BRIEFER ARTICLES, AND POINTS TO PONDER

IS THE 10-YEAR WILDLIFE CYCLE INDUCED BY A LUNAR CYCLE?[1]

The 10-year cycle long has been one of the most intriguing problems in population dynamics. Despite Cole's (1951, 1954) skepticism about the reality of population cycles, there is statistical evidence for an approximately 10-year cycle in a number of northern North American species including snowshoe hare (*Lepus americanus*), ruffed grouse (*Bonasa umbellus*), Canada lynx (*Lynx canadensis*), several other mammalian predators, and even Atlantic salmon (*Salmo salar*) (MacLulich 1957, Keith 1963, Bulmer 1974, and others).

This paper presents a simple model, based on a lunar cycle, for prediction of peak years of animal abundance. This research developed from an earlier finding of a correlation (P < 0.0005) between spring drumming activity of ruffed grouse and moon phase (Archibald 1976). That work was done at the University of Minnesota, and financial support there was provided by NIH Training Grant No. 5 T01 GM01779 and the Atomic Energy Commission (COO-1332-110). D. L. Allen, R. F. Dale, D. S. Gilmer, M. W. Jaffe, C. M. Kirkpatrick, J. M. Mitchell, Jr., F. H. Montague, Jr., and H. P. Weeks made helpful comments on drafts of the manuscript.

Explanations of the cycle have been primarily of two types, one involving an intrinsic cause such as a predator-prey interaction, and the other an extrinsic cause such as a climatic periodicity (Lack 1954: 212, and previous workers). The persistent period and approximate regional and interspecific synchrony are the cycle's features that are both most intriguing and most difficult to explain. The hypothesis that the cycle is induced by a cyclic extrinsic factor has the advantage that both the period and synchronization are explained (Moran 1953). Nu-

merous extrinsic factors have been proposed, e.g., the early sunspot hypothesis (Elton 1924) and the lunar hypothesis (unrelated to mine) of Siivonen and Koskimies (1955), but none has proven adequate (Keith 1963:102–107, 116).

The parameters of my model are based on a cyclic astronomic phenomenon, the nodal cycle of the moon. The nodal cycle causes appreciable changes in lunar declination, in times of moonrise and moonset, and in the height and timing of tides (McLaughlin 1961: 128, Macmillan 1966:44). The period of the nodal cycle is 18.6 years (Baker 1959:131), but certain phenomena occur twice during the cycle, or every 9.3 years (as will be confirmed later).

The model which I used to predict peak years of abundance is:

$$P_n = 1950.22 \pm 9.3 \, n$$

where P_n is the date (in years) of the nth peak before or after the year 1950, 9.3 is the period, and 1950.22 represents the vernal equinox (21 March) in 1950. At this time, the moon's declination attained a maximum reached once during the 18.6-year nodal cycle (Baker 1959:133).

The model gives a good fit to reported years of peak abundance of three species over a 121-year period (Table 1). The average difference between predicted and mean reported peaks is 0.30 years ($n = 14$). By experimentation, I determined that a 9.26-year period yields the minimum average difference. For each species, the reported data are averages that represent large geographical areas and begin with the earliest records that I believe are reliable for the purpose. I chose to terminate the lynx series with 1913 because lynx fur returns dropped considerably after the first world war (Bulmer 1974).

The correlation (Table 1) suggests but cannot prove the hypothesis that the nodal cycle

Table 1. Comparison of reported and predicted years of peak abundance of Canada lynx, snowshoe hare, and ruffed grouse in northern North America.

Canada lynx[b]	Snowshoe hare[c]	Ruffed grouse[d]	Mean peak year	Predicted peak years of abundance[e]	Difference (years)
1829			1829	1829.3	−0.3
1838			1838	1838.6	−0.6
1847			1847	1847.9	−0.9
1857	1857?	1857?	1857	1857.2	−0.2
1866	1865	1866	1865.7	1866.5	−0.8
1876	1876	1877	1876.3	1875.8	0.5
1885.5	1886.5	1887	1886.3	1885.1	1.2
1895?	1896	1898	1896.3	1894.4	1.9
1905	1904.1	1904.6	1904.6	1903.7	0.9
1913?	1912.4	1914.2	1913.2	1913.0	0.2
	1923.6	1922.6	1923.1	1922.3	0.8
	1932.2	1932.6	1932.4	1931.6	0.8
	1941.6	1941.2	1941.4	1940.9	0.5
	1951.5	1949.2	1950.4	1950.2	0.2

$$\bar{d} \quad 0.30$$
$$SD \quad 0.804$$

The header spanning "Canada lynx", "Snowshoe hare", "Ruffed grouse", and "Mean peak year" is: Reported peak years of abundance[a]

[a] Peak years for species are not directly comparable since data are from different regions (Lack 1954:210) and based on different types of records.
[b] Fur returns, Northern Department totals, Hudson's Bay Company (Elton and Nicholson 1942:228–229).
[c] Pre-1900, fur returns, Hudson's Bay Company (MacLulich 1957:296). Post-1900, median years of reported abundance computed from Keith (1963:42).
[d] Pre-1900, peak abundance (Schorger 1947:54). Post-1900, median reported peak years or last years of abundance, excluding maritime provinces, computed from Keith (1963:57).
[e] $P_n = 1950.22 − 9.3$ n.

is the factor underlying the periodicity and approximate synchrony of the 10-year cycle. This hypothesis must be viewed as tentative, for its validity cannot be established statistically (Moran 1949, Hickey 1955) and I cannot document the mechanism.

Under the working hypothesis that the nodal cycle governs the 10-year cycle, several types of mechanisms appear plausible. The lunar factor could operate directly on one or more cyclic prey species, with secondary effects on predators and alternate prey. Or, the factor could affect both predators and prey directly (Elton and Nicholson 1942, and others). Alternatively, the mechanism might involve an indirect effect on plants or weather, possibly via an effect on some intermediate factor such as atmospheric ozone (Huntington 1945:492–507), ultraviolet (Rowan 1950), or forest fires (Grange 1949:191–192). Many combinations of effects are conceivable, and the effect(s) need not occur in more than 2–3 consecutive years per decade.

I know of only one previous instance where a cyclic population phenomenon has been attributed to the nodal cycle. Pettersson (1912:185) claimed that the greatest herring catches off southwestern Sweden consistently occurred in years of maximum lunar declination (every 18.6 years) between 1763 and 1911. According to his hypothesis, good fishing years resulted from periodic ingress of herring, in turn related to upheavals of deep water which seemed to depend on lunar declination. The possibility that such upheavals of cold water might influence terrestrial climate was noted in Huntington (1931).

Consider the possibility of a direct lunar effect. Fig. 1 illustrates a lunar phenomenon that has the 9.3-year periodicity. Since the full moon rises at about sunset, moonrise lag serves as an *index* of changes in nocturnal illumination during the nodal cycle. (I suspect that the mechanism may involve a cyclic lunar effect on photoperiod.) At a given northern latitude, say 50°, moonrise lag at full moon is greatest near the vernal equinox and least near the autumnal equinox (Krogdahl 1962:104). In the latter case, known as the harvest moon effect, there is an 18.6-year cycle. However, the situation with re-

spect to a related variable is turned about: *moonset* lag at full moon is greatest near the autumnal equinox, with a 9.3-year period. There is no evidence of a resulting cyclic effect on rates of natality, mortality, or dispersal in any cyclic species. However, it is interesting to note that the five peaks of grouse abundance recorded at Cloquet, Minnesota since 1930 (Marshall 1954:110, Gullion, personal communication) have alternated in amplitude, and the higher grouse peaks consistently have coincided with the higher peaks in moonrise lag shown in Fig. 1. In the last half of the nineteenth century, alternation in amplitude also was evident in peak snowshoe hare fur returns of the Hudson's Bay Company: 1857, 95,534; 1865, 144,519; 1876, 104,123; 1887, 137,685; 1896, 96,000 (MacLulich 1957:296). But, in contrast to grouse at Cloquet, lower hare peaks coincided with higher peaks in moonrise lag.

Within the framework of intrinsic hypotheses, the periodicity and approximate synchrony of the 10-year cycle have been difficult to explain convincingly. The persistent period is explained only with the tenuous assumption that major disturbing influences are absent or unusually infrequent (Lack 1954:216, Hickey 1955, and others). Effects of such random disruptive influences "will affect the future course of the cycle and thus become incorporated into the future history of the series" (Moran 1953:165). In Keith's (1974:43–48) conceptual model, the periodicity in hares was attributed to the combined effects of a hare-vegetation interaction and a predator-hare interaction, which intiate and sustain the decline, respectively. While I do not doubt their existence, I question whether these interactions are sufficient, in themselves, to explain the persistent periodicity, particularly since declines may begin at markedly different peak densities (Rowan 1950, Lack 1954:214, Keith 1963:108–109). To explain synchrony between regional hare populations, Keith (1974:45) postulated a "recurrent weather phenomenon of almost continent-wide scope" that would occur during the increase phase of the cycle.

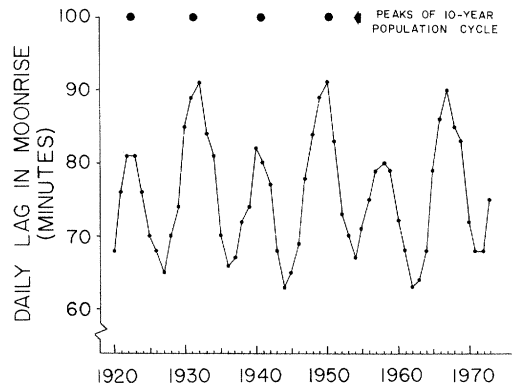Keith (1974:45, and earlier writers) be-

Fig. 1. Lag in time of moonrise on the 2 days nearest the full moon closest to the vernal equinox at latitude 50°N, 1920–1973. Lunar data from American Ephemeris and Nautical Almanac; peaks of 10-year cycle from Table 1.

lieved that periodic declines in ruffed grouse are caused by increased predation due to a "predator shift" as hares decrease. The "predator shift" hypothesis has been challenged (Hoffmann 1958, Lack 1966:286, and others) because it demands that grouse consistently decline after hares, yet the evidence (Hoffmann 1958, Keith 1963:130) indicates a tendency for grouse to peak or decline first. Rusch and Keith (1971:821) argued that "cases of grouse declining before hares could result from concentration of raptors emigrating from areas where hares had already declined." This is improbable, however, because it seems likely that the newly arrived predators initially would prey primarily on hares. In contrast, Gullion (1970) attributed declines in ruffed grouse to reproductive failure resulting from adverse (snow) conditions in the preceding winter. I suspect that all prey species involved in the 10-year cycle are affected by the nodal cycle, but perhaps in different ways. I believe that this explanation is far more plausible than, for example, the claim (e.g., Bulmer 1974:713) that the cycle in Atlantic salmon resulted from the hare cycle.

Can a lunar hypothesis shed any light on the puzzling question of the geographic extent of the 10-year cycle? Based on Keith (1963:116) and Bulmer (1974), I conclude

that a pronounced 10-year cycle in terrestrial species generally is restricted to the boreal forest in the interior of large land masses above about latitude 45°N. Within the northern hemisphere, the latitudinal restriction (and perhaps differences in size and timing of peaks) may be related to latitudinal differences in lunar phenomena. For example, the amplitude of moonrise lag (shown for 50°N in Fig. 1) at 60°N is twice that for 30°N. (As with other lunar phenomena, there is no appreciable longitudinal variation.) Confinement of the cycle largely to continental interiors might be accounted for in two ways. Perhaps maritime fog and clouds reduce visibility of moonlight enough to prevent expression of direct lunar effects. Alternatively, maritime influences may preclude significant lunar effects on climatic phenomena. Absence of the cycle in the southern hemisphere may result from the dearth of large land masses below 45°S, other than Antarctica which lacks ecologically equivalent species.

Despite its unprovability, my hypothesis seems convincing enough to justify further research. At present, it should be viewed as tentative—with approximately equal parts of skepticism and openmindedness.

LITERATURE CITED

ARCHIBALD, H. L. 1976. Spring drumming patterns of ruffed grouse. Auk. 93(4):808–829.

BAKER, R. H. 1959. Astronomy. 7th ed. Van Nostrand, Princeton, New Jersey. 547pp.

BULMER, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. J. Anim. Ecol. 43(3): 701–718.

COLE, L. C. 1951. Population cycles and random oscillations. J. Wildl. Manage. 15(3):233–252.

———. 1954. Some features of random population cycles. J. Wildl. Manage. 18(1):2–24.

ELTON, C. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Br. J. Exp. Biol. 2(1):119–163.

———, AND M. NICHOLSON. 1942. The ten-year cycle in numbers of the lynx in Canada. J. Anim. Ecol. 11(2):215–244.

GRANGE, W. B. 1949. The way to game abundance. Chas. Scribner's Sons, New York. 365 pp.

GULLION, G. W. 1970. Factors affecting ruffed grouse populations in the boreal forests of northern Minnesota, USA. Finnish Game Res. 30:103–117.

HICKEY, J. J. 1955. Some American population research on gallinaceous birds. Pages 326–396 in A. Wolfson, ed. Recent studies in avian biology. Univ. Illinois Press, Urbana. 479pp.

HOFFMANN, R. S. 1958. The role of predators in "cyclic" declines of grouse populations. J. Wildl. Manage. 22(3):317–319.

HUNTINGTON, E. 1931. The Matemak conference on biological cycles, 1931. Science 74 (1914):229–235.

———. 1945. Mainsprings of civilization. Wiley, New York. 660pp.

KEITH, L. B. 1963. Wildlife's ten-year cycle. Univ. Wisconsin Press, Madison. 201pp.

———. 1974. Some features of population dynamics in mammals. Int. Cong. Game Biol. 11:17–58.

KROGDAHL, W. S. 1962. The astronomical universe. 2nd ed. Macmillan, New York. 585pp.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343pp.

———. 1966. Population studies of birds. Clarendon Press, Oxford. 341pp.

MACLULICH, D. A. 1957. The place of chance in population processes. J. Wildl. Manage. 21 (3):293–299.

MACMILLAN, D. H. 1966. Tides. American Elsevier Publishing Co., New York. 240pp.

MARSHALL, W. H. 1954. Ruffed grouse and snowshoe hare populations on the Cloquet Experimental Forest, Minnesota. J. Wildl. Manage. 18(1):109–112.

MCLAUGHLIN, D. B. 1961. Introduction to astronomy. Houghton Mifflin, Boston. 463pp.

MORAN, P. A. P. 1949. The statistical analysis of the sunspot and lynx cycles. J. Anim. Ecol. 18(1):115–116.

———. 1953. The statistical analysis of the Canadian lynx cycle. I. Structure and prediction. Aust. J. Zool. 1(2):163–173.

PETTERSSON, O. 1912. The connection between hydrographical and meteorological phenomena. Quart. J. Roy. Meteor. Soc. 38(163):173–191.

ROWAN, W. 1950. Canada's premier problem of animal conservation: a question of cycles. New Biol. 9:38–57.

RUSCH, D. H., AND L. B. KEITH. 1971. Seasonal and annual trends in numbers of Alberta ruffed grouse. J. Wildl. Manage. 35(4):803–822.

SCHORGER, A. W. 1947. The ruffed grouse in early Wisconsin. Trans. Wisconsin Acad. Sci., Arts, Letters 37:35–90.

SIIVONEN, L., AND J. KOSKIMIES. 1955. Population fluctuations and the lunar cycle. Finnish Game Found., Pap. Game Res. 14. 22pp.

HERBERT L. ARCHIBALD, Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907.