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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

John D. C. Linnell, Ronny Aanes & Reidar Andersen

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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,

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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

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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; $\chi^2 = 13.4$, 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

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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 (*).

			Numbers of deaths due to								
Species	Study type[1]	No of marked neonates	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

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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
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.

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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

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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).

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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*

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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 juve-

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nile 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 ungu-

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lates 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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