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The Enigma of the 10-year Wildlife Population Cycle Solved? Evidence that the Periodicity and Regularity of the Cycle Are Driven by a Lunar Zeitgeber

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Despite nearly 100 years of research, the periodicity and regularity of the 10-year wildlife population cycle remain an enigma. This paper presents the hypothesis that the 9.3-year nodal half-cycle of the moon is the zeitgeber ("time-giver") of the 10-year wildlife population cycle. The period of the population cycles of the Snowshoe Hare (*Lepus americanus*) and Ruffed Grouse (*Bonasa umbellus*) is close to 9.3 years. These wildlife cycles have stayed closely in phase with the 9.3-year nodal half-cycle for 150 years. Population density of the Snowshoe Hare and Ruffed Grouse is inversely related to a 9.3-year cycle of the moon's tidal force. There is also a 9.3-year cycle of "nights without darkness" at the equinoxes, in which the full moon rises before sunset and sets after sunrise the following morning in certain years. Snowshoe Hare and Ruffed Grouse cycles are positively correlated with this phenomenon. The nodal cycle provides explanations for the key features of the 10-year wildlife cycle: regularity, periodicity, amplitude, distribution, and synchrony. Population models based solely on the nodal cycle account for 62% of the variation in the Canada Lynx (*Lynx canadensis*) cycle and 37% in the Ruffed Grouse cycle. The mechanism(s) by which herbivore cycles might be entrained by the lunar nodal cycle could involve a cyclic effect on factors including predation, stress, photoperiod, phenology, temperature, cloudiness, ultraviolet B radiation, cosmic rays, and food plant quality.

Key Words: 10-year wildlife cycle; lunar nodal cycle; Snowshoe Hare; *Lepus americanus*; Ruffed Grouse; *Bonasa umbellus*; Canada Lynx; *Lynx canadensis*

Introduction

The 10-year wildlife cycle has been described as an "extraordinary precise metronome" by ecological, if not celestial, standards (King and Schaffer 2001). Yet, despite nearly 100 years of research, the periodicity and regularity of the 10-year wildlife cycle remain an enigma. "The key question of how the 10-year cyclic pattern is produced is still unsolved" (Yan *et al.* 2013).

Numerous hypotheses, involving both endogenous (e.g., disease, predation, food abundance) and exogenous (e.g., weather, sunspots, ultraviolet radiation) causes, have been proposed to explain the cycle (see summaries in Murray [2003] and Zimmerman *et al.* [2008]). Cyclic declines in Ruffed Grouse (*Bonasa umbellus*) have been attributed to increased predation because of a predator shift following decreases in Snowshoe Hare (*Lepus americanus*) numbers (Keith 1963), but this hypothesis has been challenged because Ruffed Grouse tend to peak and decline before Snowshoe Hare (Hoffmann 1958). The prevailing endogenous hypothesis is that the Snowshoe Hare cycle results from the tritrophic interaction between predation and food supplies, with predation as the dominant factor (Krebs *et al.* 2001). In his review, Rusch (1989) concluded that predation, primarily avian, is responsible for virtually all grouse mortality and the cyclic trend in grouse populations. In their classic paper, Elton and Nicholson (1942) concluded that the broad synchronization of the Canada Lynx (*Lynx canadensis*) cycle "makes it certain that some overriding process maintains the cycle in line over

the whole extent of Canada." In his plant stress hypothesis, Selas (2006) posited that the Snowshoe Hare cycle is forced by the sunspot cycle, through its effects on plant productivity caused by changes in ultraviolet B (UVB) radiation. Sinclair *et al.* (1993) hypothesized that Snowshoe Hare cycles are synchronized by the sunspot cycle via its effect on climatic factors. However, a causal relationship between sunspots and the Canada Lynx cycle has been rejected on a statistical basis (Moran 1949; Lindstrom *et al.* 1996). Nilssen *et al.* (2007) demonstrated that the 11-year sunspot cycle cannot explain the 10-year cycle of the Autumnal Moth (*Epirrita autumnata*) in Fennoscandia because the two cycles ran in-phase and then completely out of phase during a 114-year period.

Murray (2003) suggested the possibility that an exogenous factor could entrain or synchronize a cycle that is driven by endogenous forces. Yan *et al.* (2013) concluded that the 10-year hare–lynx cycle is the result of the joint forces of both endogenous and exogenous factors. The ideal exogenous cycle candidate would have a consistent period that matched the wildlife cycle and would shed light on its other unexplained features.

Snowshoe Hare and Canada Lynx populations tend to cycle synchronously across the boreal forests of Canada and Alaska (Krebs *et al.* 2001). Recent explanations of the spatial synchrony of 10-year-cycle species across large geographic regions have generally focused on common weather or climatic perturbations (i.e., Moran effect), dispersal, migration of natural enemies

(Liebhold *et al.* 2004), or a combination thereof. Krebs *et al.* (2013) concluded that the mobile predator hypothesis offers the most likely explanation of the synchrony and traveling waves of hare populations across northwestern North America. Analysis of the spatial synchrony of Canada Lynx populations revealed three large climatic regions in which the phase synchrony is similar, with the continental region 1–2 years ahead of the Pacific and Atlantic (Stenseth *et al.* 1999, 2004). These authors concluded that external climatic forcing associated with the North Atlantic Oscillation acts as a synchronizer within each region, but they offer no explanation for the inter-regional timing of the cycle. Krebs *et al.* (2013) rejected the "attractive" hypothesis that regional weather synchronizes local Snowshoe Hare populations because of the lack of a mechanism whereby weather could drive hare numbers.

The path of the moon across the sky is complicated by its nodal cycle. The 18.6-year lunar nodal cycle gives rise to year-to-year differences in both tidal force and the moon's "altitude" (angle or height in the sky above the horizon). The tidal force of the moon is the difference between the moon's gravitational force on the side of the earth closest to the moon and that on the side farthest from the moon (Kutner 2003). The moon and the sun produce maximum tidal forces at the equinoxes when lunar "declination" (angle relative to the equator) is zero, which happens twice during the nodal cycle or every 9.3 years, and when the sun is directly above the equator, so that solar declination is zero (Pugh 1966). Because the moon's orbit is inclined 5.1° to the earth's orbit (also known as the "ecliptic"), the declination of the moon's orbit ranges from a minimum of 18.3°N and S every lunar month to a maximum of 28.6°N and S every month during the 18.6-year period of the nodal cycle. What the observer at 55°N latitude would see is variation in the moon's altitude from as little as a high of 53.5° and a low of 16.5° two weeks later (monthly swing of 37°) to, 9.3 years later, as much as a high of 63.5° and a low of 6.5° (monthly swing of 57°).

Although the nodal cycle has been known at least as far back as Stonehenge, the biological significance of the 9.3-year nodal half-cycle remains virtually unknown. Archibald (1977) hypothesized that the length and regularity of the period, approximate regional and inter-specific synchrony, and northern geographic distribution of the 10-year wildlife population cycle arise from the 9.3-year half period of the moon's 18.6-year nodal cycle. This hypothesis has been largely ignored or dismissed as a nonsense correlation (Royama 1992), perhaps because Archibald did not provide any evidence of biological effects of the 9.3-year lunar cycle or plausible mechanism. Selas (2014) proposed a new variation of the plant stress hypothesis involving modulation of cosmic rays by a 9.3-year cyclic "lunar index" (i.e., maximum declination cycle) and the 11.1-year sunspot cycle. According to Selas, a low lunar index (i.e., maximum tidal force) increases geomagnetic activity, which reduces incoming cosmic ray particles, which increase protein mobilization and reduce production of secondary metabolites in plants, thereby increasing herbivore forage quality and, hence, enhancing herbivore performance.

The objective of this paper is to present evidence supporting the hypothesis that the 9.3-year half period of the lunar nodal cycle is the zeitgeber (literally "time-giver") of the 10-year wildlife cycle and to speculate on mechanisms by which herbivore cycles might be entrained by the lunar nodal cycle.

Methods

I compiled reports of peaks in Snowshoe Hare and Ruffed Grouse abundance (Table 1) from nine sets of data (Table 2) of several types: density surrogates, such as annual fur returns (MacLulich 1957) or spring drumming counts (Williams *et al.* 2004; Minnesota DNR 2011); simple lists of peak years in an area (Shorger 1947); and lists of peak abundance for multiple locations (Keith 1963; Hodges 2000a,b). In decades where there were two or three consecutive years of similarly high population reported in a dataset or occurring in a species, the median was used as the value of the peak year. None of these datasets is precisely accurate; all have flaws and biases of various kinds. Also, peak years are not directly comparable across species because data are based on different types of records and are from different regions. Nevertheless, the mean peak years computed by averaging across species provide a broad-scale, general picture of the timing of cycle peaks over large geographic areas during the 150-year period covered.

Predicted peak years of abundance in Table 1 were computed using the formula $P_n = 1950.22 \pm 9.3n$, where P_n is the nth peak year after or before 1950.22 (date of the vernal equinox of 1950 when lunar declination reached a peak value, which happens only once in each 18.6-year nodal cycle) and 9.3 is the period of the population cycle (Archibald 1977).

Sun and moon rise and set times were obtained from the Astronomical Sky Calendar (www.briancasey.org/artifacts/astro/skycalendar.cgi) and from the United States Naval Observatory's Complete Sun and Moon for One Day website (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). The number of minutes the full moon was above the horizon at both dusk (moonrise before sunset) and the following dawn (moonset after sunrise) were computed for April and September. Lunar declination data were obtained from the Jet Propulsion Laboratory Horizons Web-Interface (http://ssd.jpl.nasa.gov/horizons.cgi#top). Over the course of the lunar nodal cycle, the moon's declination varies about 5.1° above and below the ecliptic. For each year, the absolute value of the maximum declination from the ecliptic in the equinox month of September was determined at 50°N, 90°W, i.e., absolute value (reported declina-

TABLE 1. Reported and predicted peaks in abundance of the Showshoe Hare (*Lepus americanus*) and the Ruffed Grouse (*Bonasa umbellus*) in northern North America.

| Reported peak years of abundance | | | | |
Snowshoe Hare	Ruffed Grouse	Mean peak year	Predicted peak years	Difference* (years)
2006.0	2009.0	2007.5	2006.0	1.5
1998.0	1998.5	1998.2	1996.7	1.5
1989.2	1989.0	1989.1	1987.4	1.7
1980.0	1979.2	1979.6	1978.1	1.5
1970.8	1971.8	1971.3	1968.8	2.5
1959.8	1959.5	1959.6	1959.5	0.1
1951.5	1949.2	1950.4	1950.2	0.2
1941.6	1941.2	1941.4	1940.9	0.5
1932.2	1932.6	1932.4	1931.6	0.8
1923.6	1922.6	1923.1	1922.3	0.8
1912.4	1914.2	1913.3	1913.0	0.3
1904.1	1904.6	1904.4	1903.7	0.7
1896.0	1898.0	1897.0	1894.4	2.6
1886.5	1887.0	1886.8	1885.1	1.7
1876.0	1877.0	1876.5	1875.8	0.7
1865.0	1866.0	1865.5	1866.5	−1.0
1857.0	1857.0	1857.0	1857.2	−0.2
Mean (SD)				0.9 (0.91)
Mean period	9.3	9.5	9.4	

Note: SD = standard deviation.
*Between reported and predicted peak years.

TABLE 2. Sources of the reports of peak abundance listed in Table 1.

Species	Date range	Reference	Location	Source type
Snowshoe Hare	1857–1899	MacLulich (1957: 296)	Hudson's Bay Watershed	Fur returns
	1900–1955	Keith (1963: 42)	Northern North America	Peak abundance (median years)
	1956–1992	Hodges (2000a: 119–120)	Canada, Alaska	Peak abundance (median years)
	1956–1992	Hodges (2000b: 166–168)	Minnesota, Wisconsin, Manitoba	Peak abundance (median years)
	1993–2011	Krebs (2011: 6)	Yukon Territory	Density on study area
Ruffed Grouse	1857–1899	Schorger (1947: 54)	Wisconsin	Peak years of abundance
	1900–1951	Keith (1963: 57)	Northern North America	Peak abundance (median years)
	1949–2010	Minnesota DNR (2011: 45)	Minnesota	Drumming counts
	1956–2001	Williams *et al.* (2004: 1138)	Northern Wisconsin, North Dakota	Drumming counts

tion -23.5°). September maximum lunar declination and April and September total minutes full moon above horizon were compared for two population datasets: Ruffed Grouse spring drumming counts conducted in Minnesota from 1949 to 2010 (Minnesota DNR 2011) and spring Snowshoe Hare density in the Kluane region of Yukon Territory (Krebs 2011).

Population modeling and preparation of figures were done using SciDaVis (http://scidavis.sourceforge.net/) software. Modeling results were compared with 1949–2010 Minnesota drumming counts and 1842–1918 Canada Lynx fur returns from the Northern Department (Elton and Nicholson 1942). The classic lynx time series is arguably the best example of a near-perfect population cycle with a minimal amount of noise. This dataset was not used, however, for the peak years of abundance analysis (Table 1) because populations of Canada Lynx are not independent of populations of their main prey, the Snowshoe Hare.

Correlation between population size and lunar declination was measured with least squares regression using software supplied by Wessa (Free Statistics Software, Office for Research Development and Education, version 1.1.23-r7, www.wessa.net), even though the assumption of independence of observations in each time series is clearly violated (Liebhold *et al.* 2004).

The inadequacy of currently available correlational measures was pointed out by Liebhold *et al.* (2004): "for cyclic populations, subtle differences in the timing of cycles... may result in low statistical correlation even when populations are closely linked."

Results

The period of the cycles of the Snowshoe Hare and Ruffed Grouse shown in Table 1 is close to 9.3 years: 9.3 and 9.5 years, respectively. Selas (2014) demonstrated that the periods of both the Canada Lynx and the Autumnal Moth cycles are very close to the 9.3-year lunar nodal half-cycle. One point that seems to have been overlooked in the literature, however, is how critical the period length is. For example, if you spin backward from 2006.0 (when lunar declination reached a peak value seen only once in each 18.6-year nodal cycle) using the 9.6-year period suggested by Elton and Nicholson (1942) and Krebs *et al.* (2001), the predicted peak year 15 cycles back is 1862.0, which is almost completely out of phase with the lunar peaks in 1857.2 and 1866.5. In contrast, after 15 cycles back using the 9.3-year period, reported and predicted peaks remain in phase, with the mean herbivore peak of 1857.0 coinciding with the lunar peak at 1857.2. To become completely out of phase, a difference of 0.2 years/cycle (i.e., a period of 9.1 or 9.5 years) takes about 23 cycles (or about 214 years) and a difference of 0.1 years/cycle (i.e., a period of 9.2 or 9.4 years) takes about 46 cycles (or about 428 years); sufficient data are not available to evaluate either of these cases.

For over 150 years, reported years of peak abundance of Ruffed Grouse and Snowshoe Hare have persistently stayed in phase with predicted peak years based on the lunar model $P_n = 1950.22 \pm 9.3n$ (Archibald 1977), differing by an average of 0.9 years (Table 1). Differences between mean reported and predicted peak years appear to have become larger after about

1965, with the reported peaks consistently lagging behind the predicted peaks.

9.3-year lunar declination cycle

The 9.3-year cycle in the maximum lunar declination from the ecliptic in absolute value at the equinoxes is shown in Figure 1. The alternating higher declination peaks are years when the moon's maximum declination runs below the ecliptic. Semidiurnal (result in two high tides and two low tides per day) and diurnal (result in one high and one low tide per day) tidal factors oscillate in 18.6-year cycles, 180° out of phase, with diurnal factors largest when lunar declination is highest (1950, 1968, 1987, 2006) and semidiurnal factors highest when lunar declination is minimal (1959, 1978, 1997) (McKinnell and Crawford 2007). The semidiurnal lunar forces are 23% less when the moon reaches its maximum declination of 28.6°. The solar semidiurnal forces are reduced by 16% when the sun is at its maximum declination of 23.5° at the solstices (Pugh 1996). To sum up, tidal forces reach a maximum when the moon is in the equatorial plane (i.e., at zero declination from the ecliptic), which happens twice during the 18.6-year nodal cycle or every 9.3 years.

9.3-year moonlight cycle

The full moon can be above the horizon both before dusk and after dawn the following morning, resulting in a "night without darkness" with light levels no lower than full moonlight. This can occur on two successive nights and in several months in a row. The nodal cycle causes an 18.6-year cycle of total minutes that the full moon is above the horizon both before dusk and after the following dawn at the full moon nearest the autumnal equinox (light bars in Figure 1). The westward regression of the lunar nodes from the autumnal equinox to the vernal equinox takes 9.3 years. Then, there is a corresponding 18.6-year cycle of total minutes that the full moon is above the horizon both before dusk and
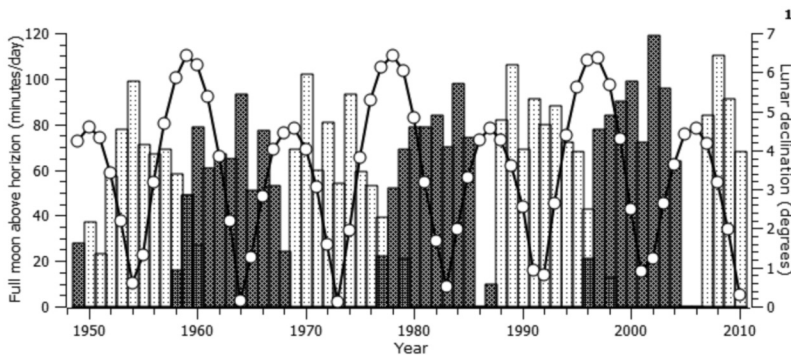

FIGURE 1. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day) and maximum lunar declination (open circles) in September relative to the ecliptic in absolute value (50°N, 90°W).

after the following dawn during the full moon nearest the vernal equinox (dark bars in Figure 1). Therefore, this phenomenon occurs every 9.3 years, alternating between the vernal and autumnal equinoxes. Nights without darkness occur multiple times in the years at or near the peak of the cycle. For example, in the September peak year 1991, there were nine nights without darkness: July 26, August 24–25, September 23–24, October 22–23, November 21, and December 20. Although the midnight sun near the summer solstice at higher latitudes is well known, there appears to be nothing in the literature about this nights-without-darkness phenomenon at the equinoxes. The only information I have found so far about "sun and full moon both up" are some anecdotal reports of confused homing pigeons flying in the wrong direction, perhaps because they mistook the rising full moon for the sun. The 9.3-year moonlight cycle is inversely related to the 9.3-year lunar declination cycle (Figure 1).

Correlations with 10-year wildlife population cycles

Ruffed Grouse drumming counts in Minnesota are positively correlated ($r^2 = 0.26$, $P < 0.001$, with 1-year lag) with September maximum lunar declination (Figure 2) and, therefore, inversely related to the moon's tidal force. During the equinox months of September and March, full and new moons always coincide with minimum lunar declination (moon over the earth's equator) (Brahde 1988). There is some tendency for grouse peaks to alternate in amplitude (i.e., every other peak is a "high" peak) (Archibald 1977). High grouse peaks are associated with years when the moon's maximum declination runs *above* the ecliptic. Because the zeitgeber effect of the 9.3-year nodal half-cycle "need not occur in more than 2–3 consecutive years per decade" (Archibald 1977), interpretation of correlation coefficients (which cover all years) is problematic.

Snowshoe Hare density in the Yukon Territory is also directly correlated ($r^2 = 0.41$, $P < 0.001$, with 2-year lag) with September maximum lunar declination and inversely correlated with the moon's tidal force (Figure 3). There is also a tendency for hare population peaks to alternate in amplitude (Archibald 1977); higher peaks coincide with years when the moon's maximum declination runs *below* the ecliptic.
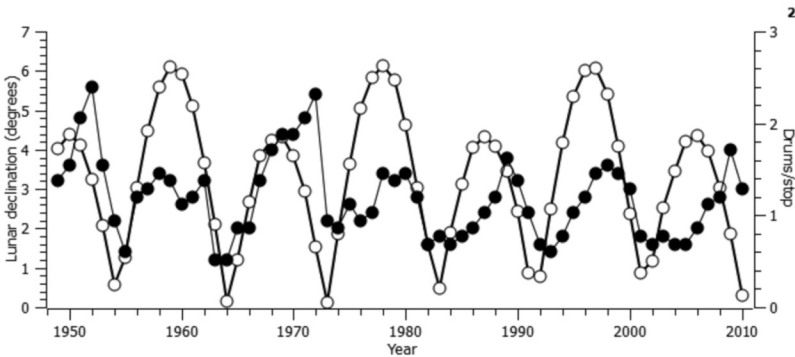

FIGURE 2. Maximum lunar declination (open circles) in September relative to the ecliptic in absolute value (50°N, 90°W) compared with spring drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949–2010 (Minnesota DNR).
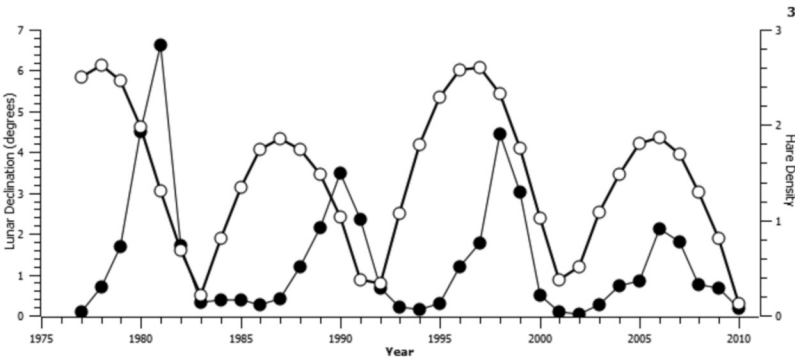

FIGURE 3. Maximum lunar declination in September (open circles) relative to the ecliptic in absolute value (50°N, 90°W) compared with spring Snowshoe Hare (*Lepus americanus*) density (closed circles) in the Kluane region of the Yukon Territory, 1977–2010 (Krebs 2011).

The cyclic nights-without-darkness phenomenon at the equinoxes generally starts to increase 1–2 years before the Snowshoe Hare peak; it peaks during the hare decline and stays relatively high throughout the hares' low phase (Figure 4). The inverse relation between Snowshoe Hare density and nights without darkness during the low phase is intriguing because explanation of the low phase remains a puzzle (Krebs *et al.* 2001). Similar to hare density, nights without darkness generally increase following an increase in Ruffed Grouse density and stay relatively high during the ensuing low (Figure 5).

Ruffed Grouse population model

The following model of Ruffed Grouse drumming is based on a single exogenous factor, the nodal cycle of the moon:

$$\text{Drums/stop}(t) = 1.27 + 0.55\sin(2\pi)/9.307 * (t-1) + 1.41)$$
$$+ 0.55\sin(2\pi)/18.6134 * (t-1) + 0.90\pi)$$

Where t is the year (yyyy) with 1-year lag; 9.307 and 1.41 are the period and phase angle of the nodal phase cycle, respectively; 18.6134 and 0.90 are the period and phase angle of the nodal amplitude cycle (Yndestad 2009); 1.27 is the amplitude; and 0.55 is half the range of observed Minnesota drumming counts.

The model output matches the observed Ruffed Grouse cycle fairly well ($r^2 = 0.39$, $P < 0.001$), in both period and alternating amplitude (Figure 6).

Canada Lynx population model

$$\text{Furs/year}(t) = 20800 + 16540\sin(2\pi /9.307 * t + 1.41\pi)$$
$$+ 16540\sin(2\pi /18.6134 * (t-9.307) + 0.90\pi)$$

Where t is the year (yyyy) with no lag on the 9.3-year phase cycle and a lag of 9.307 years on the 18.6-year amplitude cycle (to offset the higher peaks); 9.307 and 1.41 are the period and phase angle of the nodal phase cycle, respectively; 18.6134 and 0.90 are the period and phase angle of the nodal amplitude cycle (Yndestad 2009), 20800 is the amplitude and 16540 is half the range of observed Northern Department lynx fur returns between 1842 and 1918 (Elton and Nicholson 1942).
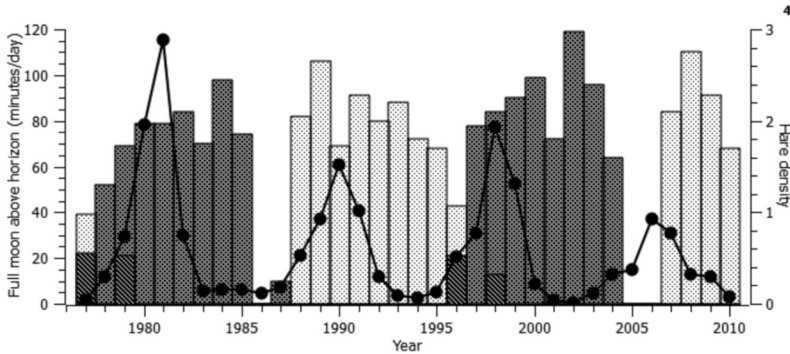

FIGURE 4. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day; 50°N, 90°W) compared with spring Snowshoe Hare (*Lepus americanus*) density (closed circles) in the Kluane region of the Yukon Territory, 1977–2010 (Krebs, 2011).
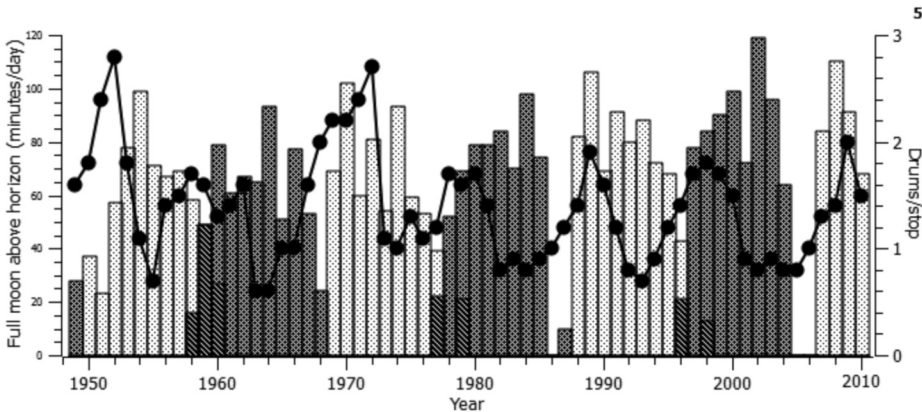

FIGURE 5. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day; 50°N, 90°W) compared with spring drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949–2010 (Minnesota DNR 2011).
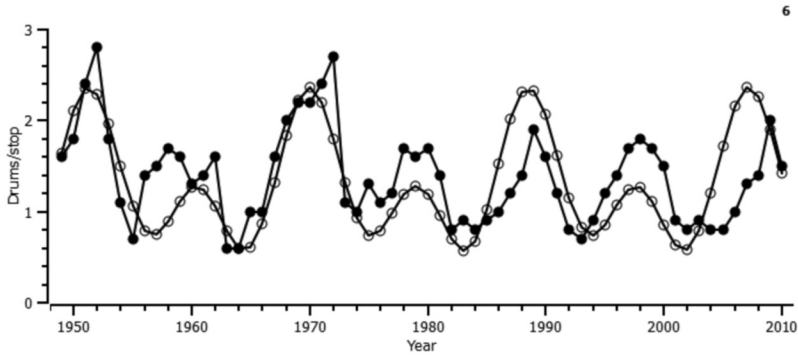
FIGURE 6. Spring drumming counts (open circles) predicted by the lunar model compared with observed drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949–2010 (Minnesota DNR 2011).
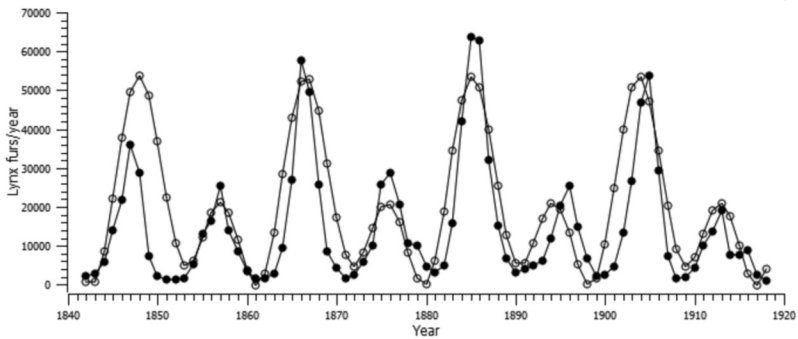

FIGURE 7. Canada Lynx (*Lynx canadensis*) fur returns predicted by lunar model (open circles) compared with observed Canada Lynx fur returns (closed circles), Northern Department, 1842–1918 (Elton and Nicholson 1942).

The model output matches the "classic" Canada Lynx cycle quite well ($r^2 = 0.62$, $P < 0.001$) in both period and alternating amplitude over the period 1842–1918 (Figure 7). Note that additional decimal places in the period values were used in the Rugged Grouse and Canada Lynx population models because the formulas are very sensitive to small differences in period length.

Discussion

Key cycle features accounted for

King and Schaffer (2001) list five important features of the 10-year wildlife cycle, and a definitive explanation for the cycle should account for all five points. The 9.3-year half period of the nodal cycle hypothesis provides a plausible explanation of each of these five features:

1. *Regularity:* Reported peak population years have stayed in phase with predicted peaks based on the 9.3-year lunar cycle for over 150 years (Table 1).
2. *Period:* The overall mean cycle period (9.4 years) is close to the 9.3-year period of the lunar cycle (Table 1).
3. *Amplitude:* Peaks in the Snowshoe Hare cycle tend to alternate in amplitude (Archibald 1977).

The trend is evident in the Hudson's Bay data from 1857 to 1896 (MacLulich 1957) and a century later at Kluane Lake (Figure 3). Schaffer (1984) noted alternating amplitude in the Canada Lynx cycle from 1821–1913. Higher peaks in the hare-lynx cycle are associated with vernal equinox peaks in the lunar cycle (Figure 4) and maximal semidiurnal tidal factors. Ruffed Grouse peaks also tend to alternate in amplitude but higher peaks in the grouse cycle are associated with autumnal equinox peaks in the lunar cycle (Figure 5), when the moon's maximum declination runs above the ecliptic (Figure 2) and diurnal tidal factors are largest.

4. *Distribution:* The 10-year cycle is a northern phenomenon restricted to latitudes above 45–50°N in North America (Archibald 1977) and even higher latitudes in northern Europe. Northern populations of Snowshoe Hares and Ruffed Grouse are cyclic, while more southerly populations exhibit little or no periodicity (Rusch 1989; Murray 2003). Several effects of the lunar nodal cycle increase significantly with latitude. For example, the full moon was above the horizon at both dusk and dawn on the night of April 29–30,

1999, for a total of 71 minutes at 40°N, 90 minutes at 50°N and 131 minutes at 60°N. Latitude is an important factor governing both the species (semidiurnal and diurnal) and maximum amplitude of tides (Pugh 1996).

5. *Synchrony:* Regional synchrony of populations over wide geographic areas has been reported for both Snowshoe Hare and Ruffed Grouse (Keith 1963), and population levels of these species tend to be closely aligned within the same areas, with peaks predominantly 1 year apart (Keith 1963). Selas (2006) found transatlantic synchrony in Snowshoe Hare/Mountain Hare (*Lepus timidus*) and Canada Lynx/Eurasian Lynx (*Lynx lynx*) series, suggesting that the cycles are triggered by a common large-scale phenomenon. Synchrony is to be expected under a lunar cycle hypothesis, because lunar phenomena, such as height in the sky, rise and set times, and gravitational pull are similar worldwide at a given latitude, varying only because of such factors as elevation and topography.

Population modeling

King and Schaffer (2001) developed a tri-trophic population dynamics model of the Snowshoe Hare cycle with browse, hare, and predator density as dependent variables and 14 parameters (but no weather factors). They concluded that the increase phase is halted by food limitation and the decline from peak numbers is due to predation. Yan *et al*. (2013) used two-level population models with rate of change of hare and lynx as dependent variables and either global weather indices or local temperature, rainfall, and snowfall with various time lags. Their simulations showed that predation and direct, as well as delayed, density dependency are necessary, but not sufficient, factors for the appearance of 10-year hare–lynx cycles and that external climatic forcing through rainfall and snowfall are essential to produce 10-year cycles.

Zimmerman *et al*. (2008) used comparative model selection to assess the correlation of numerous combinations of 13 hypothesized factors with spring drumming counts for grouse in northeastern Minnesota over a 22-year period. The hypothesized factors included goshawk abundance (predation), Eastern Tent Caterpillar (*Malacosoma americanum* [Fabricius, 1793]) abundance (aspen defoliation), weather during the breeding season, weather during the previous winter, colour phase ratios (phenotypic hypothesis), fall age ratios (recruitment), and male grouse weight (condition entering winter). The best model indicated that grouse abundance was highest during cold snowy and warm dry winters, presumably related to optimal snow-roosting conditions during periods of extreme cold. As the best model accounted for only 17% of the variation in drumming counts, these authors concluded that several interacting factors most likely cause the cycle but the mechanism remains unknown.

Using a multiple regression model, Selas (2014) found that a maximum September lunar declination index (3-year lag), March–April North Atlantic Oscillation, previous August–October North Atlantic Oscillation and sunspot numbers accounted for 38% of the variation in an Autumnal Moth index from Fennoscandia covering 113 years. A similar model, which used the Pacific–North American index instead of the North Atlantic Oscillation, accounted for 23% of the variation in a Canada Lynx population index for the period 1950–2009.

The Canada Lynx model presented here, with just the 9.3- and 18.6-year lunar parameters, accounted for 62% of the variation in the Northern Department fur returns over 77 years (Figure 7). The Ruffed Grouse model presented here accounted for 37% of the variation in the Minnesota Ruffed Grouse drumming counts over 62 years (Figure 6). This suggests that *both* the 9.3-year and 18.6-year nodal cycles play a significant role in lynx and grouse population dynamics. A prediction model with four lunar parameters including *both* the 9.3 and 18.6-year nodal periods accounted for 62% of the variation in strong-to-violent March–August tornadoes in the United States between 1950 and 2012 (Eppelbaum 2013). Schaffer's (1984) power spectrum analysis of Canada Lynx fur returns (1821–1913) showed a fundamental period of roughly 10 years and a second harmonic period of about 20 years. The obvious similarity in periods suggests that the "underlying determinism" this author sought could well be the 18.6-year nodal cycle and its 9.3-year sub-harmonic. Further research directed toward gaining an understanding of the interaction of the 9.3-year and 18.6-year nodal cycles is clearly needed. Also apparent from these model results is that, while density-dependence may well play a part in nature and is a critical component of prevailing models of cyclic populations, it is not necessary to closely mimic the cyclic population dynamics of the Canada Lynx and Ruffed Grouse.

Spatial synchrony

Regional synchrony is expected under a lunar hypothesis, and the problem to be reconciled is why the synchrony is not absolute (Krebs *et al*. 2001). Some asynchrony can be expected between even nearby populations because of differences in local conditions. Selas (2006) suggested that spatial asynchrony in hare cycles could result from asynchronous fluctuations in plant chemistry due to regional variations in UVB levels caused by differences in cloud formation or ozone distribution. If the zeitgeber effect of the lunar nodal half-cycle occurs for 3–4 years at the bottom of the cycle, more regional variation in the timing of the subsequent peak would be expected because of differences in local environmental conditions and food webs. But this explanation does not account for the tendency for synchrony of Snowshoe Hare populations to spread out from a north-central Canada in traveling waves.

Smith (1983) found that peaks in the Snowshoe Hare cycle began in a central Canada core area (Saskatchewan and Manitoba) and traveled outward in waves with 1-year and then 2-year phase lags in the peak year occurring with increasing distance. Selas (2014) found that the increasing phase lag of Canada Lynx population peaks moving away from the core area was significantly negatively related to cosmic radiation levels. In other words, Canada Lynx tend to peak first in areas of highest radiation (i.e. the "core area of the auroral oval"). Although it may be a contributing factor, the cosmic ray hypothesis seems an unlikely overall explanation for a metronomic population cycle because, first, the 9.3-year lunar cycle and the 11.1-year solar cycle will go completely in and out of phase every 103 years and, second, Selas found that the solar signal had a much stronger relation to geomagnetic activity than the lunar signal.

The earlier peaking in the core area could be due to the generally flatter topography of central Canada if the lunar zeitgeber effect on the Snowshoe Hare involves nights without darkness. The shadow effect of mountainous and hilly terrain can be expected to produce later actual rise and earlier actual set times resulting in nights without darkness occurring in fewer consecutive years (hence the lags) and with less biological impact.

Regarding the search for a mechanism, one initial question that arises is whether there is a single mechanism underlying all 10-year wildlife population cycles. Several observations suggest not. The 9.3-year cycles of the Autumnal Moth in Fennoscandia and the Douglas Fir Tussock Moth (*Orgyia pseudotsugata* [McDunnough, 1921]) in the Pacific Northwest are almost completely out of phase with the Snowshoe Hare and Ruffed Grouse cycles in North America (Archibald, unpublished data; Selas 2014), strongly suggesting a different mechanism. Also, the difference in peak amplitude alternation between the Snowshoe Hare and Ruffed Grouse cycles could result from a different mechanism.

"Correlation means little unless we see a plausible causal relationship" (Royama 1992). The two 9.3-year lunar cycles reported here provide the basis for speculative mechanistic explanations of the 10-year wildlife cycle. Other 9.3-year cycles resulting from the nodal cycle may await discovery. The 9.3-year moonlight cycle could have behavioural, physiological, chronobiological, or phenological effects. The 9.3-year declination cycle could have an impact on cyclic population dynamics through effects of oceanic and atmospheric tides on climatic factors, such as cloudiness and UVB and cosmic radiation, which, in turn, affect food plant quality.

Ruffed Grouse population peaks tend to follow maximum lunar declination by 1–2 years (Figure 2). And grouse lows are closely associated with minimum lunar declination, suggesting that the declination effect could be on food quality or palatability rather than directly on the grouse itself. The primary winter food of northern Ruffed Grouse is Trembling Aspen (*Populus tremuloides* Michaux) buds and aspen use is correlated with Ruffed Grouse density (Jakubas and Gullion 1991). These authors found that Ruffed Grouse consistently selected Trembling Aspen buds with relatively low levels of coniferyl benzoate and that high levels of this secondary metabolite were associated with declining or low grouse density. Captive Ruffed Grouse assimilated 24% less energy from aspen buds with high levels of coniferyl benzoate (Guglielmo *et al.* 1996). Jakubas and Gullion (1991) concluded that the impact of a shortage of suitable aspen in winter "may increase predation risks and energetic costs for Ruffed Grouse." It is interesting that, during four winters between 1985 and 1990, the coniferyl benzoate levels Jakubas and Gullion reported were highly correlated ($r^2 = 0.84$) with lunar declination.

Cloud conditions have more impact in terms of attenuating UVB radiation than stratospheric ozone, particularly at high latitudes (Svenoe *et al.* 1995). Pertsev and Dalin (2010) separated lunar-phase and lunar-declination effects on cloudiness; both were statistically significant with lunar declination somewhat stronger. They found a semi-monthly (13.66-day) variation in tropospheric nighttime cloudiness, with the relative amount of cloud increasing with an increase in lunar declination by absolute value. If this relation is extendable (Ray 2007) from the fortnightly half-period of the nodical month to the 9.3-year half-period of the nodal cycle, the maximum declination line in Figure 2 may also represent relative cloudiness. If so, then Ruffed Grouse density is correlated with attenuation of UVB radiation, which is generally thought to have a positive effect on food quality (van Asch and Visser 2007). The relation is particularly apparent at the Ruffed Grouse's cyclic lows, when exposure of food plants to UVB light is highest. Ayres (1993) linked reduced radiation resulting from increased cloud cover to reduced (average of 54%) secondary metabolites in food plants and their increased palatability to herbivores. In one study, Snowshoe Hares showed a strong preference for shaded Alaska Paper Birch (*Betula papyrifera* ssp. *humilis* [Regel] Hultén) shoots (Bryant *et al.* 1987). The mechanistic pathway suggested here is: increased lunar declination leads to increased cloudiness resulting in reduced UVB radiation and reduced secondary metabolites leading to increased herbivore use and higher herbivore density. This scenario is similar to the UVB plant stress hypothesis proposed by Selas (2006) as a possible cause of the Snowshoe Hare cycle, except that the driving force here is the 9.3-year lunar nodal cycle rather than the 11.1-year sunspot cycle and the intermediary is cloudiness rather than ozone.

Snowshoe Hare population peaks tend to precede maximum lunar declination by 1–2 years, and increasing hare abundance is closely aligned with increasing lunar declination (Figure 4). Like grouse, hare population lows are associated with minimum lunar decli-

nation, suggesting that maximum tidal force is detrimental, directly or indirectly, to both species. Sinclair *et al.* (1988) rejected a "fluctuating secondary compound hypothesis" to explain the Snowshoe Hare cycle because phenols declined through the increase and decline phases and increased during the low phase — exactly the opposite of what was predicted. Boonstra *et al.* (1998) posited that the low phase of the hare cycle might be related to deterioration in food quality because of the production of secondary plant defense compounds but dismissed this idea because of the failure of the fluctuating secondary compound hypothesis .

However, suppose that lower lunar declination (maximum tidal force) somehow raises the level of secondary metabolites in food plants above the threshold that the hare must stay beneath in order to grow, reproduce, and survive. In this case, the low phase of the hare cycle would continue until the lunar declination increases enough to exceed the threshold. Further study may clarify this issue.

The relative timing of the 9.3-year moonlight cycle and Snowshoe Hare density (Figure 4) suggests a possible mechanism for the Snowshoe Hare cycle, i.e., nights without darkness at the equinoxes produce a cyclic acceleration of the effects of key factors affecting the hare cycle: predation rate, predation risk, predator-induced stress, and nutritional deficiency. Predation is generally considered to be the driving factor in the hare cycle (Murray 2003). The rate of predation on Snowshoe Hares is higher when the moon is full (Griffin *et al.* 2005). Griffin and Mills (2009) found that weekly hare survival rates were about 2% lower in spring and fall compared with summer and winter rates. Spring and fall are the seasons when there is a possibility of a pelage–background colour mismatch resulting in heightened vulnerability to predation (Litvaitis 1991). The increased duration of moonlight near the peak of the 9.3-year lunar cycle can be expected to increase the time of elevated predation risk. Lima and Bednekoff (1999) suggested that animals should exhibit the greatest anti-predator behaviour in high-risk situations that are brief and infrequent. Snowshoe Hares forage almost exclusively in twilight and at night (Griffin *et al.* 2005). Lack of darkness after sunset could result in either delayed feeding or foraging restricted to areas of protective cover but lower quality food. In either case, the resulting reduced food intake may lead to declining body condition and reduced reproductive output (Boonstra *et al.* 1998). Rongstad and Tester (1971) found that the 5–10-minute daily return of Snowshoe Hares to care for their young appeared to be related to light intensity in the evening twilight period; this behaviour so crucial to juvenile survival could be affected by nights without darkness. Chronic predator-induced stress has been posited to decrease reproductive fitness during the peak and decline phases of the hare cycle (Boonstra *et al.* 1998; Krebs *et al.* 2001; Sheriff *et al.* 2010). Nights without darkness may contribute to increased stress due to conflict between predator avoidance and hunger.

The cyclic predation acceleration mechanism suggested for Snowshoe Hares may also be applicable to the Ruffed Grouse cycle (cf. Figures 4 and 5). In a large study of radio-marked grouse in northwestern Wisconsin, Lauten (1995) found that 96% of 341 known mortalities were due to predation or hunting. Bumann (2002) reported the highest predation rates in September, March, and April. Spring and fall are dangerous seasons for Ruffed Grouse; behaviour such as drumming, territorial defense, nesting, and dispersal are likely to increase predation risk at the same time that raptors are migrating. Rusch and Keith (1971) found that predation of adult males was highest during the spring and fall drumming periods. Archibald (1976) reported that moonlight was the major external factor stimulating drumming and found that nearly continuous nocturnal drumming occurred around the full moon in April. From fall to spring, however, Ruffed Grouse activity is highly crepuscular. Archibald (1973) found that late winter activity, which consisted mainly of travel to and from and feeding in aspen clones, peaked about 30 minutes before sunrise and almost precisely at sunset. Lack of darkness after sunset and before sunrise on nights without darkness could disrupt the timing, location, or duration of feeding resulting in nutritional deficiency, increased predation risk, or perhaps stress.

The lunar nodal cycle could also affect cyclic population dynamics through a cyclic impact on phenology. Temperature and photoperiod are the two most important phenological factors (van Asch and Visser 2007), and the lunar nodal cycle may play a role in both cases. First, cyclic nights without darkness at the equinoxes could confuse the perception of photoperiod. Bunning and Moser (1969) suggested that moonlight might interfere with photoperiodic time measurement in some plants and animals. Bowden (1973) posited that periods of continuous illumination at full moon could provide photoperiodic cues for insects. Interruptions in normal circadian light cycles and the resulting disruption of normal melatonin rhythms cause widespread effects involving reproduction, physiology, and behaviour (Navara and Nelson 2007). If nights without darkness at the equinoxes disrupt the circadian rhythms of Snowshoe Hares, there are several possible effects including timing of reproductive processes and molt. Change in day length is most rapid near the equinoxes and increases with latitude (e.g., ~5.5 minutes/day at 60°).

Second, there is growing evidence that climatic factors are influenced by the lunar nodal cycle. The surface climate of much of western and central Canada is strongly influenced by a large-scale atmospheric variation, the Pacific–North American (PNA) teleconnection (Mysterud *et al.* 2003). McKinnell and Crawford (2007) reported that the PNA index accounted for over

70% of the variation in average air temperature at and near Sitka, Alaska, in January. In addition, they found that the PNA index was significantly negatively correlated with the lunar nodal cycle with a 2-year lag. Yndestad (2006) found that the North Atlantic Oscillation winter index was correlated with the lunar nodal cycle. Meslow and Keith (1971) found that the onset of breeding in Snowshoe Hares was significantly correlated with the intensity of illumination (measured by cloud cover) during the previous midwinter. Major seasonal molts (which occur near the equinoxes) in the Snowshoe Hare are controlled by photoperiod (Murray 2003), whereas snow onset and disappearance are governed by temperature (Kielland *et al.* 2010). Because the nodal cycle may have a cyclic influence on both factors, there is an interesting possibility that the degree of pelage–background colour asynchrony from year to year may be cyclic as well. The lunar nodal cycle could conceivably affect Ruffed Grouse phenology through an effect on the timing of drumming, mating, or dispersal as well as the synchrony of hatching and chick food availability.

Recent research suggests that lunar declination may be an important factor in the ecology of northern latitudes. Ramos da Silva and Avissar (2005) found that the Arctic Oscillation has been "unambiguously correlated" with the 9.3- and 18.6-year oscillations of the lunar nodal cycle since the 1960s. Yasuda (2009) found a statistically significant 18.6-year periodicity, synchronized with the nodal cycle, in tree-ring chronologies in western North America over a 300-year period, and attributed this bi-decadal variability to tidal mixing. Several authors have reported 13.66-day (fortnightly) oscillations in Arctic tidal mixing, with maximum heat flux occurring at minimum lunar declination (Rogachev *et al.* 2001; Martin *et al.* 2004). According to Ray (2007), "the tidal mixing mechanism so plainly evident at near-fortnightly periods should extend in principle to the 18.6-year period." Li *et al.* (2011) found 13.6-day and 27.3-day oscillations in atmospheric pressure fields and atmospheric geopotential height (which is what climatic indices such as the PNA teleconnection and the North Atlantic Oscillation measure). The lunar forcing of these atmospheric tides reaches its maximum when the lunar declination is zero. Krahenbuhl *et al.* (2011) reported that the 27.3-day maximum lunar declination cycle influences upper tropospheric circulation by deforming high latitude Rossby waves, which are associated with the formation of weather systems. Foreman *et al.* (2006) estimated that the 18.6-year nodal modulation causes a 19% variation in the net incoming tidal energy flux of the Bering Sea basin. The 18.6-year lunar nodal cycle accounted for 59% of the variance in Pacific Halibut (*Hippoglossus stenolepsis*) recruitment from 1927 to 1983 (Parker *et al.* 1995). Based on wavelet analysis, Yndestad (2009) concluded that the biomass variability of zooplankton, capelin, cod, and herring in the Barents Sea was related to both the 18.6-year amplitude and the 9.3-year phase tide. So it seems possible that the climatic forcing that Yan *et al.* (2013) found necessary for successful modeling of the Canada Lynx cycle was actually the effect of the underlying lunar nodal cycle.

There is some evidence that the 10-year wildlife cycle has changed in recent years. Krebs *et al.* (2013) reported that the widespread regional synchrony of hare and lynx populations found in northwestern North America from 1970 to 1990 broke down after the mid-1990s. These authors found that Canada Lynx populations peaked in the early 1970s, 1980–81 and 1989–91, but there was no clear sign of a strong cyclic lynx peak after 1995. This study shows substantially greater differences between predicted and mean reported peak years after about 1965 (Table 1). Long-term monitoring of 10-year-cycle species is required to increase our understanding of cyclic phenomena (Krebs *et al.* 2013) and to assess possible links between changes in population cycles and global warming (Yan *et al.* (2013).

Just a coincidence?

Some ecologists will contend that the correlations presented here are merely a coincidence. The coincidence involves not only period but also phase: peaks of the Snowshoe Hare and Ruffed Grouse cycles are aligned with peaks of the nodal half-cycle. Period, phase, and amplitude of the Ruffed Grouse cycle in Minnesota and the "classic" Canada Lynx cycle in northern Canada can be mimicked by the lunar models presented. One school of ecological thought holds that experiments are the only way to separate causation from spurious correlation (Lambin *et al.* 2002). Unfortunately, the 9.3-year moonlight and lunar declination cycles are not subject to experimental manipulation in the field. Moreover, there does not appear to be any statistical method available to prove that the 9.3-year nodal half-cycle actually causes the timing of the 10-year cycle (Lindstrom *et al.* 1996; Berryman 2002). However, without invoking an exogenous zeitgeber, the persistent period, regularity, and synchrony of the 10-year cycle are difficult to explain convincingly. The 9.3-year moonlight cycle and 9.3-year lunar declination cycle are plausible causative factors. Previously, it was stated that the ideal exogenous factor candidate would have a consistent period that matched the wildlife cycle and would shed light on its other unexplained features. The 9.3-year nodal half-cycle of the moon meets these criteria. Unlike sunspots, the wildlife cycle has stayed in phase with the nodal half-cycle for 150 years despite major disruptive influences (e.g., Krakatoa) that might be expected to "affect the future course of the cycle and thus become incorporated into the future history of the series" (Moran 1953).

Acknowledgements

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