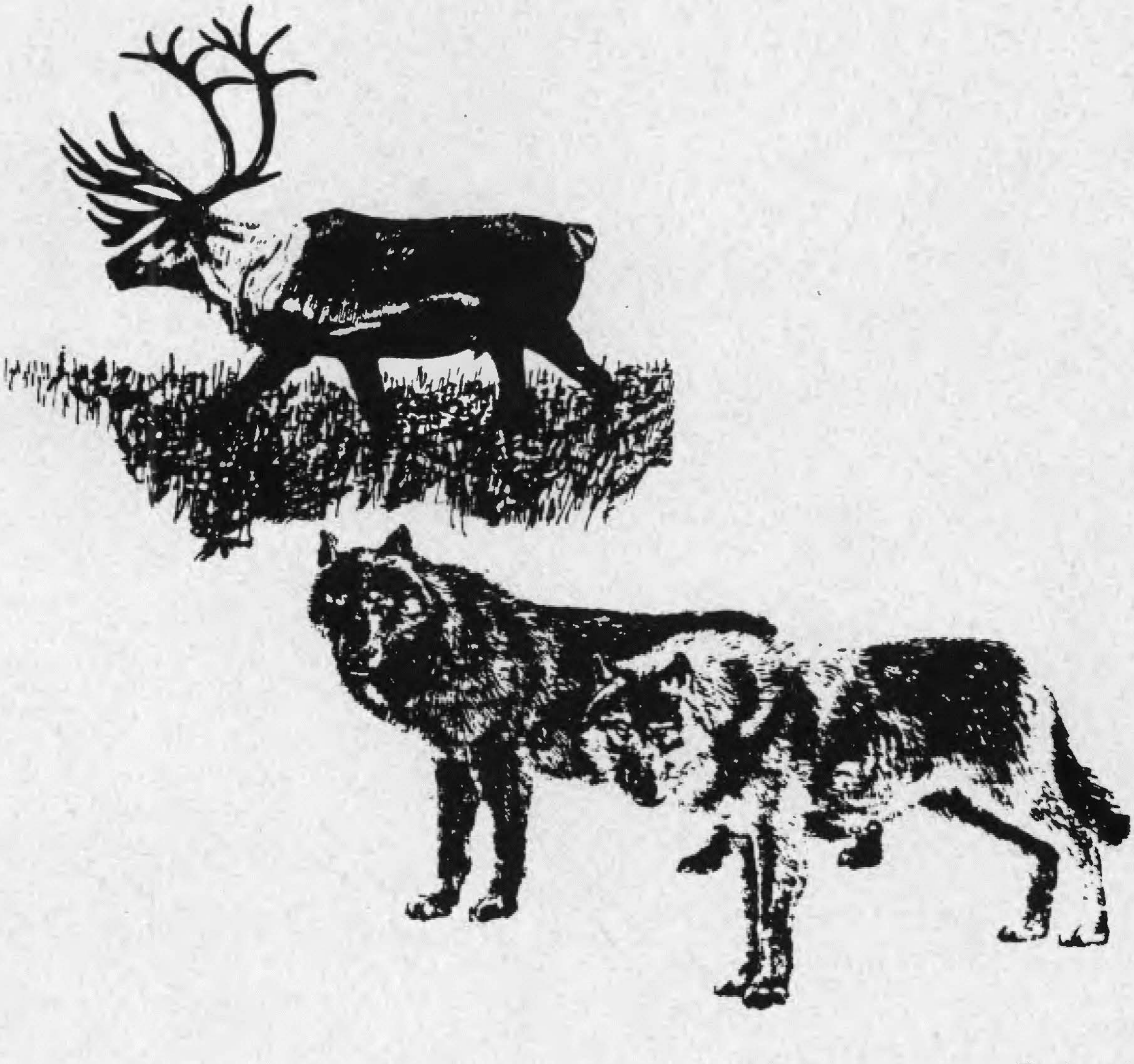
Alaska Department of Fish and Game
Division of Wildlife Conservation

Federal Aid in Wildlife Restoration
Research Progress Report

A Decade Later: Interrelationships of Predators, Ungulates, and Humans Following Wolf Reductions in an Interior Alaska Study Site

by

Rodney D. Boertje



Project W-23-5
Study 1.43
November 1992

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SUMMARY

This study involves compiling and publishing data previously collected on the interrelationships of wolves (*Canis lupus*) and their ungulate prey in Interior Alaska. Two publications are planned. One draft is presented in Appendix A, entitled "Effects of ungulate availability on wolf reproductive potential in Alaska," and was submitted to the Canadian Journal of Zoology on 14 April 1992. The second paper is in preparation and is entitled "Prolonged increases in moose and caribou densities following agency wolf reductions in an Interior Alaska study site."

The paper in Appendix A is the first to report wolf reproductive potential at high, moderate, and low prey availability. Data are from wolf carcasses collected during 3 decades by the Alaska Department of Fish and Game and supersede data analyzed by Gasaway et al. (1983). Previous studies have not identified the significant reduction in wolf reproductive potential that follows reductions in prey availability. The primary reason is that previous authors studied wolves only when moderate to high prey availability prevailed (e.g., Rausch 1967, Fuller 1989). This paper reports reproductive data from wolves collected during the first year of agency wolf reductions, when prey availability was lower than previously reported in the literature.

Key Words: Alaska, litter size, predator-prey relationships, prey availability, reproduction, ungulate biomass, wolf, wolf reproduction.

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BACKGROUND

Although the dependency of wolf (*Canis lupus*) populations on ungulates is well documented (Pimlott 1967, Mech 1970, Fuller 1989), the relationship between wolf productivity and ungulate biomass per wolf has remained ill-defined. We proposed to study the variability in Alaska wolf productivity at high, moderate, and low ungulate biomass per wolf. Ramifications may be significant for managers planning wolf reductions to enhance ungulate numbers. For example, if wolf productivity increases with prey availability, managers attempting to stabilize wolf populations may need to increase the rate of wolf reductions as ungulates increase.

In a second paper in preparation, we document the long-term effects of short-term agency wolf reductions on wolves, caribou (*Rangifer tarandus*), and moose (*Alces alces*) in Game Management Subunit 20A. This paper will (1) help managers evaluate the cost-effectiveness of intensive wolf reductions and (2) describe how and under what predator-prey relationships and environmental conditions a wolf reduction program was successful in enhancing ungulate numbers. Detailed documentation of the long-term effects of wolf reductions are lacking in the literature.

OBJECTIVES

Objectives of this study were to:

1. Review literature (1) on the effects of short-term wolf reductions on long-term ungulate population dynamics and (2) on population data and harvests of wolves, bears (*Ursus americanus* and *U. arctos*), moose, and caribou in Subunit 20A and adjacent, unmanipulated areas from 1979 to 1990.

2. Analyze data and draft figures for written and oral presentations.

3. Publish a report synthesizing the relationships of predators and prey following Alaska Department of Fish and Game wolf reductions in Subunit 20A and comparing the Subunit 20A data with adjacent, unmanipulated areas. Incorporate results into appropriate Alaska wildlife management plans and survey-inventory activities and present data to interested groups.

METHODS

Data previously collected by the Alaska Department of Fish and Game are used to satisfy study objectives. Methods for evaluating the effects of ungulate availability on wolf reproductive potential are described in Appendix A.

RESULTS AND DISCUSSION

I completed the literature review and identified the need for a separate paper on the effects of ungulate availability on wolf productivity (Appendix A). This need was identified in the research proposal for this project, but was not originally considered as a topic for a separate paper.

Work on the second paper is awaiting compilation of fall 1991 moose data and winter 1991-92 wolf data from Subunit 20A. Data from 1975 through 1990 have been compiled. A draft of this paper will be presented in next year's final report.

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APPENDIX A. Paper submitted to Canadian Journal of Zoology, April 1992 (with minor format changes).

Effects of ungulate availability on wolf reproductive potential in Alaska

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Abstract

We compared March and April wolf (*Canis lupus*) reproductive data when ungulate biomass per wolf was high, moderate, and low. The percentage of reproductively active adult females was significantly lower (66% compared with $\geq$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 more abundant. Average litter size, estimated by counting blastocysts or actual fetuses, declined significantly ($P < 0.001$) from 6.9 to 4.6 as ungulate biomass per wolf declined.

We conclude that wolf productivity will decline 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 independent of ungulate biomass per wolf.

Introduction

Although the dependency 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 per wolf has remained ill-defined. Keith (1983) found a significant linear relationship between percent 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).

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 (1948-60; 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). Rausch (1967) documented a high reproductive potential among these wolves. He concluded that a high proportion of adult female wolves ($\geq$22 months old) ovulated, conceived, and probably gave birth annually and that breeding occurred from late February through early April.

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 ungulate biomass per wolf. Wolf control programs and subsequent wolf harvests in Interior Alaska provided unique opportunities to collect wolf reproductive tracts from 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 and wolf predation continued these declines to low levels (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 also reported, but declines were nominal 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 initial year 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 provided comparisons when ungulate biomass per wolf was high.

Site description

Study areas were previously described by Rausch (1967) and Gasaway et al. (1983, 1992). Primary prey of wolves were moose (*Alces alces*) and caribou (*Rangifer tarandus*), and, to a much lesser extent, Dall's sheep (*Ovis dalli*). The wolf control area in central Alaska included northern slopes of the Alaska Range and adjacent lowlands and contained 15,300 km^2 of wolf habitat (Gasaway et al. 1983). 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 15,500 km^2 of wolf habitat (Gasaway et al. 1992).

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, 1975-76 in central Alaska and 1981-82 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., $\geq$22 months old) killed in March or April were used in these comparisons. Age was estimated by tooth development and wear; size of the reproductive tract helped distinguish long yearlings (22 and 23 months old) from older wolves (Rausch 1967). Female pups (10-11 months old) were identified by the uncalcified epiphysis at the distal end of the radius-ulna (Rausch 1967).

Uteri and ovaries were examined to determine reproductive potential. Enlargement and thickening of the uteri from increased vascularization indicated that females were reproductively active (i.e., in proestrus, estrus, or were pregnant; Rausch 1967). Also, 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 chi-square 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 high, moderate, and low 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. 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 (≥96%, $P < 0.001$) were reproductively active when ungulate biomass per wolf was moderate or high. This relationship held for 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 also 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 wolf. The difference in litter size during periods of low and moderate prey abundance were less significant ($P < 0.1$), as were the differences between moderate and high prey abundance ($P < 0.2$).

Discussion

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

Our data imply that rates of increase among wolf populations are reduced during lean years. However, lean years apparently occur rarely. We report the lowest values 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 values (112-659, $\bar{x} = 249$, n = 25). At these values, wolf mortality, not productivity, has been identified as the most significant variable limiting growth rates of wolf populations (Rausch 1967; Keith 1983; Fuller 1989).

Only when prey availability declines rapidly relative to wolf numbers do we predict that productivity becomes a significant variable limiting wolf population growth. The two examples of low reproductive potential described herein occurred following lengthy federal predator control programs, which set the stage for unusually high ungulate and wolf densities (Gasaway et al. 1983, 1992). It was during the subsequent declines in ungulates from high densities that wolf reproductive potential declined most notably. Gasaway et al. (1992) conclude that moose will not attain such high densities again in wolf-bear-moose systems unless predators are reduced. Caribou, however, have increased to high densities without human intervention (Skoog 1968).

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 successfully reproduce, even when prey are abundant. Thus, packs may continue to produce litters during lean years; only litter size would be reduced.

Acknowledgments

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Table 1. Wolf reproductive potential declines with lesser ungulate biomass per wolf, central and east central Alaska. 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, caribou, or sheep, respectively (Keith 1983, Fuller 1989).

Wolf population status	Study areas and winters	Ungulate biomass index per wolf	Percent of females ≥22 months old in proestrus, estrus, or pregnant		Average number of blastocysts or fetuses per reproductively active female			References
			n	%	n	$\bar{X}$	95% CI	
During and subsequent to federal wolf control; wolves harvest-limited	Central and east central Alaska 1957-64	High (500-850)	89	96[a]	15	6.9	±0.98	ADF&G files; Rausch 1967; Gasaway *et al.* 1983, 1992
During and subsequent to ADF&G wolf control; wolves harvest-limited	Central Alaska 1977-79, and east central Alaska 1984-89	Moderate (180-390)	37	97	12	5.7	±1.28	ADF&G files; Gasaway *et al.* 1983, 1992
Initial year of ADF&G wolf control; wolf population lightly harvested ($\bar{X}$ = 16% annually) and nutrition-limited for at least 3 years prior to wolf control	Central Alaska 1975-76, and east central Alaska 1981-82	Low (96-105)	29	66	7	4.6	±0.49	ADF&G files; Gasaway *et al.* 1983, 1992

[a] Statewide sample; original data were re-analyzed because a typographical or other error of 89% (n = 89) was evident in Rausch (1967).

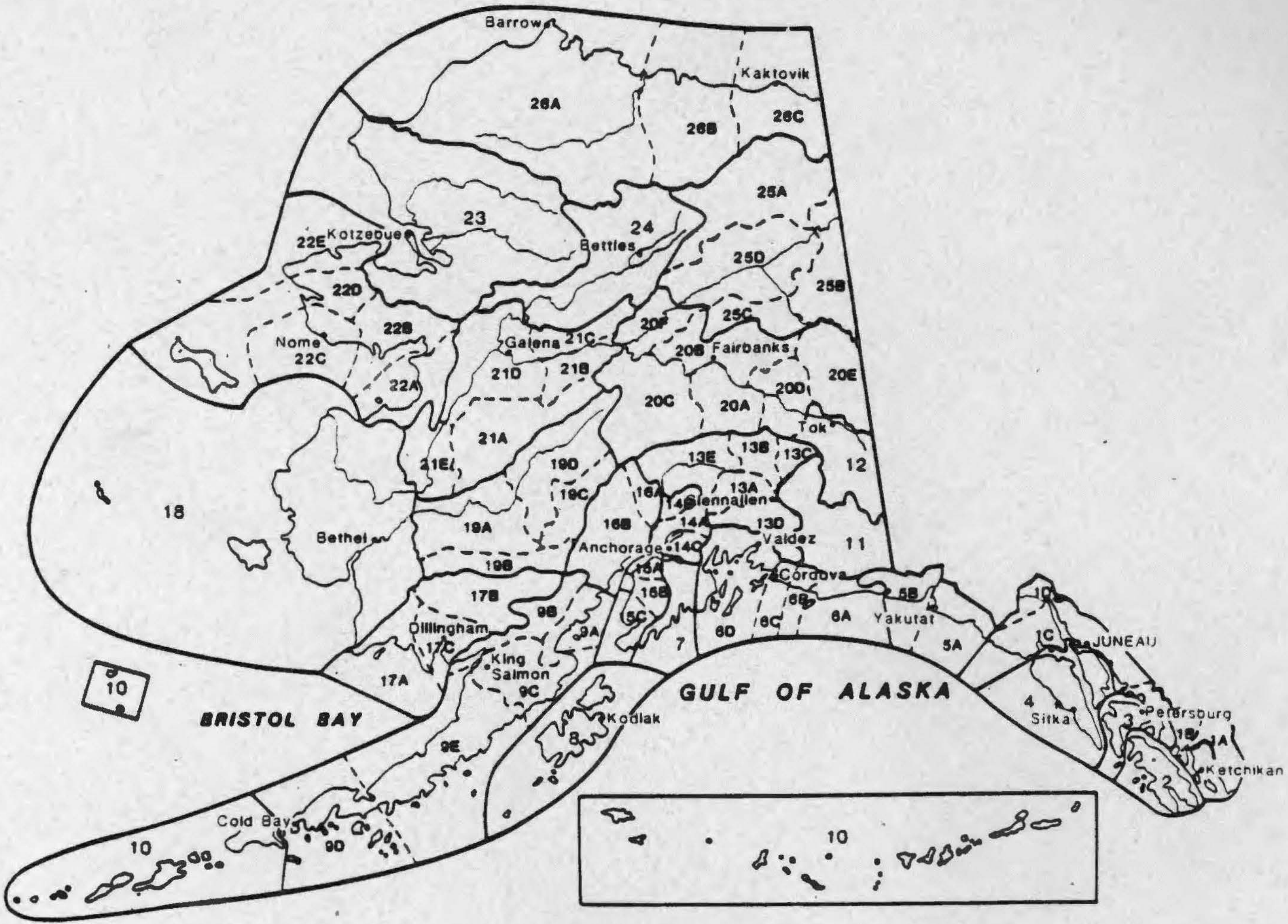
Table 2. Fat indices in reproductively active and inactive adult female wolves shot in March and April, central and east central Alaska.

	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
Reproductively active wolves, ungulate biomass moderate	26	35[a,b]	±6.6	15	106	±19.9	9	85	±11.0
Reproductively active wolves, ungulate biomass low	18	26[b]	±6.8	19	104	±19.2	14	83	±7.7
Reproductively inactive wolves, ungulate biomass 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 ($P = 0.06$).

Alaska's Game Management Units



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