but at an insignificant frequency (Bodie 1979, Trainer et al. 1983, Gaillard pers. comm.). Despite many of the studies of white-tailed deer and roe deer being carried out in agricultural areas, domestic dogs *Canis familiaris* have only occasionally been reported as predators of neonates (Nelson & Woolf 1987, Porath 1980, Andersen et al. 1995).

It appears that all mammalian predator species of a suitable size will prey on ungulate neonates when the opportunity arises. Further analysis of their relative importance would require data on their numbers in each study site, but such data were not available.

Factors affecting neonatal predation

Where the main source of neonate mortality is starvation, the role of maternal, population, and environmental factors such as age, condition, timing of birth, birth weight, population density, habitat structure and rainfall in determining variation in survival and fitness are reasonably well known (e.g. Clutton-Brock et al. 1982, Rognmo et al. 1983). Generally, the role of such factors in predation on neonates is poorly understood. Age of dam has been found to be positively correlated with survival in two white-tailed deer populations (Ozoga & Verme 1986, Mech & McRoberts 1990) which were subject to black bear and wolf predation, respectively. Capture weight did not correlate with caribou mortality in Newfoundland (Mahoney et al. 1990). Fairbanks (1993) found that low birth weight increased the probability for pronghorn fawn mortality, but failed to identify the specific causes. Similarly, lighter white-tailed deer fawns tended to be killed by canids (Nelson & Woolf 1987), possibly explained by the tendency for fawns not receiving enough milk to follow their mother, and perhaps vocalise more (Carl & Robbins 1988). However, the opposite was also indicated for another pronghorn population by O'Gara et al. (1986) who found a trend for the heavier fawns to be killed.

The density of alternative prey was theoretically shown to affect the relative efficiency of coyotes hunting pronghorn fawns as opposed to rodents/lagomorphs (Byers & Byers 1983). This theory was supported by field data showing that the availability of rodents affected the predation rates of coyotes on mule deer and pronghorn fawns (Hamlin et al. 1984, Beale 1986). Similar results were found for lynx preying on snowshoe hare *Lepus americanus* and caribou calves on Newfoundland (Bergerud 1983). This relationship could cause cyclicity in neonatal predation rates when the primary predator of neonates feeds on cyclic alternative-prey populations. But to elucidate this relationship, studies of neonatal predation are required to monitor alternative prey and should be carried out over a full cycle, which has not been done so far.

The availability of cover for hider neonates was dependent on rainfall in a Texas white-tailed deer population (Carroll & Brown 1977), and in years of high cover availability coyote predation was reduced. The cover for bedding sites available in different habitats was similarly shown to affect pronghorn fawn mortality (Bodie 1979, Barrett 1981, O'Gara et al 1986). Variation in mortality over small geographical scales was also found by Andersen (1976), Fairbanks (1993) and Nelson & Woolf (1987). The last mentioned found that the dams of predator-killed fawns tended to occupy home ranges in open habitats and fields. A similar result was found for roe deer (Andersen et al. 1995). Stochastic climatic effects also affect caribou calf mortality where variation in the timing of snow melt affects the distribution of parturient females and thus the search efficiency of wolves and bears (Bergerud & Page 1987, Adams et al. 1995). The effect of individual dam behaviour on the probability of survival has not been investigated so far, even though the intensity of maternal defence in black-tailed deer varied with population density (Smith 1987).

Chronology of neonatal mortality

Deaths from both predation and other sources show a clear temporal distribution, with mortality concentrated within the first two months post-partum, before dropping significantly in late summer and early autumn. Within this general trend there is much variation. All studies on moose show the same trend with 80% of the neonatal mortality, from both predator and non-predator causes, occurring during the first four to six weeks after birth (e.g. Ballard et al. 1991), after which period calves are better able to escape from bears and wolves. Pronghorn show a consistent pattern of low mortality in the first days post-partum rising to a peak between 10 and 20 days of age (von Gunten 1978, Barrett 1978, 1981, 1984, Trainer et al. 1983) and then declining rapidly after one month of age. Similar results have also been found for roe deer (Andersen et al. 1995). Byers & Byers (1983) hypothesised that this was due to the greater probability of detection by a predator as the hider type neonate becomes more active with increasing age, before having developed full coordination.

White-tailed and black tailed/mule deer show much greater variation in the chronology of mortality. While some studies showed that mortality is very low after the first month (Cook et al. 1971, Garner et al. 1976, Bartush & Lewis 1981, Epstein et al. 1983, 1985, Schulz et al. 1983) others showed a much more gradual phasing out of mortality during summer (Beale & Smith 1973, Dickinson et al 1980, Steigers & Flinders 1980a, Huegel et al. 1985b, Hamlin & Mackie 1989). Nelson & Woolf's (1987) study showed the same pattern as for pronghorn, where canid (coyote and feral dog) predation only began after 20 days of age, the time when white-tailed fawns grow increasingly active in the absence of the dam.

Wapiti show the sharpest drop-off rate, with 80% of the predator mortality having taken place by two weeks of age (Schlegel 1976). In the absence of mammalian predators red deer fawns suffer 80% of their summer mortality during their first week of life (Guinness et al. 1978). Caribou mortality is also largely concentrated in the first month of life (Mahoney et al. 1990), with more than 60% of mortality having taken place by four weeks of age in Newfoundland and an annual average of 85% of mortality having taken place within 15 days after parturition for the Denali herd (Adams et al. 1995). Therefore, neither predator nor non-predator related mortality is concentrated in the immediate post-partum period but takes place during a longer period of at least a month. During this period neonates presumably develop the speed and agility to better escape from predators and with increasing body size they become less vulnerable to cold and starvation. The only reports of neonatal mortality peaking later in the summer, long after parturition, were in bighorn sheep where disease was the main agent (Woodard et al. 1974, DeForge et al. 1982, DeForge & Scott 1982) and in mountain goat where predation only began in late autumn (Festa-Bianchet et al. 1994).

Proper age-specific mortality analysis is confounded by the fact that few authors present detailed age or time-specific data or use a staggered entry analysis (e.g. Pollock et al. 1989) to account for the different ages of neonates at capture (see Huegel et al. 1985b and Schwartz & Franzmann 1989). Little information is presented on the timing of mortality relative to the peak parturition date. However, the data of Aanes & Andersen (in prep) where roe deer mortality is heaviest for fawns born during the peak period, and of Adams et al. (1995) where wolf predation is concentrated into a narrow period following the birth peak, show that this temporal effect may be just as important as age in determining the pattern of predation on neonates. The results of the latter study may also reduce the significance of the observations of wolf surplus-killing of caribou calves (Miller et al. 1985), as such observations may have been carried out during the peak period only.

Non-predator mortality

Perinatal mortality

The highest rates of perinatal mortality, mainly from stillbirths, were found in three caribou studies (Miller & Broughton 1974, Miller et al. 1988, Roffe 1993). However, the results of these studies might be ascribed to different study techniques as they were based on searches for dead neonate carcasses. As discussed earlier, failure to find the birth site may cause a bias with respect to perinatal mortality. Andersen et al. (1995) found almost 30 carcasses from perinatal deaths during the capture of 148 living roe deer fawns. If these had been radio-marked before death and had been included as mortalities in the criteria which we used, the percentage of mortality would increase from 18% to 32% for this population. Such levels of perinatal mortality probably exist in most species but remain undetected.

Starvation/hypothermia

The main cause of non-predator mortality was starvation/hypothermia (see Table 1). The last part of gestation and lactation impose very high energetic costs on reproductive females (Loudon 1985). It is likely that many females in less than peak condition are unable to provide for their offspring during this period when they are totally dependent on the dam for nourishment. Abandonment appears to be a natural phenomenon under some circumstances (Smith 1987, Andersen et al. 1995) and can lead to the finding of dead fawns in which the proximate cause of death is also starvation. In farmed fallow deer *Dama*

dama stillbirth accounted for only 23% of perinatal mortality, with 70% being post-parturient. Starvation was the leading cause of this perinatal mortality (English & Mulley 1992).

Ungulate neonates are small and lack substantial reserves of white body fat, and would therefore be expected to be vulnerable to hypothermia during periods of bad weather. Of all ungulate species caribou give birth in the harshest environmental conditions. Contrary to early reports (Pruitt 1961) adverse weather was not concluded to be a significant factor affecting caribou calf survival (Miller & Gunn 1986). Experimental studies have shown that reindeer calves can tolerate temperatures as low as -22°C without shivering through increased brown fat metabolism (Soppela et al. 1986). Unfortunately no comparative data on other species are available. Species with hider strategies (Lent 1974), such as pronghorn, may gain some thermoregulatory benefits from the micro-climate of their beds (Barrett 1981). Despite this, increased mortality has been reported for pronghorn fawns in years of severe weather in the fawning season (Autenrieth 1984, 1986), and roe deer fawns have been found dead after late snowfall (Andersen et al. 1995). Correlational studies have shown greater effects of winter and spring weather than post-birth weather on juvenile survival in mule deer and bighorn sheep (Picton 1979, 1984) indicating that weather often may affect the neonate indirectly, i.e. through maternal condition or birth weight, rather than directly.

Accidents

Accidents seem to play a relatively small role in neonatal mortality, although neonatal ungulates do seem to have a propensity to drown in even the smallest bodies of water (Guinness et al. 1978, Steigers & Flinders 1980a, Bartush & Lewis 1981, Ballard et al. 1981, 1991, Hamlin et al. 1984, Huegel et al. 1985b, Franzmann & Schwart 1986, Mahoney et al. 1990, Gasaway et al. 1992, Whitten et al. 1992, Roffe 1993, Andersen et al. 1995). Deaths due to agricultural accidents also occur but at low frequency; hay-mower deaths have been reported (Strandgaard 1972, Logan 1973, Huegel et al. 1985b, Nelson & Woolf 1987, Andersen et al. 1995) as have cases of being stepped on by domestic livestock (Guinness et al. 1978, Cook et al. 1971, Barrett 1984) and traffic accidents (Logan 1973, Porath 1980, Nelson & Woolf 1987, Andersen et al. 1995).

Parasites, disease and pathological disorders

One of the few cases where disease has been found to be of numerical importance is in bighorn sheep where pneumonia was found to be a significant mortality factor of lambs (Woodard et al. 1974, DeForge et al. 1982, DeForge & Scott 1982). Although not of numerical importance the following causes of mortality have been identified (number of studies are given in parenthesis) in the genus *Odocoileus*: salmonellosis (3), pneumonia (1), septicemia (1), *Corynebacterium* infection (1), bacterial enteritis (1), bacterial hepatitis (1), staphylococcal infection (2), dermatophilosos (1), peritonitis (1), anemia (1), and circulatory collapse (1) (Robinson et al. 1970, Cook et al. 1971, Carroll & Brown 1977, Steigers & Flinders 1980b, Huegel et al. 1985b, Epstein et al. 1985); in pronghorn: salmonellosis (1), pneumonia (2), septicemia (1) and 'weak fawn syndrome' (1) (Beale & Smith 1973, Bodie 1979, Trainer et al. 1983); in caribou: pneumonia (2) and atelectasis (2) (Miller & Broughton 1974, Miller et al. 1988) and in moose: pneumonia (1) (Ballard et al. 1981, 1991). These infections and disorders typically only affect a few individuals. For purely technical reasons most studies have been unable to identify, or have not looked for, disease agents and pathological disorders. In particular, viral infections have not been extensively researched.

Ecto-parasites, usually ticks, have been found in a number of cases (e.g. Garner et al. 1976) even though only the lone star tick *Amblyomma americanus* seems to have severe and lethal local effects (Bolte et al. 1970, Logan 1973, Nelson & Woolf 1987). Few studies have examined neonates for endo-parasites.

Sex biases in neonatal mortality

Few authors present analyses of the sex ratio of neonates killed in their studies, but those that do show diverging results. Mahoney et al. (1990) and Franzmann & Schwartz (1986) found trends for male neonates to suffer higher predation rates than female neonates, while Steigers & Flinders (1980b) and Andersen et al. (1995) found severe biases towards male mortality. The picture is complicated by others studies (Cook et al. 1971, Bartush & Lewis 1981, Trainer et al. 1981, Welker 1986, Nelson & Woolf 1987, Ballard 1992) which reported no sex differences of predator killed neonates, and Hamlin & Mackie (1989) who found no overall sex difference, except in one year with particularly heavy female biased predation. Jackson et al. (1972) and Schwede et al. (1992) hypothesised that the higher level of activity characteristic of male white-tailed deer fawns would put them at greater risk of detection by predators during the hiding stage.

Effects of neonatal mortality on population dynamics

Although first summer mortality may often remove 50% of the annual neonate production from the population, its effects on population dynamics are not clear. The juvenile stage can clearly tolerate heavier mortality than the adult stages as this is more rapidly produced, and as for all iteroparous animals the population's growth rate is far more sensitive to adult mortality than to juvenile mortality (Gaillard 1992). The fact that the same predator species often prey on all age-classes and thus are involved in adult mortality as well, could cause a degree of stabilisation in the system (Taylor 1984). The large magnitude of predator-induced neonatal mortality demonstrates that predation could act as a strong limiting factor on a population's rate of increase. However, as no studies have provided convincing evidence of density-dependent neonatal predation, its role in regulating populations is unknown. Ballard's (1992) review of moose calf mortality found no cross-study relationship between moose density and bear predation, although variation in habitat and predator composition between study sites would reduce the significance of such comparisons.

As most researchers do not follow their marked neonates through to winter or subsequent survival, little is understood about the compensatory or additive nature of neonatal predation. Results from predator removal programs (Beasom 1974, Stout 1982, Stewart et al. 1985) which showed significant increases in the number of offspring per female in autumns following control, and the low mortality rates from captive populations and predator free environments (see Table 2, Loudon 1985) indicate that neonatal predation is largely additive during the summer period. Indirect studies on moose (reviewed by Boutin 1992) and one on mule deer (Bartmann et al. 1992) provide evidence that increased summer survival may be compensated for by decreased late winter survival. Obviously an understanding of this feature of neonatal mortality/predation is a prerequisite to understanding its full role in population dynamics. When quantifying the numerical impact that a given predator species has on its ungulate prey, predation on neonates must clearly be taken into account as failure to do so would greatly underestimate its effect.

Evolutionary consequences of predation on neonates

Mortality patterns are major predictors of mammalian life history variation (Promislow & Harvey 1991), and especially juvenile survival has been shown to be the major determinant of individual reproductive success among mammals (Clutton-Brock 1988). As ungulates invest a relatively large component of their life-time reproductive success in each neonate (Stearns 1983) it should be expected that selection for behaviours that reduce neonatal mortality would be strong. Ungulates use four strategies (namely hiding, swamping, montane following, and group defence) when rearing their neonates (Lent 1974, Geist 1981). The present review has shown predation to be the major proximate cause of neonatal mortality. It is therefore expected that these four neonatal security strategies would primarily be directed at protecting neonates from predation. This supports the conclusions from North American studies which attribute the parturient behaviour of female moose and caribou to predator avoidance primarily (Stephens & Peterson 1984, Bergerud et al. 1984, Bergerud 1985, Seip 1992). However, it forces us to be careful when interpreting the adaptiveness of breeding female behaviour for ungulate populations presently living in predator-free environments (e.g. in much of Europe). The extent to which past selection for predator avoidance affects ungulate behaviour in the absence of predators is unknown.

However, as starvation/hypothermia is the second major proximate cause of neonatal mortality, and may also interact with predation through its effect on offspring vulnerability, there may exist a trade-off between efforts to simultaneously reduce these two mortality factors. When examining neonatal security strategy, both these mortality factors need to be considered. Different components of the strategy, such as timing and synchrony of birth (Bunnell 1982, Rutberg 1987, Skogland 1989), choice of birth site (Stephens & Peterson 1984), and mother-offspring spacing behaviour (Lent 1974, Geist 1981) may be adaptations to different mortality factors.

Conclusions

Predation was usually the major proximate cause of neonatal mortality in populations that still co-existed with their predators. In other cases neonatal mortality was lower. After predation, starvation was the leading cause of mortality. Mainly medium and large, generalist terrestrial predators (canids and ursids) kill the neonates. Mortality, including predation tended to be concentrated in the first month post-partum, although it extended for up to three months in some cases. Generally, both sexes were preyed upon, although in some studies male biases were found. Little is known about the long-term compensatory or additive nature of neonatal predation, and therefore its effects on ungulate population dynamics are unclear, apart from the obvious conclusion that it has the potential to be a major limiting factor. Predation may obviously have a major effect on individual fitness, although data on individual factors affecting predation are sparse. The magnitude of neonatal predation must have made up a strong selection pressure in the evolution of ungulate neonatal rearing behaviour and mother/young interactions, although the importance of adequate maternal nutrition must not be forgotten.

Increasing predator populations in much of Europe may be expected to reduce the numbers of neonate ungulates surviving the summer. While this will reduce the number of harvestable juveniles available to hunters in autumn, it is unclear if it will have any effect on the overall ungulate population density. With the very high densities at which wild ungulate populations occur in much of Europe today, it is unlikely that the increased loss of neonates alone will have a significantly negative effect. Eventual predation on older age classes is likely to have a much larger effect.

Future research should concentrate on elucidating the compensatory or additive nature of neonatal predation, the effects of individual dam characteristics and environmental factors such as weather, habitat and alternative prey, and the consequences of different behavioural strategies. Data on the number of neonates killed annually by each predator species will also assist in estimating the impact of predation and contribute to determining how important neonates are for the predators.

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References

Adams, L.G., Singer, F.J. & Dale, B.W. 1995: Caribou calf mortality in Denali National Park. - Journal of Wildlife Management 59: 584-594.

Alldredge, A.W., Deblinger, R.D. & Peterson, J. 1991: Birth and fawn bed site selection by pronghorns in a sagebrush-steppe community. - Journal of Wildlife Management 55: 222-227.

Anderson, A.E. 1975: Evaluation of radio telemetry. - Colorado Division of Wildlife Game Research Report W-38-R-29: 413-473.

Andersen, A.E. 1976: Evaluation of radio telemetry. - Colorado Division of Wildlife Game Research Report W-38-R-31: 464-502.

Andersen, R., Linnell, J.D.C. & Aanes, R. 1995: Rådyr i kulturlandskapet. Sluttrapport. (In Norwegian with English summary: Roe deer in agricultural landscapes: final report). - NINA fagrapport 10: 1-80.

Ashcroft, G.E.W. 1986: Attempted defence of a lamb by a female bighorn sheep. - Journal of Mammalogy 67: 427-428.

Autenrieth, R.E. 1984: Little lost pronghorn fawn study - condition, habitat use and mortality. - Proceedings Biennial Pronghorn Antelope Workshop 11: 49-70.

Autenrieth, R.E. 1986: Antelope-feral horse-livestock range relations. - Idaho Department of Fish and Game Final Report Project W-160-R: 1-85.

Ballard, W.B. 1992: Bear predation on moose: a review of recent North American studies and their management implications. - Alces Supplement 1: 162-176.

Ballard, W.B. 1994: Effects of black bear predation on caribou - a review. - Alces 30: 25-35.

Ballard, W.B., Spraker, T.H. & Taylor, K.P. 1981: Causes of neonatal moose calf mortality in south central Alaska. - Journal of Wildlife Management 45: 335-342.

Ballard, W.B., Whitman, J.S. & Reed, D.J. 1991: Population dynamics of moose in south-central Alaska. - Wildlife Monographs 114: 1-49.

Barrett, M.W. 1978: Pronghorn fawn mortality in Alberta. - Proceedings Biennial Pronghorn Antelope Workshop 8: 429-444.

Barrett, M.W. 1981: Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. - Journal of Wildlife Management 45: 120-131.

Barrett, M.W. 1984: Movements, habitat use and predation on pronghorn fawns in Alberta. - Journal of Wildlife Management 48: 542-550.

Bartmann, R.M., White, G.C. & Carpenter, L.H. 1992: Compensatory mortality in a Colorado mule deer population. - Wildlife Monographs 121: 1-39.

Bartush, W.S. & Lewis, J.C. 1981: Mortality of white-tailed deer fawns in the Wichita Mountains. - Proceedings Oklahoma Academy Science 61: 23-27.

Beale, D.M. 1978: Birth rate and fawn mortality among pronghorn antelope in western Utah. - Proceedings Biennial Pronghorn Antelope Workshop 8: 445-448.

Beale, D.M. 1986: Pronghorn antelope productivity on semi-desert range in western Utah. - Proceedings Biennial Pronghorn Antelope Workshop 12: 41-42.

Beale, D.M. & Smith, A.D. 1973: Mortality of pronghorn antelope fawns in western Utah. - Journal of Wildlife Management 37: 343-352.

Bear, G.D. 1989: Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. - Colorado Division of Wildlife, Special Report No. 651-12.

Beasom, S.L. 1974: Relationships between predator removal and white-tailed deer net productivity. - Journal of Wildlife Management 38: 854-859.

Berger, J. 1991: Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. - Animal Behaviour 41: 61-77.

Bergerud, A.T. 1971: The population dynamics of Newfoundland caribou. - Wildlife Monographs 25: 1-55.

Bergerud, A.T. 1983: Prey switching in a simple ecosystem. - Scientific American 249: 116-124.

Bergerud, A.T. 1985: Antipredator strategies of caribou: dispersion along shorelines. - Canadian Journal of Zoology 63: 1324-1329.

Bergerud, A.T. & Page, R.E. 1987: Displacement and dispersion of parturient caribou at calving as antipredator tactics. - Canadian Journal of Zoology 65: 1597-1606.

Bergerud, A.T., Butler, H.E. & Miller, D.R. 1984: Antipredator tactics of calving caribou: dispersion in mountains. - Canadian Journal of Zoology 62: 1566-1575.

Bodie, W.L. 1979: Factors affecting pronghorn fawn mortality in central Idaho. - M.Sc. thesis, University of Montana.

Boer, A.H. 1988: Moose Alces alces calf mortality in New Brunswick. - Canadian Field Naturalist 102: 74-75.

Bolte, J.R., Hair, J.A. & Fletcher, J. 1970: White-tailed deer mortality following tissue destruction induced by lone star ticks. - Journal of Wildlife Management 34: 546-552.

Bon, R. & Cugnasse, J.M. 1992: Expanding and self adjusting collar for mouflons. - Wildlife Society Bulletin 20: 396-398.

Borg, K. 1991: Rådjur, dödsorsaker, miljöpåverkan och rättsmedicin. - Swedish Nature Protection Agency Report 3921: 1-108. (In Swedish).

Boutin, S. 1992: Predation and moose population dynamics: a critique. - Journal of Wildlife Management 56: 116-127.

Bunnell, F.L. 1982: The lambing period of mountain sheep: synthesis, hypotheses, and tests. - Canadian Journal of Zoology 60: 1-14.

Byers, J.A. & Byers, K.Z. 1983: Do pronghorn mothers reveal the locations of their hidden fawns? - Behavioural Ecology and Sociobiology 13: 147-156.

Byers, J.A. & Moodie, J.D. 1990: Sex specific maternal investment in pronghorn and the question of a limit on differential provisioning in ungulates. - Behavioural Ecology and Sociobiology 26: 157-164.

Carbyn, L.N. & Trottier, T. 1987: Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. - Canadian Journal of Zoology 65: 2072-2078.

Carl, G.R. & Robbins, C.T. 1988: The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. - Canadian Journal of Zoology 66: 239-246.

Carroll, B.K. & Brown, D.L. 1977: Factors affecting neonatal fawn survival in southern-central Texas. - Journal of Wildlife Management 41: 63-69.

Caughley, G. 1966: Mortality patterns in mammals. - Ecology 47: 906-918.

Chadwick, D.H. 1983: A Beast the Colour of Winter. - Sierra Club Books. San Francisco, 208 pp.

Clarkson, P.L. & Liepins, I.S. 1993: Grizzly bear, Ursus arctos, predation on musk ox, Ovibos moschatus, calves near the Horton River, Northwest Territories. - Canadian Field-Naturalist 107: 100-102.

Clutton-Brock, T.H. 1988: Reproductive success. - University of Chicago Press, London, 538 pp.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red Deer. Behaviour and Ecology of Two Sexes. - Edinburgh University Press, Edinburgh, 378 pp.

Connolly, G.E. 1981: Limiting factors and population regulation. - In Wallmo, O.C. (ed.); Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, pp. 245-286.

Cook, R.S., White, M. & Trainer, D.O. 1967: Radiotelemetry for fawn mortality studies. - Bulletin Wildlife Disease Association 3: 160-165.

Cook, R.S., White, M., Trainer, D.O. & Glazener, W.C. 1971: Mortality of young white-tailed deer fawns in south Texas. - Journal of Wildlife Management 35: 47-56.

Corneli, P.S., von Gunten-Moran, B. & O'Gara, B. 1984: Pronghorn fawn mortality on the National Bison range. - Proceedings Biennial Pronghorn Antelope Workshop 11: 41-48.

DeForge, J.R., Jessup, D.A. & Jenner, C.W. 1982: Disease investigations into high lamb mortality of desert bighorn in the Santa Rosa Mountains, California. - Transactions Desert Bighorn Council 26: 76-81.

DeForge, J.R. & Scott, J.E. 1982: Ecological investigations into high lamb mortality. -Transactions Desert Bighorn Council 26: 65-76.

Dickinson, T.G., Wampler, G.E., Garner, G.W. & Simpson, C.D. 1980: Mortality of desert mule deer fawns in Pecos County, Texas. - Proceedings Annual Conference Western Associations Fish Wildlife Agencies 60: 581-592.

Downing, R.L. & McGinnes, B.S. 1969: Capturing and marking white-tailed deer fawns. - Journal of Wildlife Management 33: 711-714.

English, A.W. & Mulley, R.C. 1992: Causes of perinatal mortality in farmed fallow deer (Dama dama). - Australian Veterinary Journal 69: 191-193.

Epstein, M.B., Feldhamer, G.A. & Joyner, R.L. 1983: Predation on white-tailed deer fawns by bobcats, foxes and alligators: predator assessment. - Proceedings South Eastern Association Fish and Wildlife Agencies 37: 161-172.

Epstein, M.B., Feldhamer, G.A., Joyner, R.L., Hamilton, R.J. & Moore, W.G. 1985: Home range and mortality of white-tailed deer fawns in coastal South Carolina. - Proceedings South Eastern Association Game Fish Agencies 39: 373-379.

Fairbanks, W.S. 1993: Birthdate, birthweight, and survival in pronghorn fawns. - Journal of Mammalogy 74: 129-135.

Fancy, S.G. & Whitten, K.R. 1991: Selection of calving sites by Porcupine herd caribou. - Canadian Journal of Zoology 69: 1736-1743.

Festa-Bianchet, M. 1988: Birthdate and survival in bighorn lambs (Ovis canadensis). - Journal of Zoology, London 214: 653-661.

Festa-Bianchet, M., Urquhart, M. & Smith, K.G. 1994: Mountain goat recruitment: kid production and survival to breeding age. - Canadian Journal of Zoology 72: 22-27.

Firchow, K.M. 1980: Population ecology of pronghorns in southeastern Colorado. - Proceedings Biennial Pronghorn Antelope Workshop: 43-44.

Fowler, C.W. 1987: A review of density dependence in populations of large mammals. - Current Mammalogy 1: 401-441.

Fox, J.L. & Streveler, G.P. 1986: Wolf predation on mountain goats in southeastern Alaska. - Journal of Mammalogy 67: 192-195.

Franzmann, A.W. & Peterson, R.O. 1978: Moose calf mortality assessment. - Proceedings North American Moose Conference and Workshop 14: 247-269.

Franzmann, A.W. & Schwartz, C.C. 1986: Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai peninsula, Alaska. - Alces 22: 139-153.

Franzmann, A.W., Schwartz, C.C. & Peterson, R.O. 1980: Moose calf mortality in summer on the Kenai Peninsula, Alaska. - Journal of Wildlife Management 44: 764-768.

Fuller, T.K. & Keith, L.B. 1981: Woodland caribou population dynamics in northeastern Alberta. - Journal of Wildlife Management 45: 197-213.

Gaillard, J.M. 1992: Some demographic characteristics in ungulate populations and their implications for management and conservation. - In: Spitz, F., Janeau, G., Gonzalez, G. & Aulagnier, S. (eds.); Ongulés/Ungulates 91.S.F.E.P.M. - I.R.G.M, Toulouse, pp. 493-495.

Gaillard, J.M., Delorme, D., Boutin, J., Laere, G.V., Boisaubert, B. & Pradel, R. 1993: Roe deer survival patterns: a comparative analysis of contrasting populations. - Journal of Animal Ecology 62: 778-791.

Garner, G.W., Morrison, J.A. & Lewis, J.C. 1976: Mortality of white-tailed deer fawns in the Wichita Mountains, Oklahoma. - Proceedings Annual Conference South Eastern Association Fish and Wildlife Agencies 30: 493-506.

Garner, G.W., Whitten, K. & Mauer, F.J. 1985: Methodology for studying neonatal mortality of caribou in remote areas. - Proceedings 2nd North American Caribou Workshop, pp. 139-152.

Garrott, R.A., Bartmann, R. M. & White, G.C. 1985: Comparison of radio transmitter packages relative to deer fawn mortality. - Journal of Wildlife Management 49: 758-759.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O. & Larsen, D.G. 1992: The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. - Wildlife Monographs 120: 1-59.

Geist, V. 1981: On the reproductive strategies in ungulates and some problems of adaptation. - In: Scudder, G.G.E. & Reveal, J.L.

(eds.); Evolution Today. Proceedings of the Second International Congress of Systematic and Evolutionary Biology, pp. 111-132.
Gray, D.R. 1983: Interactions between wolves and musk oxen on Bathurst Island, N.W.T., Canada. - Acta Zoologica Fennica 174: 255-257.
Grubb, P. 1974: Population dynamics of the soay sheep. - In: Jewell, P. A., Milner, C. & Morton-Boyd, J. (eds.); Island survivors: The ecology of the soay sheep of St. Kilda. The Athlone Press, London, pp. 242-273.
Guinness, F.E., Clutton-Brock, T.H. & Albon, S.D. 1978: Factors affecting calf mortality in red deer (Cervus elaphus). - Journal of Animal Ecology 47: 817-832.
Hamlin, K.L. 1979: Co-operation by coyote pairs attacking mule deer fawns. - Journal of Mammalogy 60: 849-850.
Hamlin, K.L. & Mackie, R.J. 1989: Mule deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. - Final Report, Montana Department of Fish Wildlife and Parks, Project No. W-120-R-7-181-401, 401 pp.
Hamlin, K.L., Riley, S.J., Pyrah, D., Dood, A.R. & Mackie, R.J. 1984: Relationships among mule deer fawn mortality, coyotes and alternative prey species during summer. - Journal of Wildlife Management 48: 489-499.
Harper, W.L. 1984: Pregnancy rate and the timing of lamb losses in California bighorn sheep in the Ashnola, B. C. - Proceedings of the Biennial Northern Wild Sheep and Goat Council Symposium 4: 35-50.
Hass, C.C. 1989: Bighorn mortality: predation, inbreeding and population effects. - Canadian Journal of Zoology 67: 699-705.
Hass, C.C. 1990: Alternative maternal care patterns in two herds of bighorn sheep. - Journal of Mammalogy 71: 24-35.
Hauge, T.M. & Keith, L.B. 1981: Dynamics of moose populations in northeastern Alberta. - Journal of Wildlife Management 45: 573-597.
Hornocker, M.G. 1970: An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. - Wildlife Monographs 21: 1-39.
Huegel, C.N., Dahlgren, R.B. & Gladfelter, H.L. 1985a: Use of doe behavior to capture white-tailed deer fawns. - Wildlife Society Bulletin 13: 287-289.
Huegel, C.N., Dahlgren, R.B. & Gladfelter, H.L. 1985b: Mortality of white tailed deer fawns in south central Iowa. - Journal of Wildlife Management 49: 377-380.
Huggard, D.L. 1993: Prey selectivity of wolves in Banff National Park. II. Age, sex and condition of elk. - Canadian Journal of Zoology 71: 140-147.
Jackson, R.M., White, M. & Knowlton, F.F. 1972: Activity patterns of young white-tailed deer fawns in south Texas. - Ecology 53: 262-270.
Jedrzejewski, W., Jedrzejewska, B., Okarma, H. & Ruprecht, A.L. 1992: Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieza National Park, Poland. - Oecologia 90: 27-36.
Keister, G.P., Trainer, C.E. & Willis, M.J. 1988: A self adjusting collar for young ungulates. -Wildlife Society Bulletin 16: 321-323.
Kenward, R. 1987: Wildlife Radio Tracking. Academic Press, London, 222 pp.
Kolz, A.L. & Johnson, R.E. 1980: Self-adjusting collars for wild mammals equipped with transmitters. - Journal of Wildlife Management 44: 273-275.
Krausman, P.R., Leopold, B.D., Seegmiller, R.F. & Torres, S.G. 1989: Relationships between desert bighorn sheep and habitat in western Arizona. - Wildlife Monographs 102: 1-66.
Kunkel, K.E. & Mech, L.D. 1994: Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. - Canadian Journal of Zoology 71: 1557-1565.
Larsen, D.G. & Gauthier, D.A. 1989: Effects of capturing pregnant moose and calves on calf survivorship. - Journal of Wildlife Management 53: 564-567.
Larsen, D.G., Gauthier, D.A. & Markel, R.L. 1989: Causes and rate of moose mortality in the southwest Yukon. - Journal of Wildlife Management 53: 548-557.
Lent, P.C. 1974: Mother-young relationships in ungulates. - IUCN Publications new series 24: 14-55.
LeResche, R.E. 1968: Spring-fall calf mortality in an Alaska moose population. - Journal of Wildlife Management 32: 953-956.
Liberg, O., Johansson, A., Lockowandt, S. & Wahlström, L.K. 1993: Red fox predation as a dominant cause of neonatal mortality in roe deer fawns. - Swedish Hunters' Association Conference, Lund, Sweden, pp. 12-13.
Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994: Disease reveals the predator: Sarcoptic mange, red fox predation and prey populations. - Ecology 75: 1042-1049.
Litvaitis, J.A. & Bartush, W.S. 1980: Coyote-deer interactions during the fawning season in Oklahoma. - Southwest Naturalist 25: 117-118.
Livezey, K.B. 1990: Towards the reduction of marking reduced abandonment of newborn ungulates. - Wildlife Society Bulletin 18: 193-203.
Logan, T. 1973: Study of white-tailed deer fawn mortality on Cookson Hills deer refuge eastern Texas. - Proceedings South Eastern Association Game and Fish Commissioners 26: 27-38.
Loudon, A.S.I. 1985: Lactation and neonatal survival of mammals. - Symposium of the Zoological Society of London 54: 183-207.
Mahoney, S.P., Abbott, H., Russell, L.H. & Porter, B.R. 1990: Woodland caribou calf mortality in Insular Newfoundland. - Transactions of the International Union of Game Biologists Congress 19: 592-599.
Mathews, N.E. & Porter, W.F. 1988: Black bear predation of white tailed deer neonates in the central Adirondacks. - Canadian Journal of Zoology 66: 1241-1242.
McGinnes, B.S. & Downing, R.L. 1977: Factors affecting the peak of white-tailed deer fawning in Virginia. - Journal of Wildlife Management 41: 715-719.
Mech, L.D. 1988: The arctic wolf, living with the pack. - Voyageur Press, Stillwater, Minnesota, 128 pp.
Mech, L.D. & McRoberts, R.E. 1990: Survival of white tailed deer fawns in relation to maternal age. - Journal of Mammalogy 71: 465-467.
Messier, F. & Crête, M. 1985: Moose-wolf dynamics and the natural regulation of moose populations - Oecologia 65: 503-512.
Millar, J.S. & Zammuto, R.M. 1983: Life histories of mammals: an analysis of life tables. - Ecology 64: 631-635.
Miller, F.L. & Broughton, E. 1974: Calf mortality on the calving ground of Kaminuriak caribou. - Canadian Wildlife Service Report Series No. 26: 1-26.
Miller, F.L. & Gunn, A. 1986: Effect of adverse weather on neonatal caribou survival - a review. - Rangifer Special Issue 1: 211-217.
Miller, F.L., Gunn, A. & Broughton, E. 1985: Surplus killing as exemplified by wolf predation on newborn caribou. - Canadian Journal of Zoology 63: 295-300.

Miller, F.L., Broughton, E. & Gunn, A. 1988: Mortality of migratory barren ground caribou on the calving grounds of the Beverly herd, Northwest Territories, 1981-83. - Occasional Paper Number 65 Canadian Wildlife Service, pp. 1-24.
Nelson, M.E. & Mech, L.D. 1986: Mortality of white-tailed deer in north-eastern Minnesota. - Journal of Wildlife Management 50: 691-698.
Nelson, T.A. & Woolf, A. 1987: Mortality of white-tailed deer fawns in southern Illinois. - Journal of Wildlife Management 51: 326-329.
Nixon, C.M., Hansen, L.P., Brewer, P.A. & Chelsvig, J.E. 1991: Ecology of white-tailed deer in an intensively farmed region of Illinois. - Wildlife Monographs 118: 1-77.
O'Gara, B.W., McNay, M.E. & Bodie, W.A. 1986: Effects of fawn activity and bedding cover on susceptibility to predation. - Proceedings Biennial Pronghorn Antelope Workshop 12: 58-66.
O'Pezio, J.P. 1978: Mortality among white-tailed deer fawns on the Seneca Army Depot. - New York Fish and Game Journal 25: 1-15.
Ozoga, J.J. & Clute, R.K. 1988: Mortality rates of marked and unmarked fawns. - Journal of Wildlife Management 52: 549-551.
Ozoga, J.J. & Verme, L.J. 1982: Predation by black bears on newborn white-tailed deer. - Journal of Mammalogy 63: 695-696.
Ozoga, J.J. & Verme, L.J. 1986: Relation of maternal age to fawn-rearing success in white-tailed deer. - Journal of Wildlife Management 50: 480-486.
Ozoga, J.J., Bienz, C.S. & Verme, L.J. 1982: Red fox feeding habits in relation to fawn mortality. - Journal of Wildlife Management 46: 242-243.
Peterson, R.O. 1988: The pit or the pendulum: issues in large carnivore management in natural ecosystems. - In: Agee, J.K. & Johnson, D.R. (eds.); Ecosystem management for parks and wilderness. University of Washington Press, London.
Picton, H.D. 1979: A climatic index and mule deer survival in Montana. - International Journal of Biometeorology 23: 115-122.
Picton, H.D. 1984: Climate and the prediction of reproduction of three ungulate species. - Journal of Applied Ecology 21: 869-879.
Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.
Porath, W.R. 1980: Fawn mortality estimates in farmland deer range. - In: Hine, R. L. & Nehls, S. (eds.); White-tailed deer population management in the north central states. North Central Section of the Wildlife Society, pp 55-63.
Promislov, D.E.L. & Harvey, P.H. 1991: Mortality rates and the evolution of mammal life histories. - Acta Oecologia 12: 119-137.
Pruitt, W.O. 1961: On post-natal mortality in barren ground caribou. - Journal of Mammalogy 42: 550-551.
Ratcliffe, P.R. & Rowe, J.J. 1979: A golden eagle (Aquila chrysaetos) kills an infant roe deer (Capreolus capreolus). - Journal of Zoology, London 189: 532-535.
Reynolds, H.V. & Garner, G.W. 1987: Patterns of grizzly bear predation on caribou in northern Alaska. - International Conference on Bear Research and Management 7: 59-67.
Rideout, C.B. 1978: Mountain goat. - In: Schmidt, J.L. & Gilbert, D.L. (eds.); Big game of North America. - Stackpole Books, Harrisburg, pp. 149-160.
Robinson, R.M., Hidalgo, R.J., Daniel, W.S., Rideout, D.W. & Marburger, R.G. 1970: Salmonellosis in white-tailed deer fawns. - Journal of Wildlife Diseases 6: 389-396.
Roff, D.A. 1992: The evolution of life histories. - Chapman and Hall, London, 535 pp.
Roffe, T.J. 1993: Perinatal mortality in caribou from the porcupine herd, Alaska. - Journal of Wildlife Diseases 29: 295-303.
Rognmo, A., Mårkussen, K.A., Jacobsen, E., Grav, H.J. & Blix, A.S. 1983: Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth and mortality. - Rangifer 3: 10-18.
Rutberg, A.T. 1987: Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. - American Naturalist 130: 692-710.
Salwasser, H., Holl, S.A. & Ashcraft, G.A. 1978: Fawn production and survival in the North Kings River deer herd. - California Fish & Game 64: 38-52.
Schlegel, M. 1976: Factors affecting calf elk survival in north central Idaho. A progress report. - Proceedings Western Association State Game and Fish Commissioners 56: 342-355.
Schultz, J.H. & Ludwig, J.R. 1985: A possible cause of premature loss for deer fawn transmitters. - Journal of Mammalogy 66: 811-812.
Schultz, J.H., Ludwig, J.R. & Frydendall, M. 1983: Survival and home range of white-tailed deer fawns in southeastern Minnesota. - Minnesota Wildlife Research Quarterly 43: 15-23.
Schwartz, C.C. 1991: Interrelationship of black bears to moose and forest succession in the northern coniferous forest. - Wildlife Monographs 113: 1-58.
Schwartz, C.C. & Franzmann, A.W. 1989: Bears, wolves, moose and forest succession, some management considerations on the Kenai peninsula, Alaska. - Alces 25: 1-10.
Schwede, G., Heindrichs, H. & Wemmer, C. 1992: Activity and movement patterns of young white-tailed deer fawns. - In: Brown, R. D. (ed.); Biology of Deer. Springer-Verlag, London, pp 56-62.
Seip, D.R. 1992: Factors limiting woodland caribou populations and their inter-relationships with wolves and moose in southeastern British Columbia. - Canadian Journal of Zoology 70: 1494-1503.
Sinclair, A.R.E. 1985: Does interspecific competition or predation shape the African ungulate community? - Journal of Animal Ecology 54: 899-918.
Skogland, T. 1989: Comparative social organisation of wild reindeer in relation to food, mates and predator avoidance. - Advances in Ethology 29: 1-74.
Skogland, T. 1991: What are the effects of predators on large ungulate populations? - Oikos 61: 401-411.
Smith, C.A. 1986: Rates and causes of mortality in mountain goats in south east Alaska. - Journal of Wildlife Management 50: 743-746.
Smith, W.P. 1987: Maternal defence in Columbian white tailed deer: when is it worth it? - American Naturalist 130: 310-316.
Soppela, P., Nieminen, M., Saarela, S. & Hissa, R. 1986: The influence of ambient temperature on metabolism and body temperature of newborn and growing reindeer calves (Rangifer tarandus tarandus L.). - Comparative Biochemistry and Physiology 83A: 371-386.
Spinage, C.A. 1972: African ungulate life tables. - Ecology 53: 645-652.
Stearns, S.C. 1983: The influence of size and phylogeny on patterns of covariation among life history traits in mammals. - Oikos 41: 173-187.
Steigers, W.D. & Flinders, J.T. 1980a: A break away expandable collar for cervids. - Journal of Mammalogy 61: 150-152.
Steigers, W.D. & Flinders, J.T. 1980b: Mortality and movements of mule deer fawns in Washington. - Journal of Wildlife Management 44: 381-388.
Stephens, P.W. & Peterson, R.O. 1984: Wolf-avoidance strategies of moose. - Holarctic Ecology 7: 239-244.

Stewart, R.R., Kowal, E.H., Beaulieu, R. & Rock, T.W. 1985: The impact of black bear removal on moose calf survival in east central Saskatchewan. - Alces 21: 403-418.

Stout, G.G. 1982: Effects of coyote reduction on white-tailed deer productivity on Fort Sill, Oklahoma. - Wildlife Society Bulletin 10: 329-332.

Strandgaard, H. 1972: The roe deer (Capreolus capreolus) population at Kalø and the factors regulating its size. - Danish Review of Game Biology 7: 1-205.

Sæther, B., Solbraa, K., Sødal, D.P. & Hjeljord, O. 1992: Sluttrapport Elg-Skog-Samfunn. (In Norwegian with English summary: Final report Moose - Forest- Society). - NINA forskningsrapport 28: 1-153.

Taylor, R.J. 1984: Predation. - London: Chapman and Hall, 166 pp.

Trainer, C.E. 1975: Direct causes of mortality in mule deer fawns during summer and winter periods on Steens Mountain, Oregon - a progress report. - Proceedings Western Association Game and Fish Commissioners 55: 163-170.

Trainer, C.E., Lemos, J.C., Kistner, T.P., Lightfoot, W.C. & Toweill, D.E. 1981: Mortality of mule deer fawns in southeastern Oregon, 1968-1979. - Oregon Department of Fish and Wildlife, Wildlife Research Report 10: 1-113.

Trainer, C.E., Willis, M.J., Keister, G.P. & Sheehy, D.P. 1983: Fawn mortality and habitat use among pronghorn during spring and summer in southeastern Oregon. - Oregon Department of Fish and Wildlife, Wildlife Research Report 12: 1-117.

Truett, J.C. 1979: Observations of coyote predation on mule deer fawns in Arizona. - Journal of Wildlife Management 43: 956-958.

Tucker, R.D. & Garner, G.W. 1980: Mortality of pronghorn antelope fawns in Brewster County, Texas. - Proceedings Annual Conference Western Association Fish and Wildlife Agencies 60: 620-631.

von Gunten, B.L. 1978: Pronghorn fawn mortality on the National Bison Range. - Proceedings Biennial Pronghorn Antelope Workshop 8: 394-416.

Wallace, M.C. & Krausman, P. 1992: Neonatal elk habitat in Central Arizona. - In: Brown, R.D. (ed.); Biology of Deer. Springer-Verlag, London, pp. 69-75.

Welker, H.J. 1986: Fawn mortality in the Lake Hollow deer herd, Tehama County, California. - California Fish & Game 72: 99-102.

Wenger, C.R. & Springer, J.T. 1981: Reducing bias in predator-prey research involving telemetered young ungulates. - Third International Conference on Wildlife Biotelemetry 13-19.

White, M. 1973: Description of remains of deer fawns killed by coyotes. - Journal of Mammalogy 54: 291-293.

Whitten, K.R., Garner, G.W., Mauer, F.J. & Harris, R.B. 1992: Productivity and early calf survival in the porcupine caribou herd. - Journal of Wildlife Management 56: 201-212.

Wilton, M.L. 1983: Black bear predation on young cervids - a review. - Alces 19: 136-147.

Wilton, M.L., Carlson, D.M. & McCall, C.I. 1984: Occurrence of neonatal cervids in the spring diet of black bear in south central Ontario. - Alces 20: 95-105.

Woodard, T.N., Gutiérrez, R.J. & Rutherford, W.H. 1974: Bighorn lamb production, survival, and mortality in south central Colorado. - Journal of Wildlife Management 38: 771-774.

Zwank, P.J. 1977: Monitoring mule deer mortality. - Proceedings First International Conference on Wildlife Biotelemetry, Laramie, Wyoming, pp. 131-137.