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The Effects of Temperature on Bighorn Population Estimates in Yellowstone National Park

by

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ABSTRACT. – The effects of temperature on bighorn population estimates for Yellowstone National Park's Mt. Evert's winter range were examined. Based on work by Houston (1982), a bipartite relationship was hypothesized, whereby the effects of temperature upon the observability of sheep was predicted to be significantly different in those portions of the temperature spectrum where snowmelt occurs. Analyses of the regressions of bighorn numbers observed on mean daily ground temperature supported this hypothesis. At temperatures less than 0°C, counts increased significantly with temperature at a rate of 3.15:1, but were found to underestimate bighorn numbers and be unreliable as estimators of population trend. Counts conducted at 0° to 7°C increased with temperature at a significantly greater rate of 18.53:1. However, correction for population increases suggested this relationship reflected the intercorrelation of temperature and year; a result of selecting increasingly better census conditions over time. It was concluded that no additional benefit accrued from further increases in temperature once snowmelt occurred and that counts conducted at 0° to 7°C (the period between snowmelt and spring migration) were equally reliable. The importance of regarding snowmelt as a threshold value was underscored by the vastly different conclusions regarding bighorn population trends which have been drawn by different researchers from very nearly the same data. While previous research concluded that apparent population increases were the result of temperature-biased data, this study concluded that the apparently sigmoidal population growth was real.

INTRODUCTION

Comparable census data are generally recognized as requisites in establishing valid, quantitative population trend information. To enhance comparability, researchers have often timed censuses to coincide with specific seasons. More recently, attention has been given to optimizing for short-term environmental conditions as well.

An analysis of Rocky Mountain bighorn (*Ovis canadensis canadensis*) population estimates on the northern Yellowstone winter range (NYWR) indicated aerial counts of bighorns to be significantly, positively, and linearly correlated with average daily

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ground temperatures on the day of the count, up to 7° Celsius (C) ($r^2 = 0.52$, $P<.001$) (Houston, 1982). Beyond 7°C, bighorns migrated off the winter range. Addition of a "greenup" factor improved the regression relationship somewhat ($r^2 = 0.62$). The fact that "greenup" added little to the correlation may have been due to the intercorrelation of "greenup" and temperature (Houston, 1982). Houston postulated that the temperature-observability relationship was primarily the result of: (1) changing habitat use and foraging patterns in response to warmer temperatures and vegetation growth, and/or (2) improved observability with time as the faded, white, spring pelage of sheep became more conspicuous against brown and green backgrounds.

Application of the regression relationship to population data showed a profound influence on trend information. When corrected as though taken under "optimal" conditions (7°C and 83% "greenup"), data which had previously indicated a substantial increase in bighorn numbers (from 227 in 1971 to 471 in 1978) subsequently indicated a stable population (Houston, 1982). Though the regression of *maximum* counts on time continued to show a significant population increase between 1971 and 1978, Houston attributed this to selection for increasingly better census conditions over time.

Examination of Houston's regression model yielded the following observations. First, the model incorporated an *a priori* assumption that the temperature-observability relationship was constant throughout the temperature spectrum, up to 7°C. However, since Houston's second postulate (increased color contrast) could only become operative after snowmelt, a potentially bipartite relationship was implied; whereby the temperature-observability relationship may have been significantly different in those portions of the temperature spectrum where snowmelt occurs. Second, by attributing the apparent increase in 1971-1978 maximum counts to a "choice of increasingly better census conditions over time", a positive correlation between the two independent variables, temperature and year, was indicated. Where the intercorrelation of independent variables is high, conclusions derived from regression techniques are likely to be spurious (Zar, 1984). In this case, the resulting regression may have reflected bighorn numbers on time rather than numbers on temperature, since intercorrelation would make the two indistinguishable using multiple regression statistics.

This analysis was presented in an attempt to: (1) evaluate the possibility of the bipartite relationship implicit in Houston's postulates, and (2) examine the regression relationship in a manner which would allow the effects of temperature and of population changes over time to be distinguished.

METHODS

This analysis was part of a study of the ecology of bighorn populations on the northwest border of Yellowstone National Park (YNP). Due to the overall objectives of this study, only those data from the Mt. Evert's winter range (EWR) were considered here. Analysis was based on bighorn censuses conducted by YNP biologists on the NYWR from 1968-1978 (YNP files). Data for the EWR were separated from the larger NYWR data set by referring to the original flight reports.

Two points should be emphasized regarding these data. First, the 1968-1970 data, collected by Barmore (YNP files), are included here, despite criticisms questioning their comparability to later counts (Houston, 1980), because Barmore's more intensive study of the EWR made it likely that the EWR data were comparable to later counts, even though his counts for the entire NYWR may not have been. Also, data for 1970 included one of the most intensive bighorn surveys conducted on the NYWR (Houston, 1982). Second, EWR bighorns were treated as an autonomous population despite some known interchange with populations wintering further upriver along the Yellowstone (Houston, 1982). Linear regression analysis indicated a signifcant positive correlation ($P<.05$) between estimates of the number of sheep wintering on the EWR and those wintering further upriver. Since counts in both groups were apparently increasing simultaneously, interchange appeared unlikely to have been a significant factor in the population dynamics of either area, and unlikely to bias this analysis. Radio-telemetry work (Keating, 1982) and the distribution of a pinkeye epidemic during the winter of 1981-1982 (Meagher, 1982) also suggested minimal interchange. Due to its proximity to and history of human activity, limiting this anlysis to the EWR also minimized bias resulting from increased coverage over time – a bias which Houston (1982) noted in the NYWR data.

Since the data used here were not identical to those analyzed by Houston, they were subjected to the same linear regression analysis employed by Houston to ensure comparability of results. Data analyzed here exhibited a similar positive correlation with temperature ($r^2 = 0.47$ versus $r^2 = 0.52$), indicating that any difference in findings was unlikely to be a result of differing data sets.

Temperature data were identical to those used by Houston (1982). Temperature alone was considered in this analysis since "greenup" added very little to Houston's regression model, and no data on plant phenology were available for the 1968-1970 counts. The upper threshold of 7°C observed by Houston was incorporated as an assumption in this analysis. The maximum 1976 count, obtained at 8°C, was an exception to this, but was retained on the rationale that any maximum count represented only a minimum estimate of the true population and its value in that capacity outweighed a slight deviation from the assumption. Another assumption implicit in Houston's postulates, and therefore in this analysis, was that mean daily ground temperature was a reasonable indicator of seasonal temperature trend.

Based on Houston's postulates, a bipartite temperature-observability relationship was hypothesized and the two components labelled as: (1) distributional effect, and (2) contrast effect. The mechanisms of these two would necessarily be different. The distributional effect would result from differences in habitat use and would involve spatial changes which affect observability. The contrast effect would result from changes in vegetation and snowcover which would increase the color contrast between the sheep and their habitat and would be observed only at temperatures sufficient to effect snowmelt. This hypothesis predicted that the temperature-census regression would differ significantly between temperatures above and below 0°C. To test this hypothesis, separate linear regressions were derived for those observations taken between 0 and 7°C and those taken at less than 0°C. The resulting regression equations were then analyzed for equality (Zar, 1984).

To test constancy of population size between 1968 and 1978, maximum counts for each year were plotted against time and apparent high and low population periods were grouped. Using a sign test (Zar, 1984), residuals derived from the regressions of counts on temperature for these two groups were then tested for equal distribution about the regression equations.

RESULTS

Fifty-three counts taken between 1968 and 1978 were plotted against mean daily ground temperature on the day of the census (Fig. 1). Linear regressions were signifi-

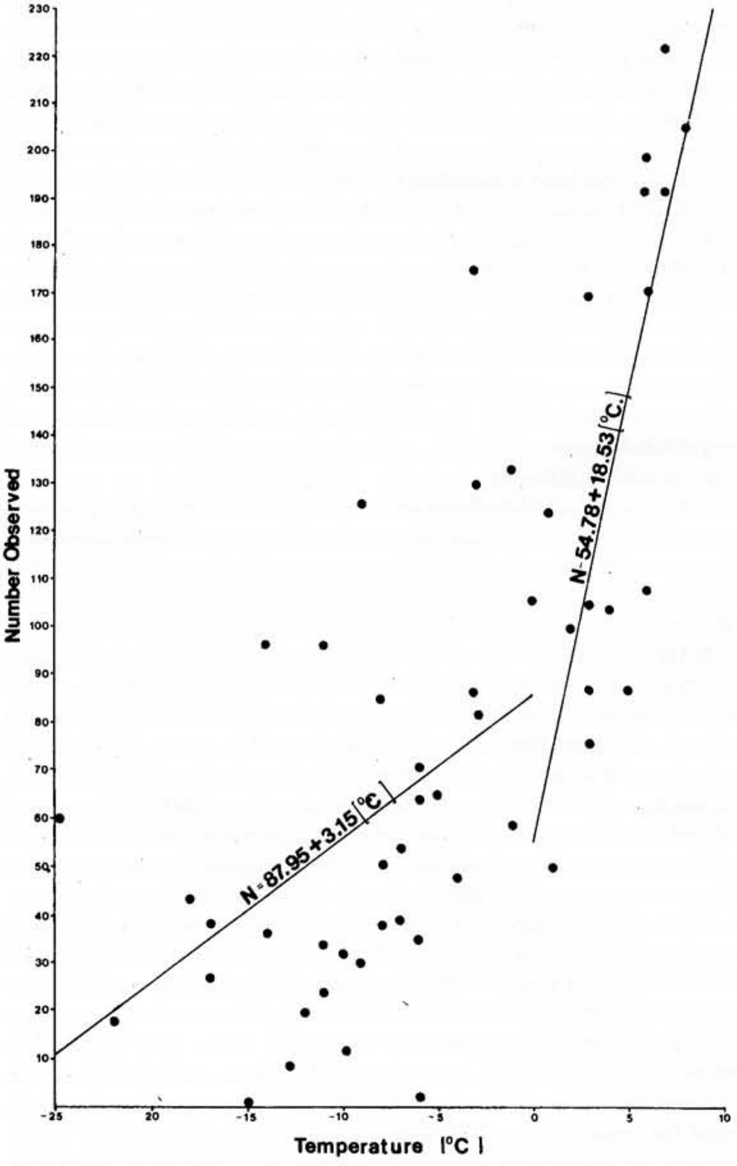

Fig. 1. Regression relationships between mean daily ground temperature at Mammoth, Wyoming, and the number of bighorns observed on the Mt. Evert's winter range for temperatures less than 0°C and 0 to 7°C.

cant for counts conducted at temperatures less than 0°C ($r^2 = 0.21$, $P<.01$) and at temperatures between 0 and 7°C ($r^2 = 0.57$, $P<.001$). A Student's-t test showed the slopes of these two regressions ($b = 3.15$ and $b = 18.53$, respectively) to be significantly different ($P<.001$).

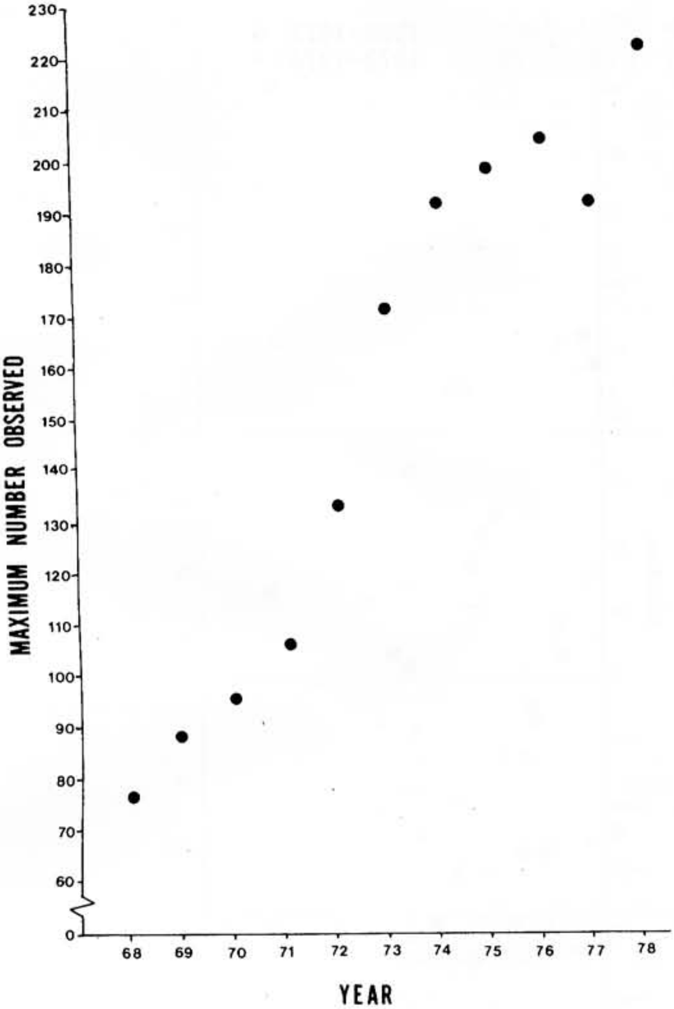

Fig. 2. Maximum population counts on time for bighorns on the Mt. Evert's winter range, 1968-1978.

Maximum counts were plotted against time (Fig. 2) and apparent low and high population periods were grouped (1968-1972 and 1973-1978, respectively). For counts conducted at temperatures less than 0°C, sign tests showed residuals from the regression for both the 1968-1972 and 1973-1978 periods to be distributed equally about the regression ($P = .52$ and $P = 1.00$, respectively) (Fig. 3). For counts conducted at temperatures between 0° and 7°C, residuals from the regression were found to be unequally distributed about the regression equation for both the 1968-1972 and 1973-1978 periods ($P = .13$ and $P = .04$, respectively), with counts from 1968-1972 and 1973-1978 clustered below and above the regression, respectively (Fig. 4).

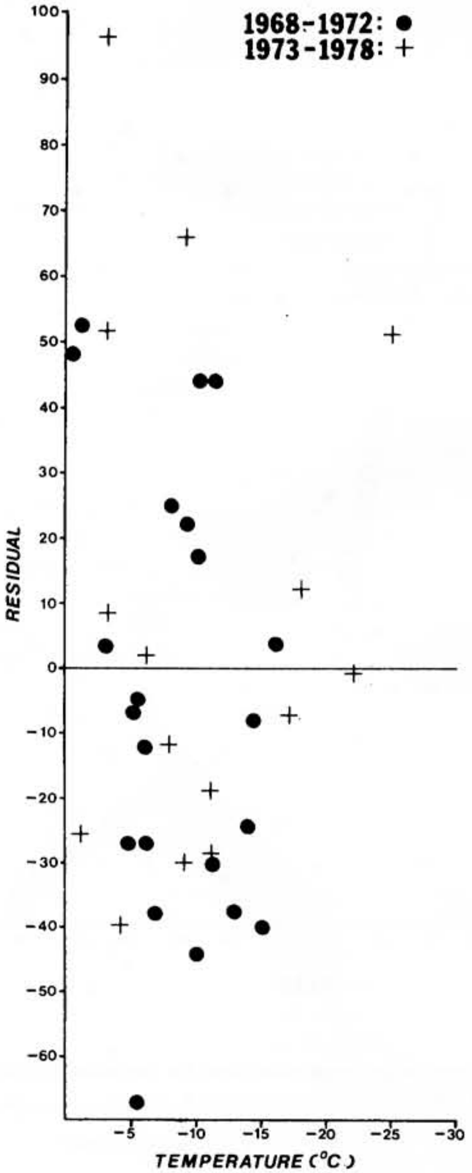

Fig. 3. Residuals of the temperature-census regression, shown relative to the regression of bighorn numbers observed on temperatures less than 0°C and divided into apparent high and low population year groups (1968-1972 and 1973-1978, respectively).

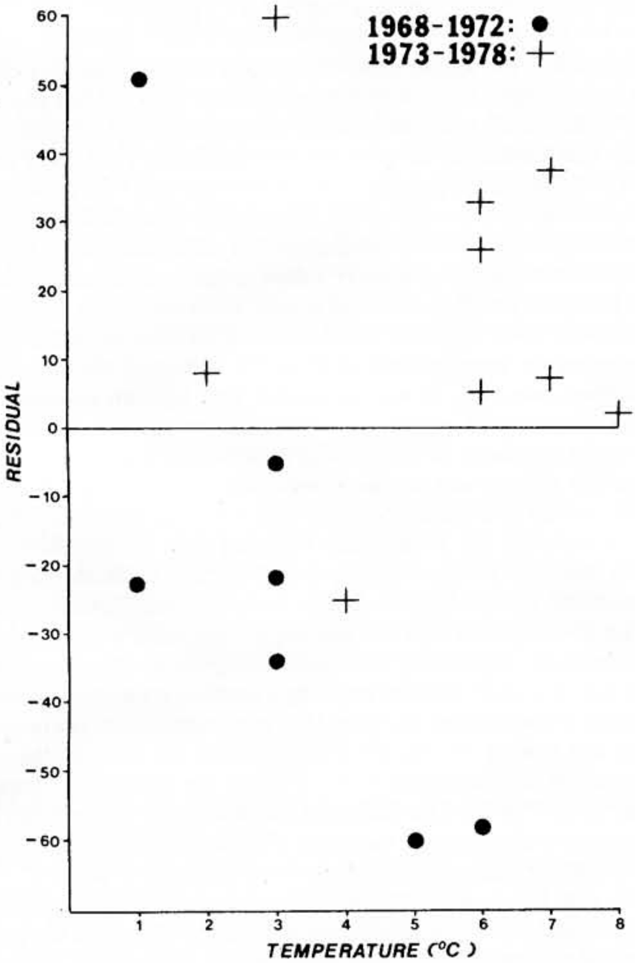

Fig. 4. Residuals of the temperature-census regression, shown relative to the regression of bighorn numbers observed on temperatures of 0 to 7°C and divided into apparent high and low population year groups (1968-1972 and 1973-1978, respectively).

DISCUSSION

Analyses of the regressions of bighorn numbers observed on mean daily ground temperature on the day of the census supported the hypothesis of a bipartite temperature-observability relationship. Censuses were found to increase significantly with temperature, up to 7°C, though the relationship was found to be significantly different in different portions of the temperature spectrum.

At temperatures less then 0°C, census counts increased with temperature according to the relationship:

$$N = 87.95 + 3.15\ (°C)$$

When this portion of the temperature-census data was analyzed for evidence of a real increase in bighorn numbers, residuals from apparent high and low population periods were found to be evenly distributed about this regression. This indicated either: (1) there was no real increase in the population between the 1968-1972 and 1973-1978 periods, or (2) differences in population levels for those two time periods were indistinguishable in the sub-zero portion of the temperature-observability relationship. Two lines of reasoning supported the conclusion that differences were indistinguishable. First, the coefficient of determination (r^2) showed that temperature accounted for only 21% of the observed variation in census counts, while maximum counts had increased 292% (from 76 in 1968 to 222 in 1978). Second, an analysis of the residuals from a similar regression for temperatures of 0° to 7°C indicated the apparent increase in bighorn numbers was real. It was concluded that bighorn censuses conducted at temperatures less than 0°C tended to underestimate bighorn numbers and were so variable as to be unreliable in establishing population estimates.

Initial analysis also showed census counts conducted at 0° to 7°C to increase with temperature, though at a markedly faster rate than counts conducted at lower temperatures. However, if this relationship reflected only differences in observability, rather than a change in the underlying population, then residuals from apparent high and low population year groups should have been distributed evenly about the regression. The fact that apparent high and low population years were clustered above and below the regression, respectively, indicated the regression of population estimates on temperature was not "real", but was probably a spurious relationship resulting from the intercorrelation of temperature and year. (For maximum counts, the intercorrelation of temperature and year ($r = .56$, $P<.05$) accounted for 91% of the correlation of maximum count on temperature ($r = .61$, $P<.05$); the correlation of maximum count on year was .95 ($P<.001$).) This indicated the absence of a significant temperature-observability relationship beyond the point of snowmelt, and suggested that censuses were equally reliable when conducted anywhere between 0° and 7°C.

Concurring with Houston (1982), this analysis suggested that bighorn aerial census information tended to be more reliable when conducted between the period of snowmelt and spring migration. It differed significantly, however, in suggesting that the temperature-observability relationship was subject to a threshold, whereby no additional benefit accrued from further increases in temperature once snowmelt had occurred. The importance of this seemingly minor difference in the temperature-observability model was underscored by the vastly different conclusions regarding population trends which were drawn from very nearly the same data. Using a strictly linear model, Houston (1982) concluded that the NYWR bighorn population had remained stable during the 1971-1978 period. Evaluating the EWR data in light of the threshold model derived here, the apparently sigmoidal growth trend shown in Figure 2 was concluded to be real. Nine of the 11 maximum counts were obtained at temperatures of 0° to 7°C. Of the other two years, the second highest counts were obtained at temperatures of 0° to 7°C and were sufficiently comparable to maximum counts (87 versus 96 for 1970 and 124 versus 133 for 1972) that the regression of numbers on time was virtually unaffected ($r^2 = .907$ versus $r^2 = .912$).

These conclusions were not inconsistent with Houston's (1982) data for the entire NYWR, which showed a fairly random distribution of years about the regression for temperatures below 0°C, maximum counts which all lay between 0° and 10°C, and maximum counts which ascended, more or less, by year (with earlier years which tended to lie below the regression). Such similarities were not surprising, but did not indicate that conclusions derived here regarding population trends were applicable over the entire NYWR. The NYWR data represented an average over a much larger area. Since the Mt. Evert's estimate accounted for nearly one-half of the NYWR estimate (222 of 471 in 1978), it was to be expected that the Mt. Evert's data would significantly influence that average. However, temperature-census relationships and population trends on Mt. Evert's may differ significantly from other areas of the park, given that: (1) the EWR lies at a much lower elevation than many of the other bighorn winter ranges in the NYWR (thus, its relationship to mean daily ground temperature at Mammoth would be expected to be different), and (2) Mt. Evert's lies within the boundary line area – a fact which may subject it to pressures not found in other areas of the park (Houston, 1982).

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REFERENCES

HOUSTON, D. B. (1980): The northern Yellowstone elk. Yellowstone National Park files. 908 p. Unpublished report.

HOUSTON, D. B. (1982): The Northern Yellowstone Elk, Ecology and Management. Macmillan Publishing Co., Inc., New York. 474 p.

KEATING, K. A. (1982): Population ecology of Rocky Mountain bighorn sheep in the upper Yellowstone River drainage, Montana/Wyoming. M.S. Thesis, Montana State University, Bozeman. 79 p.

MEAGHER, M. (1982): An outbreak of pinkeye in bighorn sheep, Yellowstone National Park: A preliminary report. Proc. N. Am. Wild Sheep and Goat Conf. 3; 198-201.

ZAR, J. H. (1984): Biostatistical Analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.: 718 p.

Int. J. Biometeor., 1985, Vol. 29, no. 1, p. 56.

Abstracts Noted*

Reviews and abstract of a wide range or publications appear in the periodic issues of "Nature and Resources" published by UNESCO. The following, which are judged of particular interest to ISB members, are reproduced with permission and acknowledgements to UNESCO.

(1) From Vol. XIX, No. 3 – July to September 1983.

The Role of Fire in Northern Circumpolar Eco-systems

Ed. by Ross, W. Wein and David A. MacLean
John Wiley & Sons Litd, Baffins Lane, Chichester, West Sussex PO19 1UD, United Kingdom, 1983. 322 pp. £ 27.95.
During the past twenty years scientists have come to view fire in the forest from a new perspective: from being regarded as an unmitigated threat, it is increasingly seen as an integral part of ecological processes. This volume presents contributions from Canadian, American, Finnish and Soviet scientists, who examine temperate-region fire concepts – about which a good deal is known – in an effort to identify which of these theories also apply to the circumpolar north, and which are unique to northern ecosystems. The book is divided into five sections. The first section considers "Past and Present Fire Frequencies" from postglacial times to the present. Next, the section "Physical Effects of Fire" examines fire behaviour in northern forests, shrublands, and organic soils, as well as effects of fire on the ground thermal regime and nutrient cycling in the northern ecosystems. There are two chapters on "Concepts of Fire Effects on Individuals and Species", paying special attention to plant individuals and species, and small-mammal and bird communities. "Fire Effects in Selected Vegetation Zones" includes reviews of the role of fire in jack pine, black spruce, and *Abies*-dominated forest ecosystems as well as the lichen-dominated tundra and forest tundra. A final section is devoted to "Fire Control and Management" with chapters on the particular problems of fire control and prevention in peatlands and on fire management in wilderness areas and parks.

(2) From Vol. XX, No. 2, April-June 1984.

Acid Rain in Europe and North America: National Responses to an International Problem
By Gregory S. Wetstone and Armin Rosencranz
Environmental Law Institute, Suite 600, 1346 Connecticut Avenue, N.W., Washington, DC 20036, United States of America, 1983. 244 pp.
This report examines the nature and severity of the acid-rain problem, what nations are doing about it, and how national and international laws and policies might respond. While the emphasis is on government policy-making, the scientific debate over the causes and repercussions of acid rain is treated in detail. There are four parts:
A review of the scientific issues, many of which are highly controversial, and of the range of available pollution-control technologies.
A survey of laws and policies relevant to the production and control of acid pollution in each of the six European and North American nations chosen for study.
An analysis of national and international laws and institutions available to promote control of acid pollution.
Thoughts on the significance of acid rain, and on the need for changes better to control this and similar environmental problems of international scope.