Alaska Department of Fish and Game
Division of Wildlife Conservation

Federal Aid in Wildlife Restoration
Research Progress Report

Development and Testing of A General Predator-Prey Computer Model for Use in Making Management Decisions

by

Mark E. McNay

Project W-24-1
Study 1.46
October 1993

STATE OF ALASKA
Walter J. Hickel, Governor

DEPARTMENT OF FISH AND GAME
Carl L. Rosier, Commissioner

DIVISION OF WILDLIFE CONSERVATION
David G. Kelleyhouse, Director
Wayne L. Regelin, Deputy Director

Additional copies of this report and other Division of Wildlife Conservation publications may be obtained from:

Publications Specialist
ADF&G, Wildlife Conservation
P.O. Box 22526
Juneau, AK 99802
(907) 465-4190

PROGRESS REPORT (RESEARCH)

State: Alaska

Cooperator: Layne G. Adams, U.S. National Park Service

Project No.: W-24-1 Project Title: Wildlife Research and Management

Study No.: 1.46 Study Title: Development and Testing of a General Predator-Prey Computer Model for Use in Making Management Decisions

Period Covered: 1 July 1992-30 June 1993

SUMMARY

A prototype of a general predator-prey model was completed using Lotus 1-2-3 software. The model requires 38 user inputs estimated from routine survey and inventory activities or extrapolated from intensive predator-prey studies. The model generates 65 outputs related to population characteristics of predator and prey populations. Primary among those outputs are estimates of ungulate population size and allowable harvests over an 8-year period. The model allows the user to select any number of alternate predator and prey management scenarios. Work began on a user's manual to assist in the use and interpretation of model inputs and outputs.

Historical data from the western Subunit 20B wolf management program were compiled and reanalyzed. Within the 8,340-km^2 Minto Study Area, 72 wolves (*Canis lupus*) were removed by government trapping and aerial gunning and public wolf harvest during the November 1984-April 1986 period. The wolf population declined from an estimated 67 wolves in November 1984 to 14 wolves in April 1986. Following 5 years of no government wolf control the population increased to an estimated 61 wolves in April 1991, representing an annual finite growth rate of 34% despite average wolf harvest by hunters and trappers of 7.2 wolves annually during the 1986-91 period.

Key Words: alternate prey, black bear, caribou, grizzly bear, moose, Predator-Prey model, ungulates, weather severity, wolf, wolf control.

CONTENTS

BACKGROUND

In 1991, a comprehensive wolf management planning process stimulated increased public involvement in management of Alaska's big game species. Public requests to intensively manage for sustained high harvests of moose (*Alces alces*), caribou (*Rangifer tarandus*), and sheep (*Ovis dalli*) from manipulated predator-prey systems were countered by public requests for lower, "natural" yields of big game from unmanipulated predator-prey systems. Those conflicting public values placed additional responsibilities on managers to more clearly predict consequences of proposed management programs.

In response to past controversy over predator-prey management, biologists in Alaska, other northern states, and the Yukon have conducted significant research into the general behavior of large ungulate-large carnivore ecological systems. Those advances in predator-large prey ecological research, and the wide availability and use of personal computers, have created an opportunity to develop additional tools for management decisions.

Starfield and Bleloch (1991) defined models and their use as, "... any representation or abstraction of a system or process. We build models to (1) define our problems, (2) organize our thoughts, (3) understand our data, (4) communicate and test that understanding, and (5) make predictions."

In concept, building a predictive model for an Alaskan game population is simple. Changes in population size follow imbalances between factors that cause the population to increase (birth, immigration) and factors that cause the population to decrease (death, emigration). In practice, however, measurement of those factors may be difficult or impossible. Therefore models are always simplifications of reality and never exactly describe the real world. "The quality of a model does not depend on how realistic it is, but on how well it performs in relation to the purpose for which it is built" (Starfield and Bleloch 1991).

For managers, models can be categorized as either conceptual system models or management working models. Conceptual system models such as low-density dynamic equilibrium (Gasaway *et al.* 1992) and multi-density equilibria models (Haber 1977) describe the long-term dynamics of systems, but tell the manager little about the allowable harvest in the coming year, or about expected levels of predation under current predator-prey conditions. Conversely, management working models such as those for estimating allowable yields of prey populations (Fuller 1989), or for estimating finite wolf (*Canis lupus*) population growth rates from an ungulate biomass index (Keith 1983), can be used by managers to explore short-term consequences of management actions or short-term biological responses in unmanipulated systems.

There are abundant examples of models that have been used to describe predator-prey-human interactions in northern ecosystems (Keith 1983; Van Ballenberghe and Dart 1983; Ballard *et al.* 1986, 1987; Bergerud and Elliot 1986; Fuller 1989; Hayes *et al.* 1991; Schwartz and Franzmann 1991; Gasaway *et al.* 1992). Each is based on empirical evidence of basic relationships between components of the predator-prey system. As more studies are completed, many of those basic relationships appear to be consistent and, therefore, somewhat predictable. Models built to describe those relationships often relate to only a portion of the system, e.g., maximum sustained yield of moose (Van Ballenberghe and Dart 1983) or number of moose calves consumed by black bears (*Ursus americanus*) (Schwartz and Franzmann 1991). Few are available to Alaskan managers in the form of easily used computer models.

Model construction requires estimates of production and survival of young, estimates of mortality rates, differences between immigration and emigration, harvest levels, and estimates of population size. Production and survival of young among caribou, moose, and sheep are estimated annually through routine survey and inventory programs and are reported in annual management reports (e.g., Morgan 1990). Estimates are expressed as young:100 females or as percent young in the population. When combined with total population estimates, absolute numbers of juvenile animals recruited each year into ungulate populations can be estimated. Total population estimates from stratified random sampling for moose (Gasaway *et al.* 1986), aerial photography for caribou (Davis *et al.* 1979), or total counts in key areas for sheep (Heimer and Watson 1986) are periodically made by area biologists.

Causes of mortality are generally considered in three categories, harvest by hunters, predator-caused mortality, and other natural mortality. Harvest is determined annually from mandatory hunter reports and in some cases substantiated with check stations (McNay 1992). Other natural mortality is often related to severe weather (Coady 1974, Gasaway *et* *al.* 1983) and qualitative estimates can be based on winter severity indices. Site-specific intensive monitoring of moose and caribou populations have provided quantitative estimates of weather-related natural mortality (Ballard *et al.* 1991, Davis *et al.* 1991) that may be generally applicable to other areas with similar weather and habitat conditions.

Black and grizzly bears (*Ursus arctos*) are significant predators of moose, and grizzly bears commonly prey upon caribou. Estimates of predation levels by bears upon moose and caribou require intensive radiotelemetry studies that are rarely part of routine survey and inventory programs. However, several intensive studies completed in Alaska and the Yukon provide a sufficient range of bear predation values to model potential impacts of bear predation on moose and caribou populations (Franzmann and Schwartz 1986; Ballard *et al.* 1987; Boertje *et al.* 1988; Adams *et al.* 1989; Bangs *et al.* 1989; Larsen *et al.* 1989; Osborne *et al.* 1991).

Black bears on two study sites in Southcentral Alaska killed an estimated 34% and 35% of neonatal moose calves (Schwartz and Franzmann 1991). Similarly, black bears killed an estimated 40% of moose calves in an Interior Alaska study (Osborne *et al.* 1991). Predation by grizzly bears on adult moose was documented in both Alaskan (Boertje *et al.* 1988, Ballard *et al.* 1990) and Yukon (Larsen *et al.* 1989) studies. Boertje *et al.* (1988) reported adult male grizzly bears killed adult moose and caribou at a rate of approximately one kill per 26 bear days in spring and Ballard *et al.* (1990) reported adult grizzly bears killed adult moose at a rate of one kill per 43.7 bear days in spring. Larsen *et al.* (1989) reported grizzly bears killed 2-3% of collared adult female moose in each of 3 years 1983-85. Kill rates by grizzly bears on moose calves were reported as 5.1, 5.4, and 5.3 calves per adult grizzly, respectively, in Yukon (Larsen *et al.* 1989), east-central Alaska (Boertje *et al.* 1988), and Southcentral Alaska (Ballard *et al.* 1990). In Denali Park, grizzly bear predation on neonatal caribou calves varied from 17% to 22% of calves produced between 1985 and 1987 (Adams *et al.* 1989).

As obligate carnivores, wolves prey upon ungulates at more consistent rates than do bears. Using data from Alaskan (Peterson *et al.* 1984), Canadian (Fuller and Keith 1980), and their own studies, Ballard *et al.* (1987) described a relationship between pack size and kill rates which recognized that a reduction in average pack size results in a proportionately smaller reduction in wolf predation rates (Hayes *et al.* 1991). Fuller (1989) used results from 25 North American studies to propose a general relationship describing a theoretical carrying capacity for wolves, and Keith (1983) described a general relationship from seven North American studies between the ungulate biomass index and the finite growth rate of wolf populations.

These relationships can be combined to model wolf predation rates, wolf population response to changing ungulate densities, and, conversely, ungulate population responses to changing wolf densities. Predation rates by bears on ungulates, while not as predictable as those by wolves, can be estimated from predation rates observed in studies of systems similar to those being modeled. In addition, responses of ungulate populations to extreme weather can be modeled using data describing thresholds of critical weather such as described for moose by Coady (1974). Historical weather records could be used to produce probability estimates for the occurrence of severe weather events.

GOAL

To develop a computer model to assist Alaskan wildlife managers in making annual management decisions regarding big game predator-prey systems, and to verify model effectiveness and sensitivity by modeling predator-prey systems that have been intensively studied and/or manipulated.

OBJECTIVES

1. Review literature of predator-prey studies to identify basic relationships of Alaskan predator-prey systems.

2. Construct a general predator-prey model using Lotus 1-2-3 software.

3. Write a manual describing model function and basis for model assumptions, including guidelines for model use.

4. Compile and analyze predator-prey data for western Subunit 20B for the period 1984-89. Prepare a report describing predator-prey dynamics in western Subunit 20B.

5. Validate and refine model functions to simulate known dynamics of intensively studied predator-prey systems.

6. Train area biologists in use of the model and application to current management problems.

7. Write Final Report and prepare presentations for public and scientific meetings.

METHODS

Development of Predator-Prey Management Model (Jobs 1-3 and 5)

A prototype predator-prey management model was developed using Lotus 1-2-3 software. The model was organized using submodels to simulate the effects of (1) variable calf production and mortality, (2) alternate prey on wolf population dynamics and predation rates, (3) various wolf management actions on wolf population dynamics, (4) bear predation on adult ungulates, and (5) weather severity on ungulate natural mortality rates. The submodels provide inputs into an ungulate population and harvest model that calculates changes in the primary prey population size and calculates allowable harvest by hunters to meet specified management objectives for up to an 8-year period. The model begins with user inputs of post-hunt population characteristics that are readily available from fall surveys of moose. For species such as sheep and caribou where survey information is routinely collected during summer, the model will accept summer data and project a post-hunt beginning population.

Predation rates by wolves on subadult and adult ungulates are based on the function Y = 13.84-3.22(lnX), where Y = adjusted days per kill (adjusted to moose equivalents of prey) and X = mean pack size (Ballard *et al.* 1987). Season (winter vs. summer), wolf population size, and alternate prey also affect wolf predation rates through equations that modify the basic predation function. Wolf numerical response to changes in total ungulate biomass are simulated using the function Y = 1.125 + 0.042(X), where Y = the predicted annual finite growth rate of the wolf population and X = ungulate biomass per wolf (Keith 1983). Wolf harvest options selected by the user allow simulated management of wolf populations at levels below those predicted by the basic wolf response function.

Predation on adult and subadult moose and caribou by grizzly bears during the May through September period is fixed in the current model. Future versions of the model may incorporate variable predation rates by bears pending additional review of the literature regarding bear predation on ungulates. Predation by wolves and black and grizzly bears on neonates is dependent upon user inputs in the current version of the model. Similarly, changes in black and grizzly bear populations are dependent upon user inputs, but use of black and grizzly bear population dynamic submodels will be investigated during the next reporting period.

To simulate the effects of varying weather conditions on the primary prey species, the user may (1) specify each of the eight winters as mild, moderate, or severe; or (2) select a stochastic probability function that assigns winter severity to each winter based on the frequency of mild, moderate, or severe winters experienced in Interior Alaska between 1965 and 1992. Severe weather increases the annual non-predation mortality rate for adults and for young of the year. Mild and moderate weather years have no effect on adults or subadults, but mild weather decreases the non-predation mortality of young of the year. Future versions of the model will incorporate a restricted random variable as the winter severity factor.

The model works with one primary prey species for population and harvest projections, but will accept up to seven alternate prey species for calculation of the ungulate biomass index. Wolf predation rates are calculated using a biomass index rather than absolute numbers of animals, and the model converts population size to a biomass index when the primary prey species name is entered by the user. Biomass values are converted back to absolute numbers of the primary prey species before projected population values are printed.

Compile and Analyze Predator-Prey Data for Western Subunit 20B for the Period 1984-90 (Job 4)

Work began on a manuscript describing the response of an Interior Alaska moose population to a government wolf removal program in western Subunit 20B. Existing wolf survey data, hunter and trapper reports, and wolf harvest records were reviewed to compile wolf population estimates for regulatory years 1984, 1985, and 1990. Moose population estimates for 1985 and 1989 were reanalyzed, revised, and submitted as part of the Subunit 20B Management Report (McNay 1993). A synopsis of the analysis to date appears below and in the Results and Discussion section.

In February 1980, the Alaska Board of Game authorized a wolf reduction program in Subunit 20B to reduce the effects of wolf predation on moose. Until 1984 wolf reduction efforts concentrated in eastern Subunit 20B. Between October and April 1984-85 and 1985-86, wolves were trapped and shot from helicopters and airplanes by government personnel within the 8,340-km^2 Minto Study Area in western Subunit 20B. Non-government hunters and trappers also killed wolves within the study area during the August-March open season during 1984-85 and 1985-86.

Estimates of wolf population size were made from aerial reconnaissance surveys conducted between November and April in 1984-85 (pre-removal) and 1985-86 (post-removal), and in March 1991 (recovery). Each survey day 1-4 pilot/observer teams searched assigned portions of the study area, concentrating search efforts along likely wolf travel routes. Each portion of the study area was repeatedly searched on different survey days during each annual survey period. Wolf numbers were estimated from wolves observed during the survey or from tracks in fresh snow. Color composition and size of packs helped differentiate packs.

During fall 1984, 3 of the estimated 10 packs occupying the study area contained radio-collared wolves, and during fall 1985, 4 of the estimated 9 packs contained radio-collared wolves. Radio collars allowed identification of packs occupying adjacent or overlapping territories. Information from trappers, hunters, and harvest records were compared with survey results to refine population estimates.

RESULTS AND DISCUSSION

Development of Predator-Prey Management Model (Jobs 1-3 and 5)

A prototype predator-prey management model was completed that allows managers to project ungulate population estimates and allowable harvests through eight annual cycles. In the prototype, five submodels calculate inputs for the main ungulate population and harvest model (Figs. 1-6).

The model currently requires 38 inputs from the user and provides 65 outputs (Appendix A). Many of the inputs are acquired through standard survey and inventory activities, but other inputs are not routinely available for each managed population. The user must extrapolate from other studies for non-routine data inputs. Consequently, accuracy of inputs will be variable and users will be encouraged to explore a range of possible outcomes, rather than use the model as a definitive predictor of predator and prey population response. To facilitate that application, the final version of the model will use stochastic variables and multiple iterations of each data set to output possible population and harvest responses graphically. Work began on a user's manual to assist in the model's use and interpretation (Appendix B).

Compile and Analyze Predator-Prey Data for Western Subunit 20B for the Period 1984-90 (Job 4)

During each of the two winters 1984-85 and 1985-86, 36 wolves were killed within the Minto Study Area. The wolf population declined approximately 79%, from an estimated 67 wolves in November 1984 to 14 wolves in April 1986 (Table 1). An attempt was made to remove entire packs during the wolf removal effort and the number of packs (2 or more wolves) declined from an estimated 10 packs in November 1984 to 3 packs in April 1986 (Table 2). Four single wolves were also identified in spring 1986, two were known survivors from packs that had been removed. The government wolf removal program ended in April 1986.

By April 1991, wolf numbers had recovered to an estimated 61 wolves in 12 packs, representing an annual finite growth rate of 34% (λ = 1.34) between April 1986 and April 1991. Pack territories left vacant after the 1984-86 wolf removal program were reoccupied by April 1991 (Fig. 7). Harvest of wolves by the public continued during the 5 years of wolf population recovery (1986-90), averaging 7.2 wolves annually (Table 1). Immigration from the surrounding lightly exploited wolf population was probably important in the rapid recovery of the Minto Study Area wolf population.

ACKNOWLEDGMENTS

Study costs were supported by funds from Federal Aid in Wildlife Restoration and the State of Alaska. R. DeLong assisted in developing an early version of the predator-prey model and C. Gardner made several suggestions for its improvement and use. Raw data from the 1984-86 wolf management program in Subunit 20B were provided by D. Haggstrom and were collected by E. Crain, D. Haggstrom, P. Karczmarczyk, P. Valkenburg, and others. R. Boertje, E. Crain, R. DeLong, R. Eagan, and R. Hunter assisted in wolf surveys during 1991. E. Lenart assisted with preparation of figures.

LITERATURE CITED

Adams, L. G., B. W. Dale, and B. Shults. 1989. Population status and calf mortality of the Denali caribou herd, Denali National Park and Preserve, Alaska. Nat. Res. Prog. Rep. AR-89/13. Nat. Park Serv., Anchorage, Alas. 131pp.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98. 54pp.

____, S. M. Miller, and J. S. Whitman. 1986. Modeling a Southcentral Alaskan moose population. Alces 22:201-243.

____, ____, and ____. 1990. Brown and black bear predation on moose in southcentral Alaska. Alces 26:1-8.

___, J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildl. Monogr. 114. 49pp.

Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult female moose on the Kenai Peninsula, Alaska. J. Wildl. Manage. 53:557-563.

Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64:1515-1529.

Boertje, R. D., W. C. Gasaway, D. V. Grangaard, and D. G. Kelleyhouse. 1988. Predation on moose and caribou by radio-collared grizzly bears in east-central Alaska. Can. J. Zool. 66:2492-2499.

Coady, J. W. 1974. Influence of snow on behavior of moose. Nat. Can. 101:417-436.

Davis, J. L., P. Valkenburg, and S. J. Harbo. 1979. Refinement of the aerial photo-direct count-extrapolation caribou census technique. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Final Rep. Proj W-17-11. Juneau. 23pp.

___, ___, M. E. McNay, R. M. Beasley, and V. L. Tutterrow. 1991. Demography of the Delta caribou herd under varying conditions of natural mortality and human harvest and assessment of field techniques of acquiring demographic data. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Final Rep. Proj. W-22-5 through W-23-3. Juneau. 112pp.

Franzmann, A. W., and C. C. Schwartz. 1986. Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. Alces 22:139-154.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105. 41pp.

___, and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583-602.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84. 50pp.

___, R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl. Monogr. 120. 59pp.

___, S. D. DuBois, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biol. Pap. 22, Univ. Alaska, Fairbanks. 108pp.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Thesis. Univ. British Columbia, Vancouver. 817pp.

Hayes, R. D., A. M. Baer, and D. G. Larsen. 1991. Population dynamics and prey relationships of an exploited and recovering wolf population in the southern Yukon. Yukon Dep. Ren. Res., Whitehorse. 67pp.

Heimer, W. E., and S. M. Watson. 1986. Comparative dynamics of dissimilar Dall sheep populations. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Final Rep. Proj. W-22-1 through W-22-5. Juneau. 101pp.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 *in* L. N. Carbyn, ed. Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Rep. Ser. 45. Ottawa.

Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. J. Wildl. Manage. 53:548-557.

McNay, M. E. 1992. Caribou management report, Subunit 20A. Pages 89-103 *in* S. M. Abbott, ed. Survey-Inventory Manage. Rep. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Proj. W-23-3 and W-23-4. Juneau.

____. 1993. Moose management report, Subunit 20B. Pages 244-266 *in* S. M. Abbott, ed. Survey-Inventory Manage. Rep. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Proj. W-23-3 and W-23-4. Juneau.

Morgan, S. O., ed. 1990. Moose survey-inventory progress report. Annu. Rep. of Survey-Inventory Activities. Vol. XX. Part VIII. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restor. Proj. W-23-2. 427pp.

Osborne, T. O., T. F. Paragi, J. L. Bodkin, A. J. Loranger, and W. N. Johnson. 1991. Extent, cause, and timing of moose calf mortality in western Interior Alaska. Alces 27:24-30.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. 113. 58pp.

Starfield, A. M., and A. L. Bleloch. 1991. Building models for conservation and wildlife management. Burgess Int. Group, Inc., Edina, Minn. 253pp.

Van Ballenberghe, V., and J. Dart. 1983. Harvest yields from moose populations subject to wolf and bear predation. Alces 18:258-275.

PREPARED BY:

Mark E. McNay
Wildlife Biologist III

SUBMITTED BY:

Daniel J. Reed
Regional Research Coordinator

APPROVED BY:

D. G. Kelleyhouse

David G. Kelleyhouse, Director
Division of Wildlife Conservation

Steven R. Peterson

Steven R. Peterson, Senior Staff Biologist
Division of Wildlife Conservation

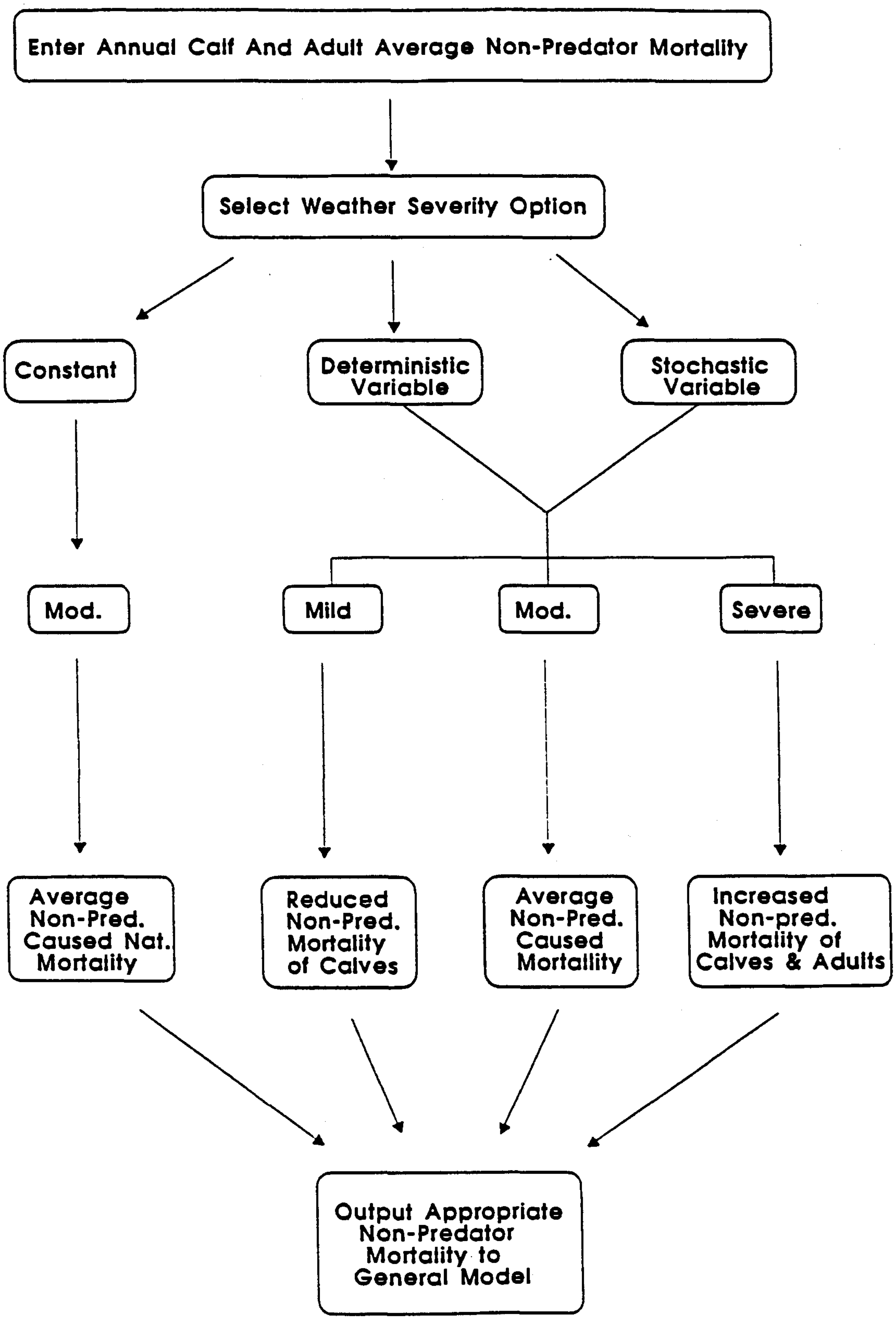

Figure 1. Weather Severity Submodel

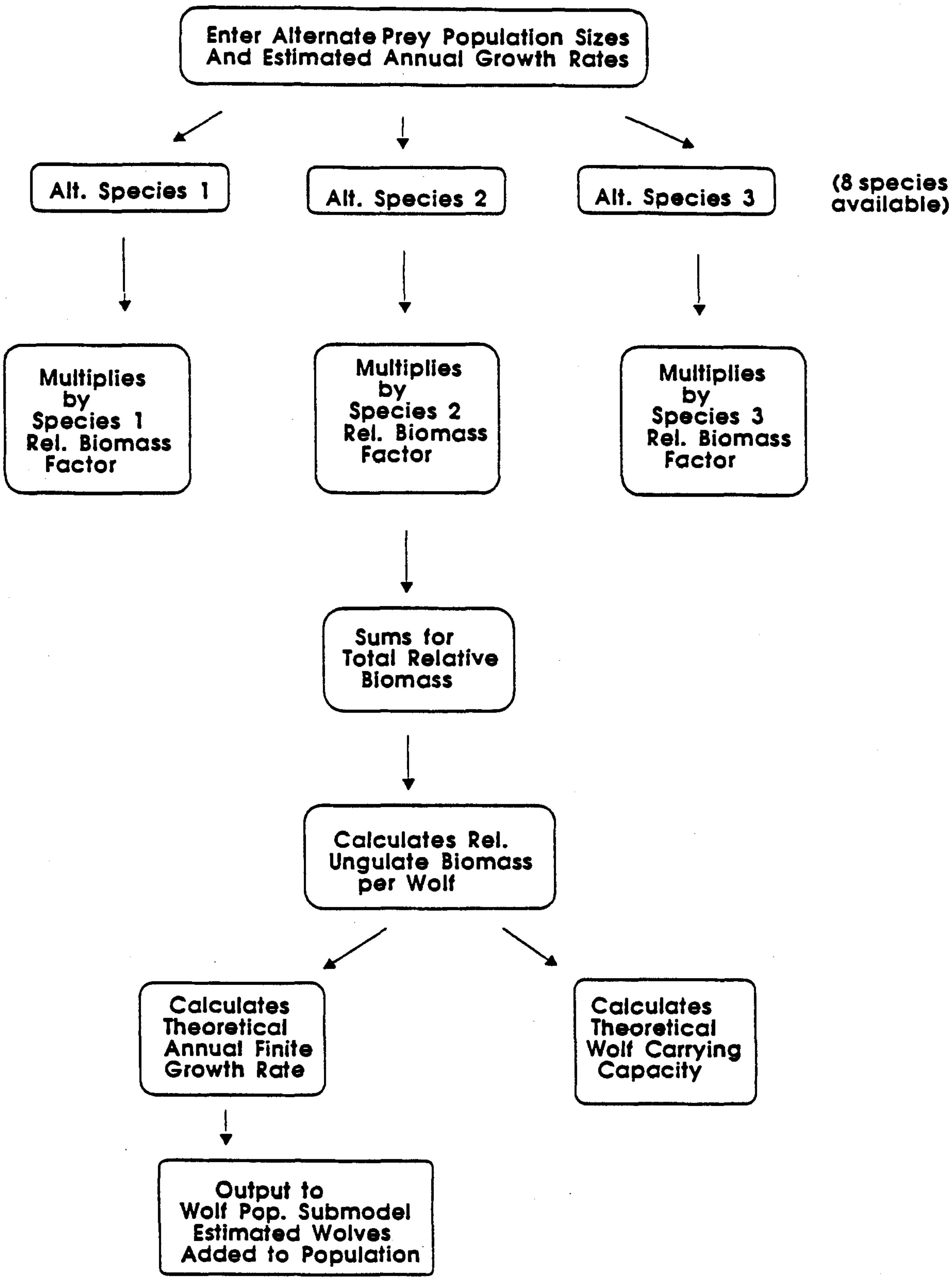

Figure 2. Alternate Prey and Relative Biomass Index Submodel

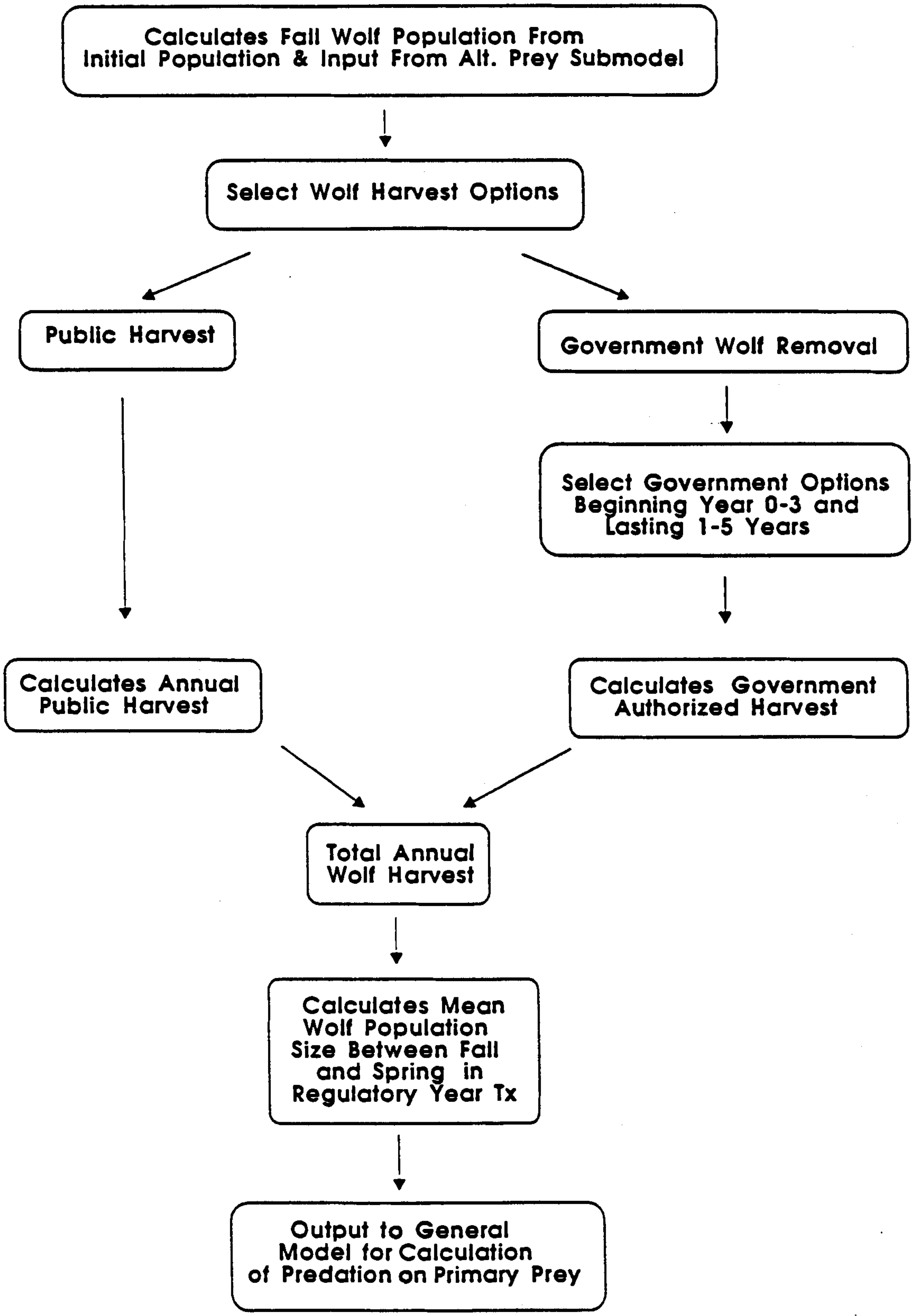

Figure 3. Wolf Population and Harvest Submodel

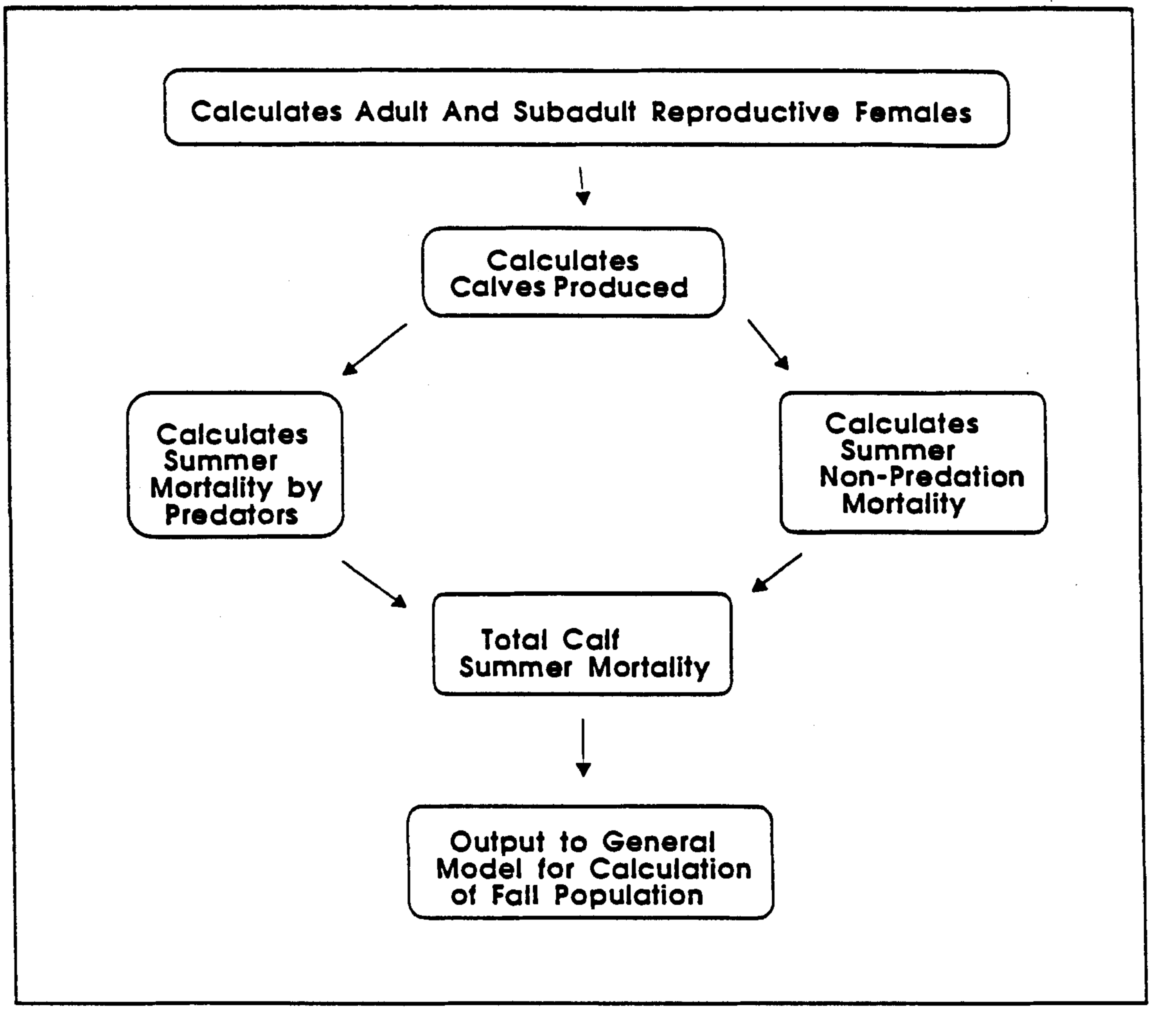

Figure 4. Calf Production And Mortality Model

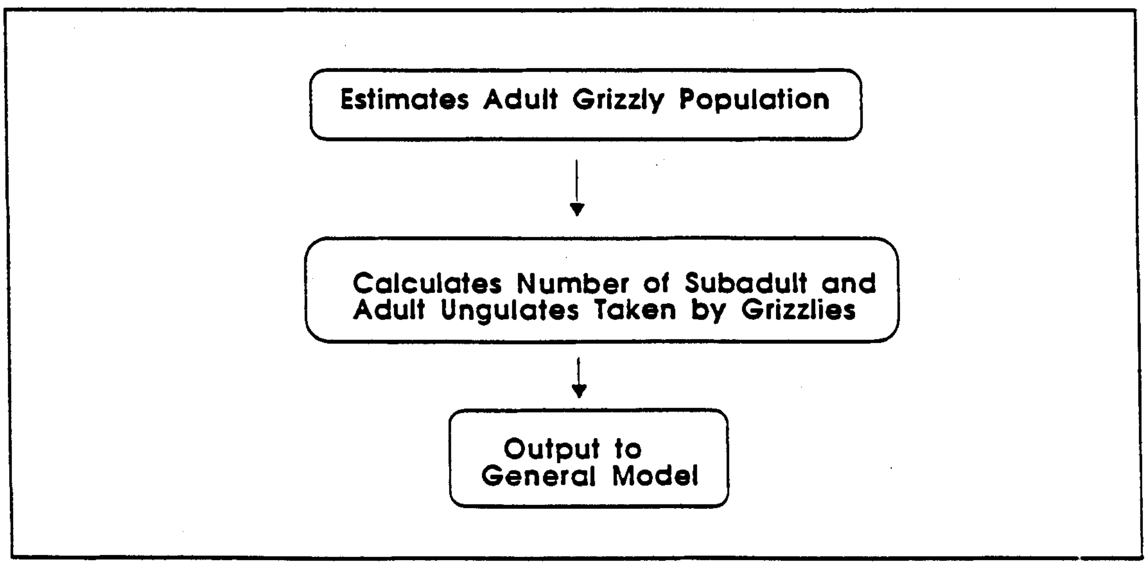

Figure 5. Grizzly Predation Submodel

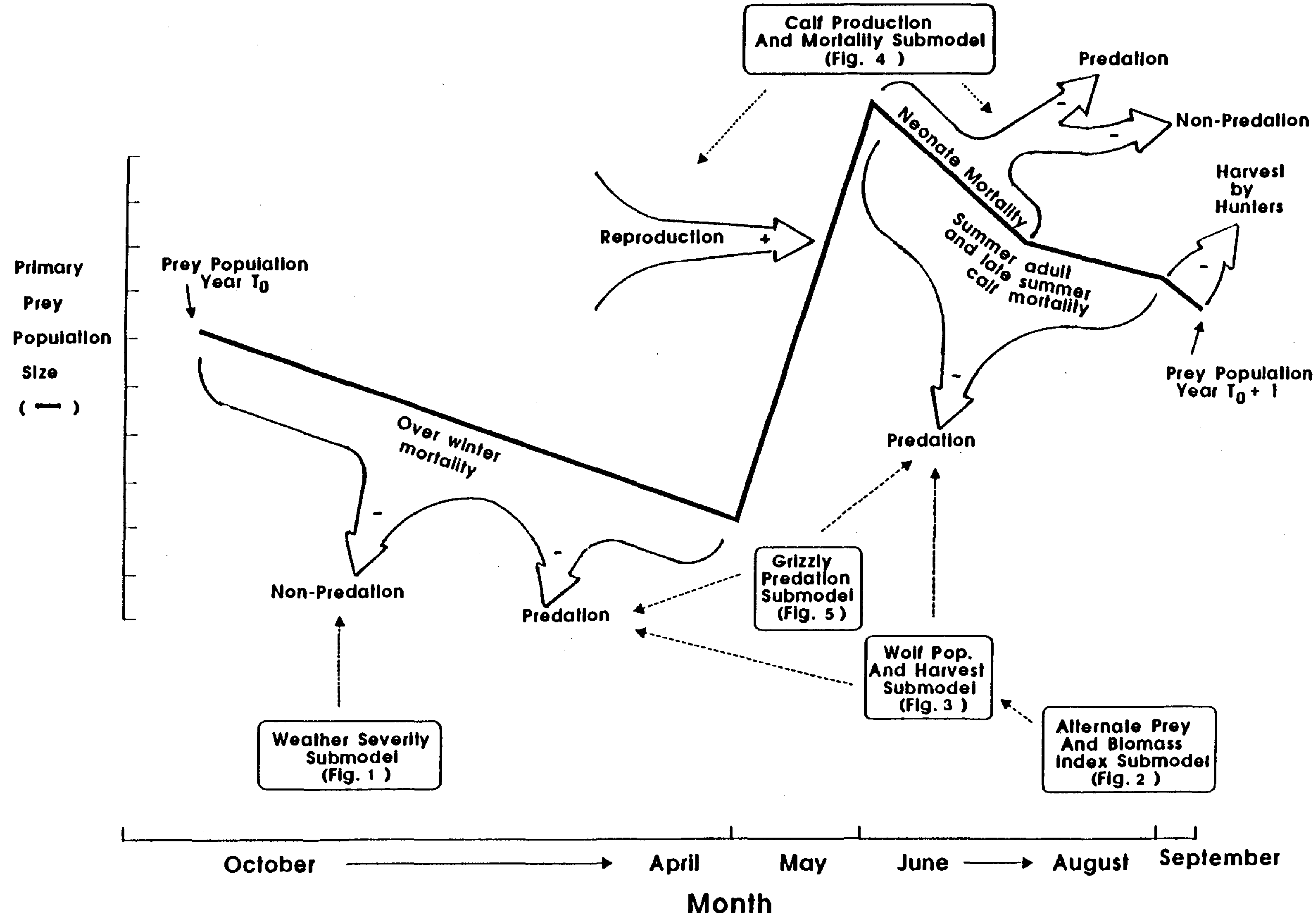

Figure 6. Structure of general Predator-Prey Management Model through 1 annual population cycle.

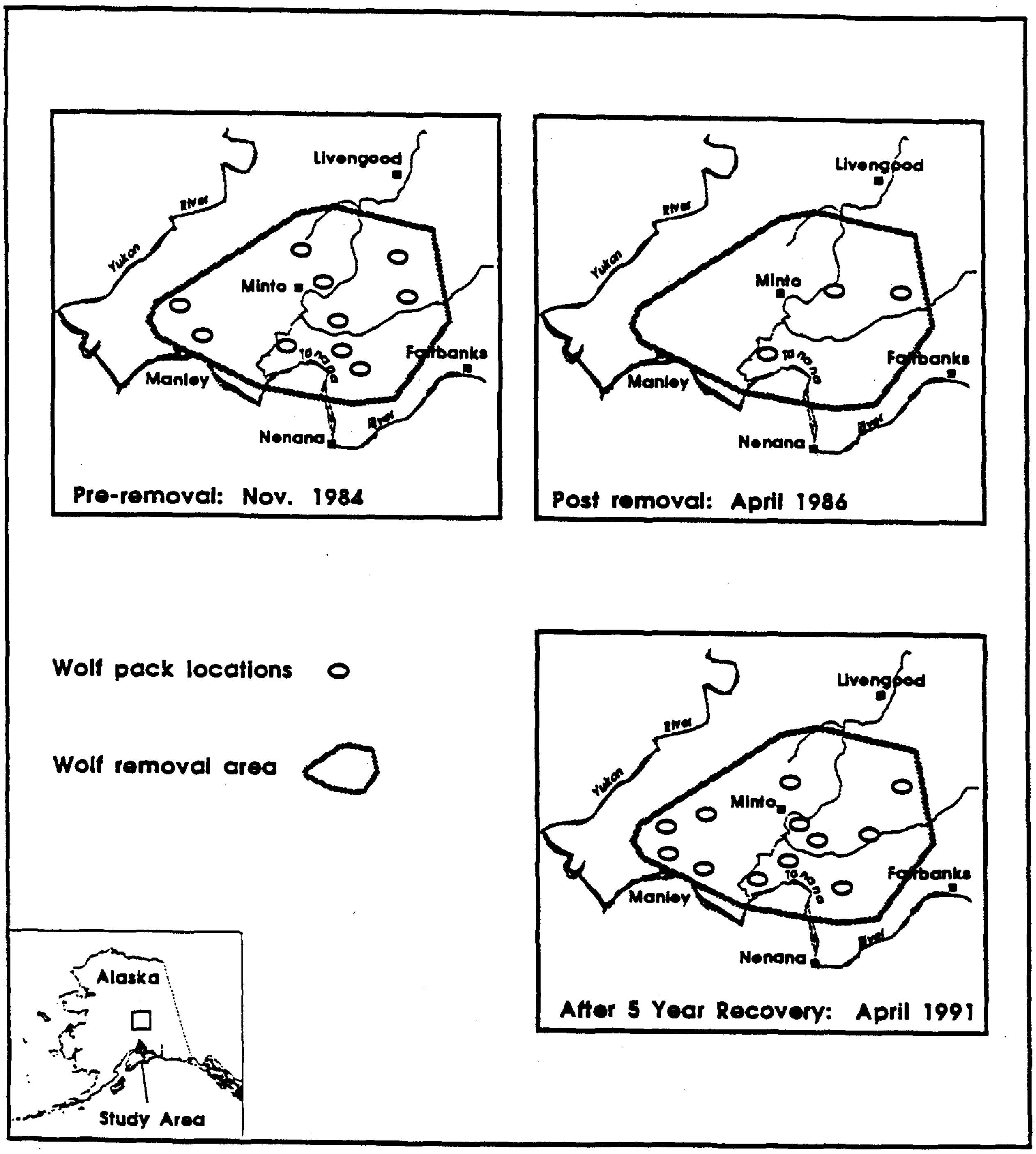

Figure 7. General locations of wolf packs in wolf removal area during pre-removal, post removal and recovery periods.

Table 1. Wolf population estimates, harvests, and survey effort in the 8,340-km^2 Minto Study Area, 1981-91.

Winter	Fall wolf population	No. of wolves killed			Late winter wolf population	Percent of pre-removal population remaining in late winter	Percent of fall population killed	Survey effort (flight hours)
		ADF&G	Public	Total				
1981-82	--	0	9	9	--	--	--	0
1982-83	--	2	16	18	--	--	--	0
1983-84	--	5	4	9	--	--	--	0
1984-85	67	27	9	36	31	46	54	156[a]
1985-86	50	32	4	36	14	21	72	220[a]
1986-87	--	0	2	2	--	--	--	0
1987-88	--	0	4	4	--	--	--	0
1988-89	--	0	13	13	--	--	--	0
1989-90	--	0	12	12	--	--	--	0
1990-91	66	0	5	5	61	na[b]	8	70

[a] These values include flight hours flown by fixed-wing aircraft during wolf removal program.

[b] Not applicable, no wolf removal program during this period.

Table 2. Fall and spring estimates of wolf pack size, Minto Study Area, 1984-86 and 1990-91.

Pack name	Pack size estimates Fall 1984	Spring 1985	Fall 1985	Spring 1986	Fall 1990	Spring 1991
Hutlinana	--	--	--	--	6	6[a]
COD Lake	--	--	--	--	2	2[a]
Dugan	--	--	--	--	5	5[a]
Baker	5[b]	5[b]	7	0	7	7
Chatanika	7	1	0	0	6	3
Globe	5	2	2	2	3	3
Manley	5	2	2	0	3	3
Minto Lakes	3	0	0	0	3	2
Sawtooth	7	5	3	0	0	0
Standard	6	1	3	1	4	4
Swanneck	9	7	12	3	12	12
Tatalina	14	3	2	0	9	8
Tolovana	4	4	5	5	6	6
Washington	0	0	10	1	0	0
Lone Wolf	2[c]	1[c]	4[c]	2[c]	0	0
Totals	67	31	50	14	66	61

[a] These packs do not correspond to any packs identified in 1984-86.

[b] This area was not surveyed in 1984. Estimate is based on fall 1985 survey and kill records. Of seven killed in 1985-86, two were pups suggesting a minimum of five wolves present in 1984-85.

[c] Includes only lone wolves documented by sightings, harvest, or radio-tracking that were not associated with known packs.

APPENDIX A. User Inputs and Model Outputs for General Predator-Prey Management Model and Associated Submodels

USER INPUTS

General Predator-Prey Management Model Inputs

Primary Prey Species
Primary Prey Population Size
Calf:Cow Ratio
Bull:Cow Ratio
Overwinter Non-predation Calf Mortality Rate
Annual Cow Non-predation Mortality Rate
Annual Bull Non-predation Mortality Rate
Summer Calf Non-predation Mortality Rate
Desired Annual Growth Rate
Desired Bull:Cow Ratio
Type of Hunt: 0 = No Hunt, 1 = Males Only, 2 = Either Sex
Annual Finite Growth Rate of Black Bear Population
Annual Finite Growth Rate of Grizzly Bear Population
Current Black Bear Population Size
Current Grizzly Bear Population Size
Current Number of Wolves in Early Winter
Current Number of Wolf Packs in Early Winter
Predator Load by Wolves (i.e., proportion of wolf diet that consists of primary prey species)
Winter Kill Factor by Wolves (generally 1.0, i.e., virtually total diet consists of ungulate prey)
Summer Kill Factor by Wolves (generally <1.0, i.e., predation rate by wolves on ungulates decreases in summer)
Size of Management Area (km^2)
Number of Winter Days (Oct-Apr = 212)
Number of Summer Days (May-Sep = 153)

Calf Production and Mortality Submodel Inputs

Twinning Rate at Birth
24 month Females:Total Precalving Female Ratio
Pregnancy Rate of Females >24 month
Proportion of Neonates Produced Killed by Grizzly Bears
Proportion of Neonates Produced Killed by Black Bears
Proportion of Neonates Produced Killed by Wolves

Alternate Prey and Biomass Index Submodel Inputs

List Current Population Size and Annual Growth of Alternate Prey Species: Bison, Moose, Elk, Muskox, Caribou, Sheep, Goat

Weather Severity Submodel Inputs

Do you wish to simulate the effects of varying weather? (0 = No, 1 = Yes)

Categorize weather for each year as mild = 1, moderate = 2, severe = 3, or enter 4 if you want the computer to select weather conditions.

Wolf Population and Harvest Submodel Inputs

Annual public wolf harvest
(Proportion wolf population harvested;
i.e., enter 0.15 for 15%)

Is there government wolf control?
(0 = No, 1 = Yes)

When will it start?
(Select year 0, 1, 2, 3)

How many years will wolves be regulated?
(1 to 5 years)

What is spring wolf population objective?

Will entire packs be removed?
(0 = No, 1 = Yes)

MODEL OUTPUTS

General Predator-Prey Management Model Outputs

Total Prey Population
Adult Population
Number Fall Males
Number Fall Females
Number Fall Calves
Calf:Cow Ratio
Bull:Cow Ratio

Number in Fall Population Killed by Wolves
Number in Fall Population Killed by Grizzly Bears
Number in Fall Adult Population Dying from Non-Predation Mortality
Number in Fall Calf Population Dying from Non-Predation Mortality
Number September Harvestable Animals
Total Population Growth with No Harvest
Total Population Growth with Male Only Harvest
Total Population Growth with Either Sex Harvest
Proportion Harvest of Total Population
Number Harvestable Males to Achieve Desired Bull:Cow Ratio
Number Harvestable Females to Achieve Desired Bull:Cow Ratio
Number of Black Bears
Number of Grizzly Bears
Black Bear Density
Grizzly Bear Density
Fall Prey:Wolf Ratio
Fall Prey:Predator Ratio
Recruitment Index (Primary Prey)

<u>Calf Production and Mortality Submodel Outputs</u>

Number of:
Calves Produced
Calves Killed by Grizzly Bears
Calves Killed by Black Bears
Calves Killed by Wolves
Calves Dead of Other Causes
Calves Killed by All Predators
Total Calves Dead
Calves Alive October 1
Calves Killed by Wolves During Winter (Oct-Apr)
Female Calves Killed by Wolves During Winter (Oct-Apr)
Females in Spring Pre-parturition
Adult Females in Spring Pre-parturition
24 month Females in Spring Pre-parturition
Pregnant Adult Females
Pregnant 24 month Cows

<u>Alternate Prey and Biomass Index Submodel Outputs</u>

Alternate Prey Species Population Sizes: 8 species
Alternate Prey Species Biomass Indices: 8 species
Relative Ungulate Biomass Per Wolf
Total Relative Ungulate Biomass
Ungulate Biomass per 1,000 km^2

Predicted Annual Wolf Population Finite Growth
Wolves Added or Lost to Population Before Harvest
Estimated Wolf Carrying Capacity (Wolves/1,000 km^2)

<u>Weather Severity Submodel Outputs</u>

Weather Severity Factor (Calves)
Weather Severity Factor (Adults)

<u>Wolf Population and Harvest Submodel Outputs</u>

Public Wolf Harvest
Wolves Killed in Government Wolf Control
Total Wolves Killed
Fall Pre-hunt Wolf Population
Spring, Post-Kill/Pre-Den Wolf Population
Number Fall Wolf Packs
Number Spring, Post-Hunt Wolf Packs
Mean Fall Pack Size
Mean Spring Pack Size
Fall Wolf Density
Spring Wolf Density
Change in Density (%) Fall to Spring
Number Packs Removed by Public Wolf Harvest
Number Packs Removed by Government Control
Total Number Packs Removed

APPENDIX B. Draft User's Manual, Section 1: Operation of Submodels

ALTERNATE PREY AND BIOMASS SUBMODEL

This submodel calculates the relative ungulate biomass values used to estimate wolf population growth rates and the "K" carrying capacity of the wolf population. The submodel contains one input and three output sections. This submodel outputs to the main ungulate population model only through fall wolf population values calculated in row 54 (N54..AI54).

Input

There are two inputs for each prey species:

1. The number of animals currently in each big game prey population within the system (i.e., subunit, herd, mountain range, etc.); and

2. An estimate of the average annual growth rate of each of those big game populations.

As the model moves through time, each alternate prey species will grow annually by the input amount. You do not have to enter a growth value for the primary prey species you entered in D7; the program will automatically use the calculated growth values from the ungulate population model. Here is an example: You have a subunit that contains sheep, caribou, and moose, and you want to estimate the future performance of the moose population. Enter "moose" in D7 and all the appropriate population information in D8 through D47. In C56 you enter the current caribou population and in D56 you enter your estimate of how much that population will grow each year (i.e., 03 = 3% per year). Similarly you enter the values for sheep in C57 and D57. The values for bison, elk, etc., should all be zero. Again, in this case, you do not need to enter a moose value because it is already entered in the main part of the model in D7 and D8. Remember to enter average growth rates. Even though a population may appear to increase 10% in 1 year it may not sustain that for 8 years; 5% may be a better long-term average.

Output

There are three sections arranged in table form:

Section A: Alternate Prey

This section simply takes the input values you entered in the ungulate population model and calculates the size of each prey species population as it moves through the years 1 through 8.

Section B: Biomass Index

This section calculates the relative biomass index for each prey species for each year. It uses relative values of 8, 6, 3, 2.5, 2, 1, 1, and 0.7 for bison, moose, elk, muskox, caribou, sheep, goats, and deer, respectively. These values are similar to those used by Keith (1983) and Fuller (1989). The relative biomass per wolf is also calculated for each year in this section. These values, total relative ungulate biomass, and relative ungulate biomass per wolf are used to predict the wolf population response to changing prey densities.

Section C: Wolf Population Growth and Carrying Capacity

This section uses information from sections A and B to predict the finite growth rate of the wolf population each year. The formulas for predicting annual wolf growth rates and annual wolf "K" values are regressions from Keith (1983) and Fuller (1989), respectively. Those regressions are general models and do not behave very well at the high and low biomass ends of the scale. Therefore, the submodel departs from the published regression when the biomass per wolf index falls below 200, graduating the predicted growth rate to zero and then to 0.9 (i.e., -10%/year) as biomass per wolf approaches zero. If the wolf density exceeds that predicted by Fuller's (1989) regression, wolf growth becomes negative (i.e., 0.9) until the wolf population falls below the predicted wolf "K," after which wolf growth is again predicted by Keith's (1983) regression.

Predicted wolf growth rates are based on a "midwinter" estimate of wolves (i.e., (fall + spring)/2). Wolves are added (or subtracted) to the spring post-hunting wolf estimates to produce a fall estimate for the following year.

Assumptions and Justifications

This submodel assumes:

1. A linear increase in wolf carrying capacity with an increase in total ungulate biomass; and

2. A linear increase in the finite growth rate with an increase in ungulate biomass per wolf (with the exception of modifications described above).

Although simplistic, the assumptions are generally true. Yet, large fluctuations in prey vulnerability could cause significant deviations from the generally linear relationships. For example, in 1992 Denali Park wolves occurred at densities higher than predicted by the general biomass index models, possibly as a result of increased prey vulnerability during severe weather years. In addition, disruption of wolf social structure caused by wolf control programs conducted throughout the spring breeding period may or may not cause reproductive success to fall short of that predicted based on wolf density and ungulate biomass alone (Gasaway *et al.* 1983, Hayes *et al.* 1991).

WEATHER SEVERITY MODEL

This model allows the user to introduce variability in overwinter mortality rates of the primary prey species due to effects of weather. A switch in D64 allows the user to disable the weather severity model. If the weather severity model is disabled then each year is assumed to have an equal, moderate effect on overwinter survival on both adults and calves.

Input Section

If "1" is selected in D64, a menu appears that asks the user to categorize the weather severity for each year in cells D70-D77. A "1" is entered for mild weather, a "2" for moderate (average) weather, and a "3" for severe weather. If "4" is chosen, the model assigns a winter severity factor from a probability function based on the weather severity recorded at Fairbanks between 1965 and 1992. Both mild and severe weather years should be considered relatively rare, occurring maybe only once or twice in a decade. For example, weather indices based on snow depth and duration in Fairbanks indicated that severe winters occurred in 1965-66, 1970-71, 1984-85, and 1990-91. Mild winters occurred in 1969-70, 1979-80, 1985-86, and 1986-87.

If dry or exceptionally hot summer weather is considered to have a negative impact on first year survival, productivity, or adult survival, then "3" would be an appropriate entry to simulate those conditions.

If any number other than "1" is selected in D64 the model automatically assumes "average" weather for all years.

Output Section

In this model, the effects of extreme weather are manifested through an increase or decrease in the overwinter natural mortality rates of adults and first year animals (i.e., calves, lambs, fawns). Among animals in their first year of life, severe weather acts to increase the average natural mortality rate, and exceptionally mild weather acts to reduce natural mortality. Among adults, severe weather acts to increase the natural overwinter mortality rate, but exceptionally mild weather does not decrease adult natural mortality. The outputs of this submodel are (1) weather severity factors for calves and (2) weather severity factors for adults. The main model draws all its weather severity information from those two values.

Assumptions and Justifications

Implicit assumptions are that:

1. First year animals are vulnerable to weather. Survival improves when environmental conditions are better than average and survival can be substantially reduced when environmental conditions are severe; and

2. Adult ungulates have evolved to endure average or better weather with little change in survival until weather becomes severe and prolonged.