Relating the 4-year lemming population cycle to a 3.8-year lunar cycle and ENSO

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Relating the 4-year lemming population cycle to a 3.8-year lunar cycle and ENSO

Archibald, H.L.

632 Tee Hi Place, Medford, Wisconsin 54451 USA

Correspondence: herb.archibald@gmail.com

Tel: 1-715-748-6536

Archibald, H. L. 2019. Relating the 4-year lemming population cycle to a 3.8-year lunar cycle and ENSO
Abstract

Reported peak years of lemming (*Lemmus* spp. and *Dicrostonyx* spp.) and Arctic fox (*Vulpes lagopus* (Linnaeus, 1758)) abundance were compiled from the literature for 12 locations spanning 127 years. The mean period of the 34 reported lemming and Arctic fox cycles from 1868 to 1994 was 3.8 years, suggesting that the period of the 4-year cycle is actually 3.8 years. Peak population years were predicted using a simple model based on a 3.8-year lunar cycle. For nearly 130 years, reported years of peak abundance of lemmings and Arctic foxes were significantly correlated with and have persistently stayed in phase with predicted peak years of abundance. Over the same period, predicted peak years of lemming abundance have been closely aligned with peak (i.e., La Niña) years of the January-March SOI (Southern Oscillation Index). From 1952 to 1995, peak flowering in Norway tended to occur close to trough June-August SOI (El Niño) years. The hypothesis proposed is that the 3.8-year lunar cycle governs the timing of the lemming cycle but it does not cause the population cycling itself. If this hypothesis is true, the heretofore unexplained source of the persistent periodicity and quasi-metronomic regularity of the lemming cycle is identified.

**Keywords** 4-year population cycle, lemming (*Lemmus* spp. and *Dicrostonyx* spp.), Arctic fox (*Vulpes lagopus*), zeitgeber, population dynamics, lunar cycles, ENSO, Southern Oscillation Index (SOI)
Introduction

The persistent 4-year population cycle of lemmings (*Lemmus* spp. and *Dicrostonyx* spp.), voles (*Microtus* spp. and *Clethrionomys* spp.) and their predators, including the Arctic fox (*Vulpes lagopus* (Linnaeus, 1758)) and the snowy owl (*Bubo scandiacus* (Linnaeus, 1758)), is among the most fascinating puzzles in population ecology. Lemmings are keystone species in Arctic tundra ecosystems of northern North America and northern Eurasia (Krebs 2011). Lemmings typically undergo 4-year cycles of considerable amplitude, and populations can have significant impact on both tundra vegetation food resources and predator population reproductive success and survival (Reid et al. 2012). Despite over 90 years of intensive research, no consensus regarding the cause(s) of the periodicity, regularity, and persistence of the lemming cycle has yet emerged.

Population cycles can be driven by either extrinsic environmental factors (weather) or intrinsic density-dependent factors which can be either exogenous (food quantity/quality, predation, parasites, tritrophic [food + predation]) or endogenous (maternal effects, social interaction) (see Korpimaki and Krebs (1996: inset p.755) for a concise summary of cycle hypotheses). Cycles of northern lemming and vole populations are generally thought to result from the interaction of intrinsic factors (e.g. density-dependence) and extrinsic factors (e.g. climate) (Krebs 1996; Aars and Ims 2002; Kausrud et al. 2008).

To explain the extraordinary periodicity, regularity, and geographic and interspecific synchrony of both the 4-year and 10-year wildlife cycles, ecologists (e.g., Elton 1924, 1942; Moran 1953) have sought a powerful, over-riding, extrinsic controlling factor. Large-scale climate patterns such as ENSO (El Niño Southern Oscillation) and NAO (North Atlantic Oscillation) are “packages of weather” that often outperform individual weather variables in
explaining climate-related variation in animal numbers (Stenseth 2007). The ecological impacts of ENSO and the NAO include effects on terrestrial vegetation, herbivores and carnivores plus marine fisheries (see review by Stenseth et al. 2002).

ENSO is one of the most significant climatic phenomena, owing to its ability to change global atmospheric circulation, which in turn influences global temperature (L’Heureux 2014). The Southern Oscillation Index (SOI) is calculated from the normalized air pressure difference between Tahiti and Darwin, Australia. The SOI is a measure of the intensity of the El Niño (low negative values, warm, wet) and La Niña (high positive values, cold, dry) phases of ENSO. Zhang (2001) reported a nearly significant tendency ($p = 0.057$) for Norway lemming (*Lemmus lemmus* (Linnaeus, 1758)) peaks in Norway to occur in SOI peak years (average annual) or 1 year later from 1862 to 1894 but not in the whole 1862–1938 period examined. However, he did find evidence of significant associations between vole peak years and SOI peak years in France (1885-1930), northern Finland (1946-1992), and Poland (1946-1975). In this study, analysis of the relationship between lemming population peaks and ENSO was concentrated in two seasons thought to be particularly important influences on lemming population levels: January-March to reflect winter snow conditions and June-August to reflect food plant production.

Published values for lemming cycle periods include the following (in years): 3.4 (Framsted et al. 1997), 3.6 (Elton 1924: 115), 3.6 (Elton 1942: 426), 3.6 (Selås 2016), 3.69 (Gruyer et al. 2008), 3.8 (Kalela 1949), 3.85 (Elton 1942: 421), 3.86 (Wing 1962), 3.92 (Gruyer et al. 2008), and 4.0 (Gilg et al. 2009). The mean of 167 cycle lengths in Fennoscandia from 1862 to 1998, reported by Angerbjörn et al. (Figure 3: 2001), was 3.71 years.

Lemming cycles typically often have 4:4:3:4:4-year, 4:3:5:4:3-year, or similar pattern of intervals between peak years of abundance. Higher than normal or “spring” tides (which are
unrelated to season) occur when the sun, earth, and moon are in alignment, which happens only at full and new moon (i.e., syzygy). According to Wilson (2012) “Spring tides that occur on roughly the same day of the year follow a 4:4:3:4:4-year spacing pattern with an average spacing of \((4 + 4 + 3 + 4 + 4)/5 = 3.8\) years”. So there is a remarkable resemblance between the 4:4:3:4:4-year interval patterns of the lemming cycle and the 3.8-year peak spring tidal cycle.

The 24.8-hour lunar day and 29.53-day lunar month cycles produce several environmental cycles including tides, illumination levels, and geomagnetic fields (Kronfeld-Schor et al. 2013). For animals, these cycles affect predation risk, predator avoidance behavior, foraging timing and habitat use, and temporal synchronization of spawning and other reproductive behavior (see Kronfeld-Schor et al. 2013 for a review). These lunar cycles also affect the germination, growth, fruiting, water uptake, and leaf movement of plants (see Zurcher 2011 for review). Longer-term lunar cycles may also have biological significance. Population cycles of the Canada lynx (\textit{Lynx canadensis} (Kerr, 1758)), autumnal moth (\textit{Epirrita autumnata} (Borkhausen 1794)), snowshoe hare (\textit{Lepus americanus} (Erxleben, 1777)), and ruffed grouse (\textit{Bonasa umbellus} (Linnaeus, 1766)) have been linked to the 9.3-year half nodal cycle of the moon (a.k.a. lunar nodal phase cycle) (Archibald 1977; Selås 2014). Based on this correlation, Archibald (2014) hypothesized that the half lunar nodal cycle is the zeitgeber of the 10-year wildlife population cycle. Recently, Yasuda (2018) reported a statistically significant tendency for La Niña to occur in the 3rd, 12th, and 16th years after the maximum diurnal tide in the 18.6-year lunar nodal cycle over 148 years. This supported the connection between ENSO and the 18.6-year cycle suggested by Cerveny and Shaffer (2001).

The objectives of this paper are to 1) introduce a simple model based on the 3.8-year lunar cycle to predict the peak years of the lemming cycle, 2) compare predicted peak years with
reported peak years of lemming abundance and Jan-Mar values of the Southern Oscillation Index, 3) present the hypothesis that the 3.8-year lunar cycle is the zeitgeber (time-giver) of the 4-year lemming cycle, 4) speculate on mechanisms by which lemming cycles might be entrained by the 3.8-year lunar cycle. It is important to note that the hypothesis proposed here is that the 3.8-year lunar cycle governs the timing of the lemming cycle but it does not cause the population cycling by itself.

Methods

Data series were chosen to provide the most clear-cut long-term examples of regular, persistent 3–5-year cycling in lemming populations. The most complete long-term lemming population time series come from Fennoscandia and northern Canada, but the nature of the historical records from these regions is quite different. Records of lemming outbreaks in Fennoscandia date back to the 16th century (Angerbjörn et al. 2001), but there is practically no direct evidence concerning the periodicity of lemming fluctuations in northern Canada (Elton 1924) until nearly the middle of the 20th century (Elton 1942). However, since Arctic fox populations mirror the cycles of their dominant lemming and vole prey (Elton 1942; Henden et al. 2009), Hudson’s Bay Company fur returns for this predator dating back to the early 19th century were used here as a lemming proxy.

Reports of peaks of lemming and Arctic fox abundance (Table 1) were compiled for 12 locations (Table 2). The 12 location datasets used were selected to be representative, but the list is certainly not exhaustive. However, addition of more qualifying locations probably would not change the results of this study markedly. For example, the mean period of the 66 cycles in the five Fennoscandian locations from Angerbjörn et al. (2001) not included in Table 1 was 3.82 years. Henden et al. (2009) examined Norwegian county Arctic fox and red fox (Vulpes vulpes
bounty data from 1880 to 1976; the mean of the estimated period lengths of 28 clearly cyclic populations identified was 3.83 years. The most recent peak year included in Table 1 is 1994, which was the last lemming peak year (Kausrud et al. 2008) in southern Norway until 2006 (Ims et al. 2011). Collapse or dampening of population cycles of numerous species including northern lemmings and voles after 1994 may have altered the cyclic dynamics of these species as compared to the previous 100+ years (Ims et al. 2011; Cornulier et al. 2013) making their comparison problematic.

In the Northwest Territories, there was one instance of peak years falling only 2 years apart, which is not compatible with the 3.8-year block format of Table 1. So, rather than drop 1 peak year, 1971 and 1973 were averaged to create an artificial 1972 peak year. Where two consecutive years with similarly high populations were reported in a dataset, the mean was used as the value of the peak year. None of these datasets is precisely accurate; all have biases and flaws of various kinds. Also, peak years are not directly comparable between species because data are from different regions and are based on different types of records. Nevertheless, the mean peak years, computed by averaging between species, regions and continents, provide an unique picture of the timing of cycle peaks over large geographic areas during the nearly 130-year period covered.

Predicted peak years of abundance in Table 1 were computed using the lunar model $P_n = 1952.0 \pm 3.8n$, where $P_n$ is the nth peak year after or before 1952.0 (selected for best fit) and 3.8 is the period of the population cycle.

Monthly values of the SOI since 1868 were obtained from the Working Group on Surface Pressure (https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/SOI/). Sums of the January-March SOI values > 0 were used in the correlation with predicted peak lemming/Arctic fox
abundance in Table 1. Years with locally maximum SOI values were identified as SOI peak years; if there were two consecutive years with similarly high SOI values, the first was used as the value of the peak year (Zhang 2001). Sums of June-August SOI values < 0 were used in comparison with peak flowering years in Norway in Table 3.

A 2X2 contingency table analysis and Fisher’s exact probability test were used to determine whether both the mean reported years of peak lemming abundance and SOI peak years were significantly clustered within 0.8 years of predicted peak years. Statistical computations were performed using the VassarStats website (www.vassarstats.net).

To illustrate the 3.8-year recurrence of spring tides on or about the same calendar date, a syzygy (i.e., full or new moon) index based on the percentage of the moon illuminated (Orrock et al. 2004), which varies from 50 at full or new moon to 0 at first or last quarter, was employed. If the percent illuminated was > 50, the index was computed as $\text{Abs}(50 – \text{illum} \%)$. If percent illuminated was $\leq 50$, the index was $\text{Abs}(\text{illum} \% – 50)$. So the value of the syzygy index for the full moon is $100\% \text{ illum} – 50 = 50$, for the new moon is $\text{Abs}(0\% \text{ illum} – 50) = 50$, and for quadrature is $\text{Abs}(50\% \text{ illum} – 50) = 0$. The percentage of the moon illuminated on March 18–22 of each year was obtained from the Jet Propulsion Laboratory’s Horizons Web-Interface (http://ssd.jpl.nasa.gov/horizons.cgi#top). Illumination values for the 5 days around the vernal equinox were averaged for each year. Then, this average illumination value was used to compute the syzygy index for each year.

Results

The mean period of the 34 reported lemming and Arctic fox cycles shown in Table 1 is 3.8 years, providing evidence that the period of the 4-year cycle is actually 3.8 years. Selås (2016) found a 3.6-year periodicity in the lemming cycle from 1920 to 2014 on the
Hardangervidda plateau, which is located within the Norway Southwest region shown in Table 1. The mean period of Angerbjörn et al.’s (2001) Norway Southwest data from 1871 to 1994 is 3.85 years; if the small 1985 peak added by Selås (2016) is included, the mean period becomes 3.71 years. Period length is very critical: computing back from the predicted peak year 1993.8 using a period length of 3.7 years produces a predicted peak year 19 cycles back of 1923.5, which is completely out of phase (differing by 3.8 / 2 = 1.9 years) with the lunar peak years 1921.6 and 1925.4.

For nearly 130 years, reported years of peak abundance of lemmings and Arctic foxes have persistently stayed in phase with predicted peak years of abundance based on the lunar model \( Pn = 1952.0 \pm 3.8n \), differing by an average of only -0.01 years (Table 1). Mean reported peak years were consistently and regularly aligned with predicted peak years over the span of 34 cycles, separated by a mean interval of 0.53 years (Figure 1). In 31 out of 34 instances, mean reported peak years were within 0.8 years of predicted peak years (\( p < 0.0001 \)).

From 1871 to 1990, peak years of lemming and Arctic fox abundance predicted from the 3.8-year lunar cycle have consistently stayed in phase with peak years of the January-March SOI index, differing by an average of 0.32 years (Table 1). In 20 out of 28 instances, SOI peak years were within 0.8 years of the predicted peak years (\( p < 0.003 \)). But there were 6 (out of 34) 3.8-year blocks that did not contain an SOI peak year, yet there was a reported lemming/Arctic fox peak in all 34 blocks in Table 1. This shows that lemming/Arctic fox peaks tend to occur close to but are not forced by peak January-March SOI (La Niña) peaks. The mean period of the 23 intervals between successive January-March SOI peak years (Table 1) was 3.83 years. This suggests that the January-March SOI index is cyclic with a 3.8-year period.
The 12 years of peak flowering in Norway reported by Selås (1997: Figure 3) were all associated with negative June-August SOI index values (Table 3). Peak flowering years preceded peak lemming years by an average of 1.08 years, and 9 out of 12 flowering peaks occurred in June-August SOI trough years. This indicates that peak flowering in Norway tends (in 75% of the years) to occur close to trough June-August SOI (El Niño) years. The remaining 3 flowering peaks (1984, 1990, 1993) were within unusually long series of negative SOIs: 1982-3-4-5 and 1990-1-2-3-4. All 6 lemming peaks from 1977 to 1991 (Selås 2016: Figure 2) fell in the same or 1 year after flowering peaks, as expected, but only 2 out of 6 did so in the earlier years (1952–1974; Table 3).

**Discussion**

Davis (1976) suggested that detection of a zeitgeber could lead to significant advances in understanding cycles. The correlation between mean actual peak years and peak years predicted with the model $P_n = 1952.0 \pm 3.8n$ over 127 years (Table 1) suggests, but cannot prove, the hypothesis that the 3.8-year lunar cycle is the zeitgeber of the 4-year lemming cycle. This hypothesis is supported by the mean period of the 34 reported lemming and Arctic fox cycles shown in Table 1 being 3.8 years, providing evidence that the period of the 4-year cycle is actually 3.8 years. If this hypothesis is true, the heretofore unexplained source of the persistent periodicity and quasi-metronomic regularity of the lemming cycle is identified. It is important to stress that the hypothesis proposed here is that the 3.8-year lunar cycle governs the *timing* of the lemming cycle but it does not cause or force the population cycling itself.

The key features of a cycle are period, amplitude, and phase. One test of the hypothesized 3.8-year period is to experiment with other similar periods. A difference in period of just 0.1 years (i.e. 3.7 or 3.9) results in predicted peak years completely out of phase with the observed data after
19 cycles (19 X 0.1 years = 1.9 years, or half of the 3.8-year period). So, 3.8 is the only period in
the ~4-year range that fits the reported data. The question of why the phase-setting year 1952.0 in
the model $P_n = 1952.0 \pm 3.8n$ provided the best fit to the reported data remains unknown. But it is
clear that reported years of peak lemming abundance have persistently stayed in phase with
predicted peak years of abundance for nearly 130 years. Because this study concerns population
peak years only, it cannot tell us anything about the amplitude of the lemming cycle.

One of the many puzzling features of Norway lemming population dynamics in
Fennoscandia are the extended periods without a population peak in a particular region
(Angerbjörn et al. 2001; Table 1). Importantly, when cyclicity returns to a region, the peak
nearly always falls within 1 year of a predicted peak year based on the 3.8-year lunar cycle
(Table 1). This suggests that the lunar cycle determines the periodicity and regularity of
population peaks but does not cause peaks by itself. This phenomenon of missing peaks,
apparently absent in North America, is one of the many features of the 4-year lemming cycle that
remain to be explained by future research.

There was a lemming/Arctic fox peak in each of the 34 3.8-year blocks in Table 1. But
there were 6 3.8-year blocks with no Jan-Mar peak SOI value. So peak level SOI values are
usually associated with but are not necessary for peak lemming/Arctic fox abundance. In his
study of tidal influences on climate variability, Treloar (2002) found that the greatest SOI phase
shift values between 1850 and 2000 occurred at 1866.34, 1885.74, 1932.84, 1953.14, and
1972.54. Curiously, 4 out of the 5 of these dates fell near the midpoint of one of the 3.8-year
blocks that did not contain an SOI peak (Table 1).

The hypothesis that the 3.8-year lunar cycle is the zeitgeber of the lemming cycle is a
simple solution to one aspect (i.e. the timing) of the complex problem of what causes the quasi-
metronomic fluctuations of most northern lemming populations. Chitty (1996: 115) suggested that “anyone who proposes a new and doubtful hypothesis has a duty to test it”. The problem here is that lunar cycles and weather are not subject to experimental manipulation (Krebs 1988) and no statistical test can prove that the correlation between the lunar cycle and the lemming cycle or the ENSO cycle is causative (Berryman 2002).

The results of this study show that ENSO impacts lemming populations at two different phases of their cycle. First, lemming/Arctic fox peak years have corresponded closely with the January-March SOI peak (i.e., strong La Niña) years for nearly 130 years (Table 1). Successful breeding under the snow during the long northern winter is often thought to play an essential role in cyclic lemming populations reaching peak population levels (Duchesne et al. 2011; Ims et al. 2011; Reid et al. 2012). Early and deep snow cover, combined with minimal mid-winter freeze-thaw cycles, enhances both reproduction (by improving insulation in winter nests) and survival (by reducing predation by some, but not all, predators), and by improving accessibility to food (Duchesne et al. 2011). Throughout much of Canada, winter temperatures are colder than normal during La Niña years (Shabbar and Khandekar 1996). Also, winter precipitation (i.e., snowfall) in northcentral and southwestern (west of 100°) Canada is above normal in La Niña years (Shabbar et al. 1997). So, in northern North America, peak lemming abundance consistently coincides with optimal winter weather conditions. Severe winter conditions in Alaska were found to influence red-backed vole (Myodes rutilus (Pallas, 1779)) cycle amplitude but not period, suggesting that winter severity does not cause cyclicity by itself (Schmidt et al. 2017). Unfortunately, it appears that the relationship between ENSO and weather in northern Europe is not sufficiently understood (nor agreed upon) to make a similar comparison. However, modeling
of Norway lemming populations showed that winter weather and snow conditions plus a density-dependent parameter accounted for the observed population dynamics (Kausrud et al. 2008).

Second, during the increase phase, peak flowering years preceded years of peak lemming abundance by an average of 1.08 years (Table 3), supporting results of previous studies on lemmings and voles (Selås 1997; Johnsdottir et al. 1999; Selås 2016). Peak flowering usually (9 out of 12) occurred in June-August SOI trough (i.e., strong El Niño) years. El Niño leads to summer moisture deficits in the western two-thirds of Canada (Shabbar and Skinner 2004), which are not conducive to plant production. However, flower bud formation in northern climates occurs in the summer(s) preceding the flowering peak (Laine and Henttonen 1983; Selås 1997; Selås 2016), which would likely have neutral or La Niña climatic conditions. The results of this study support Zhang’s (2001) speculation that SOI cycling might cause the 3-4-year lemming/vole cycle through SOI-related climatic changes affecting food plant flowering rhythms and then affecting lemming abundance. Schmidt et al. (2017) found that abundance of red-backed voles was related to primary productivity, which in turn was determined by summer growing degree days and total precipitation as well as winter average snowfall.

To summarize, the proposed mechanistic pathway in the increase phase is: growing season (Jun-Aug) ENSO → optimal food plant growth conditions → increased food plant quantity/quality → increased lemming survival and fecundity → peak lemming abundance. In the increase to peak phase, the mechanistic scenario is: winter (Jan-Mar) ENSO → optimal winter snow conditions → increased lemming winter reproduction and survival → peak lemming abundance.

In contrast to the northern environments inhabited by lemmings, the abundance of some rodents in temperate climates has been linked to El Niño. For example, outbreaks of rodents in
semiarid northern Chile (Lima et al. 1999) and the Serengeti (Sinclair et al. 2013) are associated with increased rainfall during El Niño years (i.e. low or trough SOI values).

The 3.8-year recurrence of syzygial spring tides on or about the vernal equinox is illustrated in Figure 2. The equinox was selected because of its increased likelihood of biological significance. Spring tides on or near the equinoxes are significantly higher (and lower) than usual and are known as equinoctial spring tides (Pugh and Woodworth 2014). The “combined lunisolar forces” are increased by “about 33% at the syzygies near the solstices” (Wood 2001), and syzygial spring tidal forces also affect the atmosphere. Pertsev and Dalin (2010) reported that tropospheric cloudiness (at 56° N latitude) tends to increase with the change of lunar phase from quadrature to syzygy.

Siivonen and Koskimies (1955) proposed a since discarded lunar mechanism to explain wildlife cycles, based on the recurrence of the full moon in certain years during a critical period in which the photoperiodic system is particularly stimulated by moonlight, thereby enhancing reproduction. However, if these authors had considered both the full and new moons, they would have found a regular 3.8-year cycle (e.g., Figure 2). Critical periods do exist in nature; for example, several species of coral undergo mass spawning on the same night (but at different times) seven or eight evenings after the August full moon (Vize et al. 2005).

To support the hypothesis that animal populations might be entrained by the 3.8-year spring tidal cycle, evidence is needed that animals (or plants) are affected by both the full and new moon, or by both the first and last quarter. Golden hamster (Mesocricetus auratus (Waterhouse, 1839)) activity is highest 4 days after the full moon and a day or two after the new moon (Brown and Park 1967). Larkin and Keeton (1978) found synodic monthly oscillations in the vanishing bearings of homing domestic pigeons (Columba livia domestica (Gmelin, 1789)).
the turning points of the oscillations were at the syzygies. Mass mate-searching behavior of the harvested mangrove crab (*Ucides cordatus* (Linnaeus, 1763)) during the austral summer always occurs at the syzygies (Schmidt et al. 2012). Other examples include spawning of salt-marsh killifish (*Fundulus heteroclitus* (Linnaeus, 1766)); Hsaio et al. 1994), turning behavior of the sea slug (*Tritonia diomedea* (Bergh, 1894)); Lohmann and Willows 1987) and mud-snail (*Nassarius obsoletus* (Say, 1822)); Brown et al. 1960), and emergence of the midge (*Clunio marinus* (Halladay)); Neumann and Heimbach 1984).

One big question raised but not answered by this study: Is the ENSO cycle driven by or somehow connected with the 3.8-year lunar cycle? The correlation between predicted lemming/Arctic fox peak years and January-March SOI peak years (Table 1) suggests that ENSO might be driven by the 3.8-year lunar cycle. Zhang (2001) surmised, “There must exist some behind and deep mechanism of linking rodent outbreaks and ENSO together”. However, there is not much evidence for such a linkage. The only reference found to a relationship between a 3.8-year lunar cycle and atmospheric circulation is Wilson’s (2012) finding of a significant 3.78-year (+/- 0.06) periodicity in the peak latitude anomaly of the subtropical high-pressure ridge over eastern Australia from 1860 to 2010. However, some worldwide climate oscillations contain a periodicity of ~3.8 years (selected examples in Table 4), and it is clear that these oscillations are interconnected. For example, Li and Lau (2012) examined the late winter teleconnection between the ENSO and the NAO and found that the average NAO index values in 19 El Niño winters and 20 La Niña winters were -0.35 and 0.51, respectively: positive NAO index values are more frequent during La Niña winters, and negative winter NAO index values are more frequent during El Niño events.
The mean period of the lemming cycles in the 12 study locations in Alaska, northern Canada, Greenland, and Fennoscandia is 3.8 years (Table 1). Lemming cycle periods in these parts of the Arctic generally range from 3 to 5 years. In an analysis of 172 lemming cycles in Fennoscandia over a 137-year period, Angerbjörn et al. (2001) found cycle lengths varied as follows: 2-year, 1%; 3-year, 35%; 4-year, 54%, 5-year, 8%, 6-year, 2%.

But there is no evidence of a 3.8-year lemming cycle in Siberia. Long-term lemming time series from this part of the Arctic are limited. However, a regular 3.0-year Siberian lemming (*Lemmus sibiricus* (Kerr, 1792)) and Arctic lemming (*Dicrostonyx torquatus* (Pallas, 1778)) cycle has been reported on the Taimyr peninsula from 1961 to 1988 (Summers et al. 1998). And a 5-7-year Siberian lemming and collared lemming (*Dicrostonyx vinogradovi* (Ognev, 1948)) cycle was found on Wrangel Island from 1971 to 2010 (Menyushina et al. 2012). The 5+-year cycling at Wrangel appears to be different than the occasional (8%) 5-year cycle found by Angerbjörn et al. (2001) in Fennoscandia. The 5-year cycles in that region were interspersed with 3-year cycles resulting in a mean period of about 4 years. On this basis, the 3.8-year lunar hypothesis proposed in this study must be qualified as apparently not applicable to the Siberian Arctic region. One possible explanation is that the hypothesized 3.8-year ENSO timing signal does not reach this part of the Arctic. Assuming this is correct, it is interesting that these Siberian lemming populations still have a strong tendency to cycle, albeit at different, independent periods. Further research is needed to develop an understanding of the longitudinal and latitudinal variation of the Southern Oscillation and its effect on both weather and northern lemming populations.

The critical reader may object to findings of this study on several grounds: 1) Under a lunar hypothesis, it might seem logical that the both neighboring and more distant lemming
populations should all be exactly in phase rather than sometimes 1 (or rarely 2) year apart. And that there should consistently be peaks every 3.8 years without fail. Regional geographic synchrony, interspecific synchrony, and approximate transatlantic synchrony as evidenced in Table 1 are to be expected under a lunar hypothesis, because lunar phenomena, such as phase, rise and set times, height in the sky, and gravitational pull, are similar worldwide at a given latitude, varying only because of such factors as elevation and topography (Archibald 2014). But differences in population levels of neighboring populations are to be expected if local environmental conditions are different. Missing lemming peaks at the regional level are to be expected when environmental conditions are uniformly unfavorable throughout the region as happened between 1995 and 2005 in Fennoscandia. 2) It may seem logical to conclude that it is not biologically possible for the period of the lemming cycle to be 3.8 years - the period must be either 3.0, or 4.0, or 5.0 years. However, it clearly is possible for the lemming cycle to have an average period of 3.8 years, particularly if its timing is governed by an extrinsic factor with a 3.8-year period. 3) Some readers may reject the lunar hypothesis presented here as far-fetched (Royama 1992) or just unbelievable lunacy. Correlation is a standard, commonly-used tool employed by field ecologists to analyze relationships in their data. While correlation does not necessarily reflect causation, in this case the correlation between reported and predicted peak lemming years for over 125 years (Table 1) seems too strong to be ignored or rejected out of hand without serious consideration. 4) Readers may interpret the lunar hypothesis proposed here as an attack on the density-dependent paradigm. The lunar model $P_n = 1952.0 \pm 3.8n$ is sufficient to account for the periodicity and regularity of the lemming cycle but has nothing to say about the cyclic dynamics of lemming populations. The fluctuations of lemming populations result from a combination of intrinsic density-dependent factors such as social interactions and
dispersal and extrinsic factors such as weather and delayed density-dependent predation (Radchuk et al. 2016). Weather variations, hypothesized here to be caused by ENSO, affect lemming food quantity/quality as well as winter survival and fecundity.

In recommending that population cycle hypotheses based on exogenous environmental factors such as the lunar nodal phase cycle should be “laid to rest” in the rejected hypothesis graveyard, Myers (2018) concluded: “Although it would be satisfying to find a relationship between animal population cycles and cyclic environmental cues, there is no support for a consistent association over space and time.” On the contrary, the results of this study show a consistent, regular, persistent (>125 years) association between the peaks of lemming/Arctic fox cycles and peak years predicted by the simple lunar model $P_n = 1952.0 \pm 3.8n$ in northern North America and Fennoscandia (Table 1). And a previous study reported a consistent, regular, persistent (>120 years) relationship between the peaks of the ruffed grouse, snowshoe hare and Canada lynx cycles and the peak years predicted by the lunar model $P_n = 1950.2 \pm 9.3n$ in much of northern North America (Archibald 2014). No other models have the capability to forecast and hindcast these population cycle peaks for well over 100 years.

It is remarkable that the lemming cycle has persistently stayed in phase with the 3.8-year lunar cycle for nearly 130 years (Table 1), despite major volcanic climatic disruptions (e.g., Krakatoa 1883, Santa Maria and Pelee 1902, El Chichon 1982) 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). It seems improbable that this consistently periodic and quasi-metronomic record of peak lemming abundance is the result of the interaction of intrinsic density-dependent population dynamics and stochastic environmental factors. However, this cyclic pattern becomes
more expected if a cyclic environmental factor such as the 3.8-year lunar cycle and/or the 18.6-year lunar nodal cycle (Yasuda 2018) is the zeitgeber.

See Appendix A for a brief survey of 21st century lemming cycles.

Acknowledgments

Thanks to Nils Stenseth and Nancy Jennings for critical review of previous versions and to C. Stuart Houston and Vidar Selås for advice and encouragement. Two anonymous reviewers provided valuable suggestions. This study would not have been possible without long-term data series supplied by Charles Elton, Anders Angerbjörn, and their many colleagues. I am indebted to Ian Wilson and Zhibin Zhang, respectively, for drawing my attention to the 3.8-year lunar cycle and the lemming-Southern Oscillation Index relationship.

References


**Figure captions**

Figure 1. Mean reported peak years of abundance of lemmings and Arctic fox (red) and predicted peak years of abundance (blue) based on the lunar model $P_n = 1952.0 \pm 3.8n$.

Figure 2. 3.8-year cycle of the recurrence of syzygial “spring” tides on the 5 days around the vernal equinox, March 18–22, each year. Syzygy index: full and new moon = 50, first and last quarter = 0. The syzygy index reflects the number of days between the vernal equinox and the new or full moon closest to it.
Table 1. Reported and predicted peak years of abundance of lemmings and Arctic Fox in Norway, Greenland, and northern North America.

<table>
<thead>
<tr>
<th>Predicted Peak Year of Abundance</th>
<th>Norway Tromso</th>
<th>Norway Nordland</th>
<th>Norway No. Trondelag</th>
<th>Norway Dovre</th>
<th>Norway Southwest</th>
<th>Greenland</th>
<th>Canada Yukon</th>
<th>Canada Manitoba</th>
<th>Alaska Point Barrow</th>
<th>Canada NW Territories</th>
<th>Canada No. Quebec</th>
<th>Canada Labrador</th>
<th>Mean Reported Peak Year of Abundance</th>
<th>n</th>
<th>Difference (Predicted - Reported Peak Years)</th>
<th>SOI Jan-Mar Peak Year</th>
<th>Difference (Predicted - SOI Peak Years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993.8</td>
<td>1990.0</td>
<td>1986.2</td>
<td>1982.4</td>
<td>1978.6</td>
<td>1974.8</td>
<td>1971.0</td>
<td>1967.7</td>
<td>1967.0</td>
<td>1963.0</td>
<td>1959.0</td>
<td>1955.0</td>
<td>1952.0</td>
<td>1868.4</td>
<td>1891.2</td>
<td>1872.2</td>
<td>1974.0</td>
<td>0.4</td>
</tr>
<tr>
<td>1993.3</td>
<td>1989.9</td>
<td>1987.1</td>
<td>1982.6</td>
<td>1980.0</td>
<td>1975.0</td>
<td>1970.1</td>
<td>1966.0</td>
<td>1960.0</td>
<td>1956.0</td>
<td>1952.0</td>
<td>1948.0</td>
<td>1944.0</td>
<td>1872.2</td>
<td>1894.9</td>
<td>1890.0</td>
<td>1974.0</td>
<td>0.8</td>
</tr>
<tr>
<td>1993.6</td>
<td>1989.2</td>
<td>1987.4</td>
<td>1982.9</td>
<td>1980.3</td>
<td>1975.3</td>
<td>1970.4</td>
<td>1966.3</td>
<td>1960.3</td>
<td>1956.3</td>
<td>1952.3</td>
<td>1948.3</td>
<td>1944.3</td>
<td>1872.5</td>
<td>1895.2</td>
<td>1890.3</td>
<td>1974.0</td>
<td>1.1</td>
</tr>
</tbody>
</table>

Predicted peak years based on the lunar model \( P_n = 1952.0 \pm 3.8n \). Peak years of Southern Oscillation Index (SOI) Jan-Mar.

Mean: -0.01 ± 0.32

s.d. 0.59 ± 0.79
Table 2. Sources of the reports of peak abundance in Table 1.

<table>
<thead>
<tr>
<th>Location</th>
<th>Date Range</th>
<th>Species</th>
<th>Reference</th>
<th>Source Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal Norway, Five Regions</td>
<td>1862-1994</td>
<td>Norway Lemming&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Angerbjorn et al. (2001)</td>
<td>Peak years (classes 3, 4, 5)</td>
</tr>
<tr>
<td>Manitoba, Canada</td>
<td>1932-1990</td>
<td>Collared Lemming&lt;sup&gt;5&lt;/sup&gt;</td>
<td>Scott (1993)</td>
<td>Snap trapping</td>
</tr>
<tr>
<td>Northwest Territories, Canada</td>
<td>1919-1981</td>
<td>Arctic Fox&lt;sup&gt;6&lt;/sup&gt;</td>
<td>Obbard et al. (1987)</td>
<td>Fur harvest</td>
</tr>
<tr>
<td>Ungava District, No. Quebec, Canada</td>
<td>1867-1924</td>
<td>Arctic Fox&lt;sup&gt;6&lt;/sup&gt;</td>
<td>Elton (1942:415-416)</td>
<td>Fur returns</td>
</tr>
<tr>
<td>Moravian Stations, No. Labrador, Canada</td>
<td>1834-1925</td>
<td>Arctic Fox&lt;sup&gt;6&lt;/sup&gt;</td>
<td>Elton (1942:424-425)</td>
<td>Fur returns</td>
</tr>
</tbody>
</table>

<sup>1</sup> *Lemmus lemmus* (Linnaeus, 1758)  
<sup>2</sup> *Dicrostonyx groenlandicus* (Traill, 1823)  
<sup>3</sup> *Dicrostonyx spp* *Lemmus trimucronatus* (Richardson, 1825)  
<sup>4</sup> *Dicrostonyx richardsoni* (Merriam, 1900)  
<sup>5</sup> *Vulpes lagopus* (Linnaeus, 1758)
Table 3. Comparison between peak years of flowering\(^1\) and peak lemming abundance\(^2\) in Norway and June-August Southern Oscillation (SOI) index.

<table>
<thead>
<tr>
<th>Peak Flowering Year</th>
<th>SOI Jun-Aug Year</th>
<th>SOI Trough Year?</th>
<th>SOI Jun-Aug Value</th>
<th>Peak Lemming Year</th>
<th>Difference (Peak Flowering - Peak Lemming Years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1953.5</td>
<td>1953</td>
<td>Yes</td>
<td>-2.42</td>
<td>1955</td>
<td>-1.5</td>
</tr>
<tr>
<td>1957.5</td>
<td>1957</td>
<td>Yes</td>
<td>-1.27</td>
<td>1958</td>
<td>-0.5</td>
</tr>
<tr>
<td>1960</td>
<td>1959</td>
<td>Yes</td>
<td>-2.11</td>
<td>1962</td>
<td>-2.0</td>
</tr>
<tr>
<td>1964.5</td>
<td>1965</td>
<td>Yes</td>
<td>-5.32</td>
<td>1966</td>
<td>-1.5</td>
</tr>
<tr>
<td>1968.5</td>
<td>1969</td>
<td>Yes</td>
<td>-1.68</td>
<td>1969</td>
<td>-0.5</td>
</tr>
<tr>
<td>1972</td>
<td>1972</td>
<td>Yes</td>
<td>-4.64</td>
<td>1974</td>
<td>-2.0</td>
</tr>
<tr>
<td>1977</td>
<td>1977</td>
<td>Yes</td>
<td>-5.20</td>
<td>1977</td>
<td>0.0</td>
</tr>
<tr>
<td>1980</td>
<td>1980</td>
<td>Yes</td>
<td>-0.88</td>
<td>1981</td>
<td>-1.0</td>
</tr>
<tr>
<td>1984</td>
<td>1984</td>
<td>No</td>
<td>-1.00</td>
<td>1985</td>
<td>-1.0</td>
</tr>
<tr>
<td>1987</td>
<td>1987</td>
<td>Yes</td>
<td>-6.18</td>
<td>1988</td>
<td>-1.0</td>
</tr>
<tr>
<td>1990</td>
<td>1990</td>
<td>No</td>
<td>-0.21</td>
<td>1991</td>
<td>-1.0</td>
</tr>
<tr>
<td>1993</td>
<td>1993</td>
<td>No</td>
<td>-4.97</td>
<td>1994</td>
<td>-1.0</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean -1.08</td>
</tr>
</tbody>
</table>

\(^1\)Selås 1997:Figure 3  
\(^2\)Selås 2016:Figure 2
Table 4. Worldwide climate oscillations with a periodicity of ~3.8 years.

<table>
<thead>
<tr>
<th>Description</th>
<th>Location</th>
<th>Time span</th>
<th>Reference</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice core net accumulation</td>
<td>Yukon Territory, Canada</td>
<td>1736-1987</td>
<td>Holdsworth et al. 1992</td>
<td>3.8</td>
</tr>
<tr>
<td>Air temperature</td>
<td>Greenland</td>
<td>1901-2000</td>
<td>Box 2002</td>
<td>3.7</td>
</tr>
<tr>
<td>NAO</td>
<td>Greenland</td>
<td>1901-2000</td>
<td>Box 2002</td>
<td>3.8-4.0</td>
</tr>
<tr>
<td>Sub-tropical high pressure ridge</td>
<td>Eastern Australia</td>
<td>1860-2010</td>
<td>Wilson 2012</td>
<td>3.8</td>
</tr>
<tr>
<td>Sea surface temperature</td>
<td>Global</td>
<td>1979-2013</td>
<td>Liu and Duan 2017</td>
<td>3.8</td>
</tr>
<tr>
<td>ENSO: strong+ El Niño events</td>
<td>Southeastern Pacific Ocean</td>
<td>1803-1987</td>
<td>Quinn et al. 1987</td>
<td>~3.8</td>
</tr>
<tr>
<td>ENSO: sea surface temperature</td>
<td>Tropical Pacific Ocean</td>
<td>1950-1999</td>
<td>Salau et al. 2012</td>
<td>~3.8</td>
</tr>
<tr>
<td>ENSO: 16 coral reef reconstructions</td>
<td>Tropical Pacific and Indian Ocean</td>
<td>1897-1981</td>
<td>Wilson et al. 2006</td>
<td>3.7-3.9</td>
</tr>
<tr>
<td>Atlantic Niño: sea surface temperature</td>
<td>Tropical Atlantic Ocean</td>
<td>1870-2012</td>
<td>Nnamchi 2013</td>
<td>3.8</td>
</tr>
</tbody>
</table>

Glossary (Source: NOAA/NWS Climate Prediction Center)


El Niño: Period of warmer than average sea surface temperatures across the eastern tropical Pacific Ocean.

La Niña: Period of cooler than average sea surface temperatures across the eastern tropical Pacific Ocean.

SOI: Southern Oscillation Index. Based on the pressure difference between Tahiti and Darwin, Australia.

NAO: North Atlantic Oscillation. Fluctuation in atmospheric pressure difference between the Subtropical Azores High and Subpolar Iceland Low.

Atlantic Niño: Sea surface temperature and trade wind fluctuation in the equatorial Atlantic Ocean.
Appendix A

At this point, the curious reader is left wondering how well the 3-8-year lunar model predicts 21st century lemming peak years and whether the model applies to northern voles as well. While beyond the original scope of this paper, a survey of recent lemming and vole literature was undertaken to seek tentative answers to these questions.

Reports of 28 peaks of lemming and/or northern vole abundance were compiled for 7 locations (Table A1). To be selected, a dataset needed to contain 3 or more peaks of lemmings and/or voles from 2001 to 2017. While lemming and vole cycles collapsed or dampened in several areas across Europe in the 1980’s and 1990’s (Table 1; Ims et al. 2011; Cornulier et al. 2013), classic 3-4-year cycles have persisted in Canada and recovered in parts of Norway, Sweden, and Finland in the 21st century (Table A1).

Data from the Kluane region of the Canadian Yukon boreal forest provide an answer to both questions posed above: the lunar model predicts cyclic peaks of a vole population very accurately. From 2002 to 2017, red-backed voles (*Myodes rutilus*, Pallas 1779) in the Kluane area showed a 3.8-year cycle with peaks closely aligned (mean absolute difference = 0.3 years) with predicted peaks based on the 3.8-year lunar model (Table A1). However, it should be pointed out that this near-perfect fit was not prevalent throughout the entire 45-year time-series but rather occurred in 8 of the 11 (73 %) peaks. Peaks in 1975 and 1979 were within 0.3 years of predicted peaks. Curiously, the next 3 peaks (1984, 1987, and 1992) deviated from predicted years by a mean absolute difference of 1.4 years. But then the cycle returned to close alignment with predictions from 1998 to 2017.

In contrast to the Canadian Yukon, there were synchronous lemming and vole peaks in the other 6 locations in 2011 (Table A1), presumably having resulted from a record-breaking La
Niña that occurred that year. The highest January-March SOI value found in the 150 years from 1866 to 2017 was in 2011. Hoset et al. (2017) reported an “exceptionally massive” rodent outbreak in northern Fennoscandia in 2010-2012. These findings provide further evidence of the important influence of ENSO on lemming population fluctuations.

Considering all 7 locations, mean reported peak years of lemming and vole abundance from 2001 to 2006 were within -0.1 and 0.8 years of predicted peaks, respectively (Table A1). The next 3 mean reported peak years (2007-2014) deviated from predicted years by 1.5, 1.8, and -1.0 years, respectively. It appears that the record-breaking La Niña dominated the timing of the synchronous lemming and vole peaks found in 2011. But then from 2015 to 2017 the mean reported peak year returned to within 0.3 years of the predicted peak. We will have to wait for further research to determine whether or not the recent close alignment with the predictions of the 3.8-year lunar model continues.

The 1.8-year deviation between the mean reported peak year 2011.0 and the predicted peak year 2012.8 was by far the worst prediction in the entire study (Table 1). The Jan-Mar SOI peak of 2011 was almost exactly out of phase with the predicted years 2009.0 and 2012.8. This was unusual: 20 out of 28 (71%) of SOI peak years were within 0.8 years of predicted peak years from 1868 to 1994 (Table 1). But it was not unprecedented: the SOI peak years 1935, 1939, and 1950 deviated from predicted peak years by 1.8, 1.6, and -1.8 years, respectively (Table 1). The interrelationship between lemming and vole population cycles, the 3.8-year lunar cycle, and the ENSO cycle is an enigma that warrants further research.

Predicted peak years of abundance based on the lunar model $P_n = 1952.0 \pm 3.8n$. Peak years of Southern Oscillation Index (SOI) Jan-Mar.

<table>
<thead>
<tr>
<th>Country</th>
<th>Province/Location</th>
<th>Year</th>
<th>Reported Peak Year of Abundance</th>
<th>Predicted Peak Year of Abundance</th>
<th>Difference (Predicted - Reported Peak Years)</th>
<th>SOI Jan-Mar Peak Year</th>
<th>Difference (Reported - SOI Peak Years)</th>
<th>Mean Period n</th>
<th>Mean Period s.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canada</td>
<td>Yukon</td>
<td>2017</td>
<td>2017</td>
<td>2017</td>
<td>-0.1</td>
<td>2011</td>
<td>-0.0</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Nunavut</td>
<td>2014</td>
<td>2014</td>
<td>2014</td>
<td>0.1</td>
<td>2011</td>
<td>0.0</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Mosvatn</td>
<td>2011</td>
<td>2011</td>
<td>2011</td>
<td>-0.1</td>
<td>2011</td>
<td>-0.1</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Norway</td>
<td>Stor-Elvdal</td>
<td>2007</td>
<td>2007</td>
<td>2007</td>
<td>-0.1</td>
<td>2007</td>
<td>-0.1</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>West Central</td>
<td>2007</td>
<td>2007</td>
<td>2007</td>
<td>-0.1</td>
<td>2007</td>
<td>-0.1</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Sweden</td>
<td>West Central</td>
<td>2004</td>
<td>2004</td>
<td>2004</td>
<td>0.0</td>
<td>2004</td>
<td>-0.0</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Stor-Elvdal</td>
<td>2001</td>
<td>2001</td>
<td>2001</td>
<td>0.0</td>
<td>2001</td>
<td>-0.0</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Abisko</td>
<td>2015</td>
<td>2015</td>
<td>2015</td>
<td>-0.1</td>
<td>2015</td>
<td>-0.1</td>
<td>3.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Finland</td>
<td>Kilpisjärvi</td>
<td>2015</td>
<td>2015</td>
<td>2015</td>
<td>-0.1</td>
<td>2015</td>
<td>-0.1</td>
<td>3.3</td>
<td>1.3</td>
</tr>
</tbody>
</table>

1. Red-backed vole (*Myodes rutilus*, Pallas 1779); Source: Krebs et al. (2018)
3. Norway lemming (*Lemmus lemmus*, Linnaeus, 1758); Source: Selås (2016)
4. Bank vole (*Myodes glareolus*, Schreber, 1780); Source: Johnsen et al. (2019)
6. Norway lemming (*Lemmus lemmus*, Linnaeus, 1758) and several voles; Source: Olofsson et al. (2012)
8. Norway lemming (*Lemmus lemmus*, Linnaeus, 1758) and several voles (*Clethrionomys* spp.); Source: Lehikoinen et al. (2016)