Effects of ungulate availability on wolf reproductive potential in Alaska

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We compared wolf (*Canis lupus*) reproductive data for March and April, when ungulate biomass per wolf was high, moderate, and low. The percentage of reproductively active adult females was significantly lower (66% compared with ≥96%, $P < 0.001$) when ungulate biomass per wolf was low versus moderate or high. Reproductively inactive adult females had significantly less subcutaneous fat ($P < 0.01$) than reproductively active females when ungulate biomass per wolf was relatively abundant. Average litter size, estimated by counting blastocysts or fetuses, declined significantly ($P < 0.001$), from 6.9 to 4.6, as ungulate biomass per wolf declined. We conclude that wolf productivity declines as prey availability per wolf declines. However, only when ungulate biomass per wolf declined below levels previously reported in the literature did we observe significant declines in reproductive potential. Ungulate biomass per wolf was low because of large, rapid declines in ungulates and lesser declines in wolves. We recognize that functional relationships, e.g., prey vulnerability and feeding dominance, can influence wolf productivity independently of ungulate biomass per wolf.

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Nous avons comparé des données sur la reproduction du Loup gris (*Canis lupus*) en mars et en avril quand la biomasse d'ongulés par loup était élevée, moyenne ou faible. Le pourcentage de femelles adultes actives sexuellement était significativement plus faible (66% comparativement à ≥96%, $P < 0{,}001$) lorsque la biomasse d'ongulés par loup était faible plutôt que moyenne ou élevée. Les femelles adultes inactives sexuellement avaient significativement moins de graisses sous-cutanées ($P < 0{,}01$) que les femelles actives sexuellement lorsque la biomasse des ongulés par loup était relativement abondante. Le nombre moyen de petits par portée, estimé par comptage des blastocystes ou des fétus, diminuait significativement ($P < 0{,}001$), passant de 6,9 à 4,6 à mesure que diminuait la biomasse des ongulés par loup. La productivité des loups diminue donc lorsque le nombre de proies disponibles par loup diminue. Cependant, nous n'avons enregistré une chute significative du potentiel reproducteur que lorsque la biomasse des ongulés par loup a diminué jusqu'à atteindre des seuils plus bas que ceux jamais rapportés dans la littérature. La biomasse des ongulés par loup était faible à cause de diminutions importantes et rapides des ongulés et des diminutions moins importantes des loups. Nous reconnaissons toutefois que des relations fonctionnelles, e.g., la vulnérabilité des proies et la dominance alimentaire, peuvent influencer la productivité des loups indépendemmant de la biomasse des ongulés par tête de loup.

[Traduit par la rédaction]

Introduction

Although the dependence of wolf (*Canis lupus*) populations on ungulates is well documented (Pimlott 1967; Mech 1970; Fuller 1989; and others), the relationship between wolf productivity and ungulate biomass available per wolf has remained ill-defined. Keith (1983) found a significant linear relationship between the percentage of pups in fall or winter and ungulate biomass per wolf. However, Fuller (1989) reviewed eight studies and concluded that litter size at birth did not increase with ungulate biomass per wolf (weighted $r = 0.37$, 6 df, $P = 0.45$). In each of these eight studies, wolves were reasonably well nourished (ungulate biomass index per wolf = 161–659; methods followed Keith 1983).

Likewise, in the most extensive study of wolf productivity, Rausch (1967) compiled data from well-nourished wolves. These wolves were collected throughout Alaska from 1957 to 1964, during and immediately after effective federal wolf control (1948–1960; Harbo and Dean 1983). Ungulate biomass per wolf was extremely high during these collections (Bishop and Rausch 1974; Gasaway *et al.* 1983, 1992; Ballard *et al.* 1987), and wolves exhibited high reproductive potential. Rausch (1967) concluded that a high proportion of adult female wolves (≥22 months old) ovulated, conceived, and probably gave birth annually and that breeding occurred from late February through early April.

The objectives of this paper were to compare the reproductive potential of lightly harvested, food-limited female wolves with data from harvest-limited females collected during periods of greater prey availability. Wolf control programs and subsequent wolf harvests in interior Alaska provided unique opportunities to collect wolf reproductive tracts during periods of high, moderate, and low ungulate biomass per wolf. Shortly after Rausch's (1967) collections of wolf reproductive tracts, large declines in ungulate numbers occurred in interior Alaska, while wolf numbers remained relatively high (Gasaway *et al.* 1983, 1992). By the time the Alaska Department of Fish and Game (ADF&G) initiated wolf control programs in interior Alaska, ungulate biomass per wolf had declined to very low levels. Declines in wolf numbers were small relative to declines in ungulate numbers because of the long lag response of wolves (Peterson and Page 1983).

We examined wolf reproductive tracts collected during the first winter of these ADF&G wolf control programs to assess wolf reproductive potential when ungulate biomass per wolf was low. Continued harvest of wolves during and following control provided reproductive tracts from periods when ungulate biomass per wolf was moderate. Rausch's (1967) data were used to represent a period when ungulate biomass per wolf was high.

Study area

Study areas and ungulate densities were previously described by Rausch (1967) and Gasaway *et al.* (1983, 1992). The primary prey of wolves were moose (*Alces alces*) and caribou (*Rangifer tarandus*),

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TABLE 1. Decrease in wolf reproductive potential with lesser ungulate biomass per wolf, in central and east-central Alaska

Wolf population status	Study areas and winters	Ungulate biomass index per wolf	Females ≥ 22 months old in proestrus, in estrus, or pregnant		Avg. no. of blastocysts or fetuses per reproductively active female			Sources
			n	%	n	$\bar{x}$	95% CI	
Wolf harvest limited by federal control	Central and east-central Alaska, 1957–1964	High (500–850)	89	96[a]	15	6.9	±0.98	ADF&G files; Rausch 1967; Gasaway *et al.* 1983, 1992
Wolf harvest limited by ADF&G control	Central Alaska, 1977–1979, and east-central Alaska, 1984–1989	Moderate (180–390)	37	97	12	5.7	±1.28	ADF&G files; Gasaway *et al.* 1983, 1992
Wolves nutritionally limited during first year of ADF&G control[b]	Central Alaska, 1975–1976, and east-central Alaska, 1981–1982	Low (96–105)	29	66	7	4.6	±0.49	ADF&G files; Gasaway *et al.* 1983, 1992

NOTE: Wolves were collected in March and April and were ≥ 22 months old. Ungulate biomass index was calculated assuming values of 6, 2, and 1 for a moose, a caribou, or a sheep, respectively (Keith 1983; Fuller 1989).

[a] Statewide sample of 89 wolves taken during 13 March – 30 April, of which 85 were pregnant and 4 were reproductively inactive. Most of these carcasses came from central and east-central Alaska. The original data were reanalyzed because a typographical or other error of 89% (n = 89) was evident in Rausch (1967; p. 257).

[b] Wolf populations were lightly harvested ($\bar{x}$ = 16% annually) and nutritionally limited for at least 3 years prior to wolf control.

and, to a much lesser extent, Dall sheep (*Ovis dalli*). The wolf control area in central Alaska included the north slopes of the Alaska Range and adjacent lowlands and contained 15 300 km^2 of wolf habitat (Gasaway *et al.* 1983, p. 4). The wolf control area in east-central Alaska included the rolling, largely forested hills and mountains between the upper Tanana and Yukon rivers and contained 9700 km^2 of wolf habitat (Gasaway *et al.* 1992, p. 9).

Methods

We necropsied wolves from two wolf control areas in interior Alaska and reanalyzed wolf reproductive data from Rausch (1967). Wolves collected during the first winter of control programs, 1975–1976 in central Alaska and 1981–1982 in east-central Alaska, were shot by agency personnel. Most other wolf carcasses were provided by trappers or public aerial hunters. Only adult female wolves (i.e., ≥ 22 months old) killed in March or April were used in these comparisons. Criteria for estimating age were supported by examination of known-age wolves (Rausch 1967). Female pups (10–11 months old) were identified by the protruding uncalcified epiphysis at the distal end of the radius–ulna; yearlings (22–23 months old) and older wolves lacked this feature. Pup canines were not fully erupted in most cases and carnassials were sharp and white. Yearlings had fully erupted canines and distal surfaces of carnassials were slightly flattened and discolored. Uterine horns were 11–16 cm long and 2–3 mm wide in female pups, 13–20 cm long and 5–9 mm wide in nonreproductive yearlings and adults, and 21–33 cm long and 10–14 mm wide in reproductively active wolves.

Uteri and ovaries were macroscopically examined to determine reproductive potential. Enlargement and thickening of the uteri from increased vascularization indicated that females were reproductively active (i.e., in proestrus, in estrus, or pregnant; Rausch 1967). Ovaries were hardened in 10% formalin for at least 2 weeks, then hand-sectioned at 1-mm intervals to note presence or absence of enlarged follicles or corpora lutea (Rausch 1967). Proportions of reproductively active females in the various samples were compared using χ^2 tests of independence.

Uteri were sectioned longitudinally to count implanted blastocysts or fetuses. These counts served as indices of potential litter size and were compared at low, moderate, and high ungulate biomass per wolf using two-tailed Student's t-tests.

Fat indices of reproductively active and inactive adult female wolves were compared using Student's t-tests. Indices included depth of subcutaneous fat (mm), kidney fat (gm), and percent femur marrow fat (Neiland 1970). Depth of subcutaneous fat was totaled from maximum depth on the sternum, flank, and posterior vertebrae. The kidney fat index was calculated as the weight of fat immediately surrounding the kidney divided by the fat-free kidney weight multiplied by 100 (Riney 1955). The kidney and attached fat were removed by cutting through the fat at right angles to the spine; these cuts were made at the ends of the kidney.

Results

There appears to exist a level of prey availability below which adult female wolves suppress or delay gonadal cycles. Only 66% of adult female wolves (≥ 22 months old, n = 29) were reproductively active in March and April, when ungulate biomass per wolf was low (Table 1). Significantly more females ($\geq 96\%$, $P < 0.001$) were reproductively active when ungulate biomass per wolf was moderate or high. This relationship held for the subsample of wolves ≥ 34 months old; 67% (14 of 21 female wolves) were reproductively active when ungulate biomass per wolf was low, compared with 100% (n = 29) when ungulate biomass per wolf was moderate.

Fat indices were compared between reproductive and nonreproductive wolves to assess if fat indices could be related to reproductive potential. Reproductively inactive adult female wolves had less fat than reproductively active wolves (Table 2); however, only subcutaneous fat depths were significantly lower ($P < 0.01$). Kidney and marrow fat levels were not significantly related to reproductive status ($P > 0.2$), possibly because these fat deposits are mobilized largely after subcutaneous reserves, and therefore are less sensitive to small changes in nutritional status (Harris 1945).

In utero wolf litter size declined as ungulate biomass per wolf declined. Average *in utero* litter size declined from 6.9 to 4.6 (Table 1), and differences were highly significant ($P <$ 0.001) between periods of high and low ungulate biomass per

TABLE 2. Fat indices in reproductively active and inactive adult female wolves shot in March and April, in central and east-central Alaska

Reproductive status of wolf	Ungulate biomass index per wolf	Depth of subcutaneous fat (mm)			Kidney fat index			Femur marrow fat (%)		
		n	$\bar{x}$	95% CI	n	$\bar{x}$	95% CI	n	$\bar{x}$	95% CI
Active	Moderate	26	35[a,b]	±6.6	15	106	±19.9	9	85	±11.0
Active	Low	18	26[b]	±6.8	19	104	±19.2	14	83	±7.7
Inactive	Low	9	21[a]	±10.0	9	96	±24.4	7	81	±12.8

[a] Values were significantly different ($P < 0.01$).
[b] Values were significantly different ($P = 0.06$).

wolf. The differences in litter size during periods of low and moderate prey availability were less significant ($P < 0.1$), as were the differences between moderate and high prey availability ($P < 0.2$).

Discussion

A direct relationship appears to exist between wolf productivity and nutritional status. Indices of nutritional status included fat depth and prey availability. Wolf productivity was reduced through the suppression of estrus and reduced litter size, but suppression of estrus occurred only when prey were extremely scarce relative to wolves. Captive wolves regularly enter estrus (Packard *et al.* 1983), presumably because they are well nourished.

Our data imply that the potential rate of increase in a wolf population is reduced during lean years. However, lean years are apparently rare in most North American study sites. We report the lowest indices for ungulate biomass per wolf (96–105) in the literature, as reviewed by Fuller (1989). Other North American wolf populations had, relatively, moderate to high indices of available prey (112–659, $\bar{x} = 249$, $n = 25$). At these indices, wolf mortality, not productivity, has been reported as the most significant variable limiting growth rates of wolf populations (Rausch 1967; Keith 1983; Fuller 1989).

Our two examples of low ungulate biomass indices per wolf (96–105, Table 1) occurred following rapid declines in prey from high densities and lesser relative declines in wolf numbers. However, declines from high prey densities may not be necessary for low prey availability per wolf to occur. Gasaway *et al.* (1992, pp. 36–37) reviewed data from several Alaskan and Yukon study areas where prey availability per wolf occurred at chronically low levels; however, no ungulate biomass indices per wolf were calculated.

Although wolf productivity appears dependent in part on ungulate availability, we recognize that functional relationships can also influence reproduction. Two examples follow. First, if prey vulnerability increases from stochastic events, wolf productivity could increase regardless of changes in ungulate numbers. Second, feeding dominance by dominant females could help ensure productivity in most packs during lean years. In this example, the suppression of estrus we observed would occur largely in subordinate females less likely to reproduce successfully, even when prey are abundant. Thus, packs may continue to produce litters during lean years; only average litter size would be reduced.

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