Estonian Journal of Ecology, 2011, **60**, 2, 155–164 doi: 10.3176/eco.2011.2.06

Three-year periodicity in historical raptor-persecution data: an indication of vole cycles?

Asko Lõhmus

Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia; asko.lohmus@ut.ee

Received 21 December 2010, accepted 20 April 2011

Abstract. Reflections of three- to four-year cycles in vole abundance have been observed in the breeding performance and abundance of raptors in Estonia at least since the 1970s. To check whether such link could be used to reconstruct earlier vole cycles, too, I analysed two geographically distinct samples of reports on systematic raptor persecution in 1890–1908. These samples showed three-year periodicity and coincided in their years of minimum although vole-eating species formed only a small part of the material. The numbers of different taxa (diurnal raptors vs owls; *Buteo buteo* vs *Accipiter nisus*) were positively correlated in the material, indicating interspecific synchronity in the fluctuations. Probably the observed pattern reveals that, similarly to the recent decades, the productivity of raptors fluctuated in response to three-year vole cycles in Estonia already at the end of the 19th century. These reconstructions can explain some known historical irruptions of raptors and indicate an early general decline of diurnal raptors at least in southern Estonia.

Key words: Baltic–German wildlife management, birds of prey, cyclic populations, historical time series, numerical response.

INTRODUCTION

Regular oscillations in animal populations have been an important research topic for more than a century, allowing insights into the drivers of population dynamics, spatial processes in populations, and predator–prey dynamics. Beginning with Elton's (1924) pioneering work several studies have used data on predator populations to indicate the dynamics of their prey. Such shortcuts are particularly reasonable for documenting long-term or large-scale population processes when predators are easier to record than their prey (e.g., Sundell et al., 2004; Henden et al., 2009).

A well-known system comprising conspicuous predators and their more elusive prey is that of many species of raptors and small mammals (notably voles of the genera *Microtus* and *Clethrionomys*). The latter have been model organisms for studying periodicity and spatial synchrony in population dynamics because of their widespread distributions, synchronous dynamics of several species, and relatively short population cycles (e.g., Turchin, 2003). Many raptor species respond numerically and functionally to fluctuating vole populations, which can thus be tracked via such responses (Korpimäki, 1994; Lõhmus, 1999; Sundell et al., 2004). Yet, census data or ecological research on raptor populations is still usually limited to a few decades (only fragmentary information may date back centuries; Bijleveld, 1974), while longer time frames are needed to understand how vole populations react to slow processes such as climate or landscape change (Henden et al., 2009).

In this paper, I explore whether historical dynamics of vole populations could be restored using data on systematic raptor persecution in Estonia. Such persecution lasted from the end of the 19th century until the middle of the 20th century; it was based on a perception that raptors limit the populations of 'useful' wildlife (Randla, 1976). The likely magnitude was 0.4 million diurnal raptors and owls killed (A. Lõhmus, unpublished data). I analyse only the first decades of the persecution campaign because these data are relatively well accessible and so its feedback on vole populations by a reduction in predation pressure can be excluded (see Steen et al., 1990). Based on the fact that the reflections of three- to four-year vole cycles have been observed in the breeding performance and abundance of raptors in Estonia at least since the 1970s (Lõhmus, 1999, 2004; Lõhmus & Väli, 2004), I hypothesize that the numbers of killed raptors also fluctuated regularly a century ago. To evaluate the impact of possible confounding variables, I also explore the species composition and long-term trends in the material. Finally, I discuss the reconstructed dynamics in the light of historical irruptions of some rare raptor and owl species.

MATERIAL AND METHODS

I mostly followed Rootsmäe & Rootsmäe (1983) to find all Estonian predator persecution reports published in the journals *Baltische Waidmannsblätter* and *Neue Baltische Waidmannsblätter*. Those reports distinguish at least diurnal raptors (Accipitriformes et Falconiformes), owls (Strigiformes), corvids (Corvidae), and other predators, while many species determinations may be wrong (Martenson, 1908). There were no lists from islands, thus the analysis only covers the Estonian mainland. Two data sets could be formed.

(1) Estate reports reflecting obligatory persecution by gamekeepers and other forest officers on estate lands, and including also landlords' contribution. These reports indicate the year and location (usually estate; rarely forest district), the object (eggs or birds), the species or species group, and the numbers shot or collected; often also the amounts paid as premium. I rejected the number of collected eggs because of the small samples, and all lists with landlords' own data only because of different motivation and effort. For the period 1890–1908, altogether 167 annual estate reports were accepted for analysis; 121 of these originated from southern Estonia (Governorate of Livonia) and 46 from northern Estonia (Governorate of Estonia). These reported the killing of a total of 7483 diurnal raptors and 514 owls. Since 1894, 5–18 estate reports were published annually, but for the period 1890–1893 only two estates published their report: one in all four years, the other in 1892–1893. Thus, the averages for 1890–1893 should be regarded with caution.

I used the annual average number of killed raptors and owls per estate as an index of abundance. It was the best available area-related index as most reports did not include descriptions of hunting grounds. Eight estates published these data: the areas averaged 50 km^2 (range 13–118 km^2), but the intensities varied from 0.4 to 4.8 killed raptors per square kilometre per year, and no clear relationship between the area and birds killed emerged ($r_s = 0.25$, $p = 0.55$). Probably the estates that published their reports were prosperous and their owners were enthusiastic hunters, but the hunting lands were not necessarily extensive.

(2) The material collected in 1895–1908 by the North-Estonian Hunters' Society (NEHS) (Anonymous, 1907, 1909), which paid premium for eggs (since 1895) and claws (since 1897) of the Goshawk (*Accipiter gentilis*), Sparrowhawk (*A. nisus*), eagles, Peregrine (*Falco peregrinus*), and Eagle Owl (*Bubo bubo*) (Anonymous, 1902). Claws apparently had more value because the number of collected eggs dropped after 1897, and in 1909 the NEHS stopped financing corvid egg collecting altogether (Anonymous, 1909). Destroying a clutch makes it impossible to get claws of the young and to catch the adults who were usually shot or caught when feeding the young (Sass, 1901; Kolga, 1933). For these reasons I calculated a linear index combining egg (E) and bird (B) numbers with the least square method so that, on average, $x\text{E} + y\text{B} = 100$. Solving for actual numbers: $x = 0.1388$ and $y = 0.0654$. In total, these reports documented 7094 killed birds and 6354 collected eggs.

It was not possible to check directly whether the two data sets had any overlapping material, but a substantial overlap is unlikely as the material from northern Estonia only formed a minor part of the estate data. Moreover, a hunters' society similar to the NEHS (paying premium for selected species) was active in southern Estonia as well, and comparisons of its available reports (Vietinghoff & Engelhardt, 1901, 1902) with some largest estate reports (e.g., Engelhardt, 1904) show no overlap at all.

The species composition was explored in two samples, in which all raptor species had been identified by specialists using comparison collections and identification guides. One is a local report from mid-eastern Estonia in 1894–1904 (Engelhardt, 1904; $n = 2544$ individuals, included in the general estate data set), the other is a general report by the Hunters' Society of Livonia (including northern Latvia) in 1900 and 1901 (Vietinghoff & Engelhardt, 1901, 1902; $n = 858$ and 876, respectively). These lists do not have any overlapping material.

To detect periodicity in the time series, I used spectral analysis in STATISTICA 9.1 software. To test the null hypothesis that a series follows white-noise series, I fitted exponential distribution to periodogram distribution (Kolmogorov–Smirnov test). Note that, in the analysed period, a hunting year usually began between February and April, thus a year mentioned includes its breeding season and only the following non-breeding season.

RESULTS

Both data sets revealed three-year periodicity and coincided in the years of minimum in their overlapping parts (1897, 1900, 1903, 1906; Fig. 1). The years of maximum coincided in three latest periods (1901, 1904, 1908), while earlier maxima in the NEHS material appeared a year before the estate data. Variation in

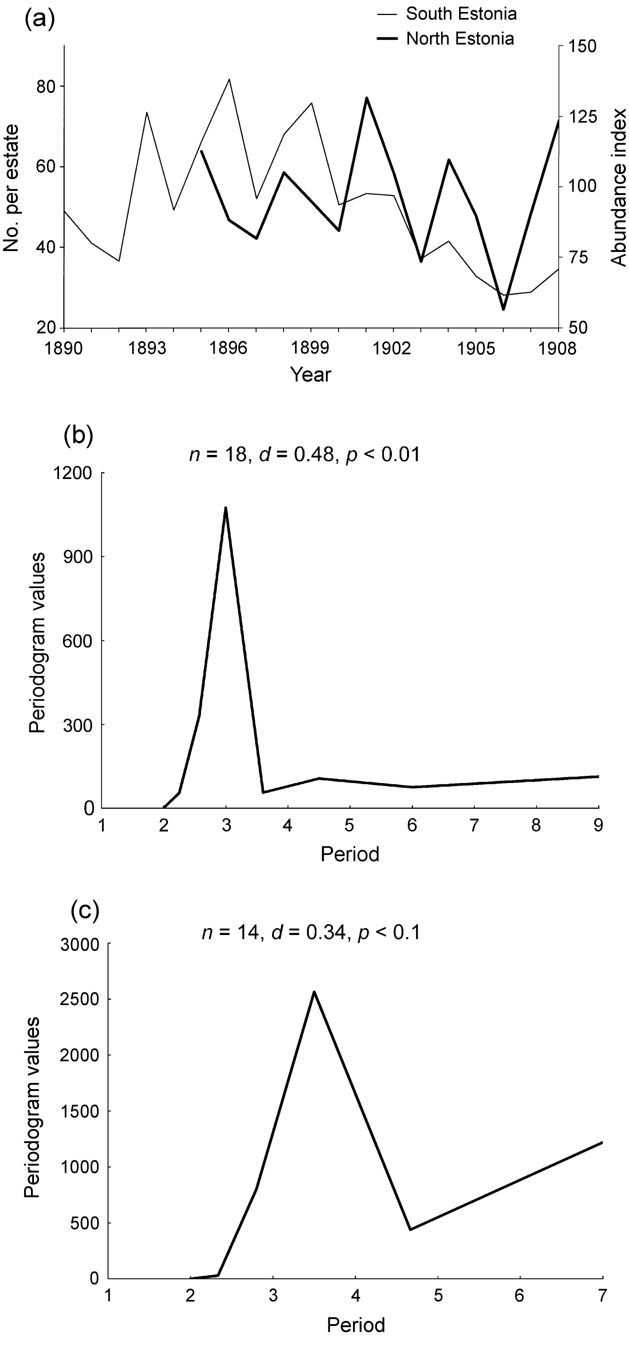

Fig. 1. (a) Variation in the numbers of killed raptors in (mainly) South Estonian estates (annual mean per estate) and in northern Estonia (an index combining the number of eggs and claws collected by hunters), 1890–1908. (b) and (c): Periodograms for these two data sets, with Kolmogorov–Smirnov test results fitting exponential distribution to periodogram distributions (data from 1890 were excluded from the estate data because of the odd number of observations).

the numbers of owls tended to follow that of diurnal raptors (Fig. 2), although the correlation was clear only in the sample from mid-eastern Estonia for vole-eating diurnal raptors (Fig. 2b; $r_s = 0.80$, $n = 10$, $p = 0.005$). In the NEHS data set no trends were observed, but in the estates the mean number of diurnal raptors killed decreased in the last ten years, 1899–1908 ($r_s = -0.87, p = 0.0012$; Fig. 2a). No such decrease was observed for owls ($r_s = -0.06$, $p = 0.87$) or the number of participating estates ($r_s = -0.27, p = 0.46$).

Among species the Sparrowhawk dominated (49% in mid-eastern Estonia and 47–48% in Livonia), followed by the Common Buzzard (*Buteo buteo*) (14% and 11–12%), Goshawk (5% and 11–15%), and Honey Buzzard (*Pernis apivorus*) (6% and 5–6%). Vole-eating raptors (*Buteo* spp., *Circus* spp., *Falco tinnunculus*, *Nyctea scandiaca*, *Surnia ulula*, *Asio* spp., *Strix uralensis*, *Aegolius funereus*) in total formed 26.5% and 23–24% of the material. In the sample from mid-eastern Estonia, the numbers of the two most common species (*A. nisus* and *B. buteo*) were positively correlated (Fig. 3).

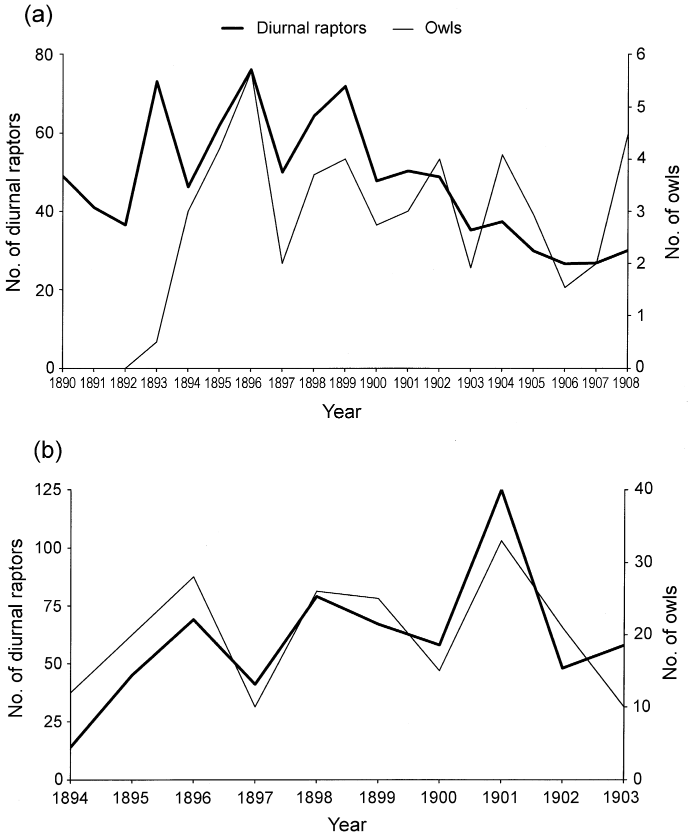

Fig. 2. Variation in the numbers of killed diurnal raptors and owls: (a) average numbers per (mainly) a South Estonian estate; (b) numbers in mid-eastern Estonia (according to Engelhardt, 1904). For (b) only vole-specialized diurnal raptors (*Circus cyaneus*, *C. pygargus*, *Buteo buteo*, *Aquila pomarina*, *Falco tinnunculus*) were considered.

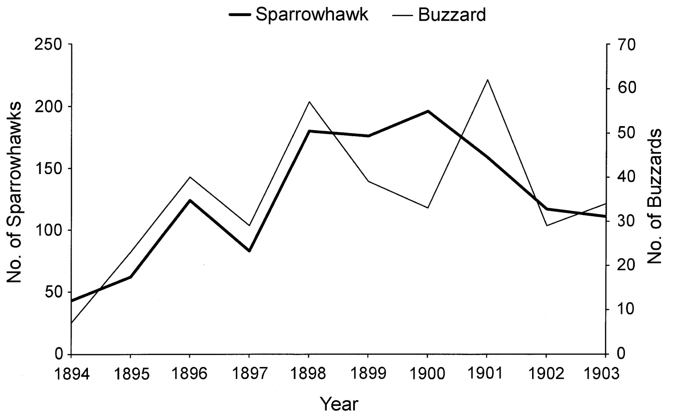

Fig. 3. Variation in the numbers of killed Sparrowhawks and Common Buzzards in mid-eastern Estonia (data from Engelhardt 1904; $r_s = 0.72$, $n = 10$, $p = 0.018$).

DISCUSSION

I observed a regular and largely overlapping three-year periodicity in historical raptor-persecution data in two distinct areas in Estonia. This periodicity resembles vole-induced fluctuations in raptor populations in the recent decades (Lõhmus, 2004; Lõhmus & Väli, 2004). There was no indication of any relevant periodicity in the persecution campaign itself, and the main result (Fig. 1) is robust to errors in species identification (Erkamo, 1990) – I only assumed that corvids had been correctly separated from raptors. Weather factors, which could influence the activity of birds or hunters, fluctuate either randomly (temperature; Karing, 1992) or have much longer cycles (27–28-year precipitation cycles; Jõgi & Tarand, 1995) in Estonia. Therefore, I argue that the pattern observed indicates three-year vole cycles in Estonia already at the end of the 19th century. This is what could theoretically be expected from the latitudinal pattern of vole cycles (Hanski et al., 1991), and it is also consistent with their recent dynamics in the adjacent southern Finland (Sundell et al., 2004).

Most likely, the regular variation in the persecution data is largely due to the fluctuating reproductive success of raptors, which is related to the vole supply in many species (Newton, 1979, 2002). The dominant technique of early raptor persecution in Estonia was a systematic search for nests to kill young and occasional shooting of adults (e.g., F., 1908; R. V., 1921; Kivisikk, 1939). Without special means, young inexperienced birds were probably also the easiest to catch. It was only after 1904 that the trapping of adults (Hermann, 1910; Anrep, 1914; Sivers, 1914) and shooting raptors near captive Eagle Owls (Schönfeldt, 1909) were reported. An effective sprung-roof trap with live bait was introduced to public in 1908 (F., 1908).

The main argument against such interpretation might be that most killed raptors were not vole specialists or, according to official determinations (which cannot be checked), the NEHS data did not include vole specialists at all. However, this may indicate a more general response in the raptor community, as known from some other studies (e.g., Hagen, 1969). Selås & Steel (1998) specifically show that brood size can follow vole cycles in the Sparrowhawk – the species forming half of the Estonian material (perhaps partly due to its relatively large broods) and showing a positive correlation with the other most abundant species, the Common Buzzard (a vole-eater). A factor that may have contributed to a general response is that, during the persecution period, the land cover of Estonia was dominated by traditionally managed agricultural lands (Mander & Palang, 1999) where voles may have played a more prominent role in food webs than nowadays.

The results also agree with two other types of observations on Estonian raptor populations. The decline in the number of killed diurnal raptors in South-Estonian estates probably indicates true population declines (typical in heavily persecuted raptor populations; Bijleveld, 1974) as no similar decrease in the persecution effort was observed. A methodological artefact is particularly unlikely given the absence of any trend in owls, which were infrequently killed (Fig. 2a); in fact the different trends may have confounded the general correlation between diurnal raptor and owl numbers. Indeed, two long-term case studies report low abundances of common mid-sized diurnal raptors until the middle of the 20th century in Estonia (Lõhmus, 1997; Tuule et al., 2011). My analysis helps to date that decline already to the first decade of the century, which is further supported by Middendorff (1910), who claimed the same for northern Estonia. The latter was not evident in the NEHS reports, but it may have been smaller or slightly delayed because the rural human population was denser and the persecution intensity much higher in the south.

Secondly, the reconstructed vole cycles can explain historical invasions of some vole-eating raptors to Estonia. The Pallid Harrier (*Circus macrourus*) has had three irruptions to Estonia, most significantly in autumns 1901 and 1911, and a probable one in 1895 (Leibak et al., 1994). Both 1901 and 1895 appeared as top years and 1911 may have been as well (it is three years after the latest detected peak in 1908). Moreover, 1895 and 1901 were irruption years also in Latvia (Viksne, 1983). A prominent invasion of the Snowy Owl (*Nyctea scandiaca*) to Estonia was detected in winter 1895/96 (Leibak et al., 1994), and that of the Tengmalm's Owl (*Aegolius funereus*) to Latvia in winter 1901/02 (Viksne, 1983). Although many nomadic owls were also observed after a minimum year, in 1906–1907, this mostly happened on the coast of the Gulf of Finland (Wasmuth, 1909), where vole dynamics may be distinct from that inland (Sundell et al., 2004). Finally, the only breeding case of the Hawk Owl (*Surnia ulula*) in the period in Estonia was confirmed in 1893 (Leibak et al., 1994) – a top year.

ACKNOWLEDGEMENTS

I thank Raivo Mänd and Vidar Selås for comments on early drafts of the manuscript. The study was supported by the Estonian Ministry of Education and Research (project 0180012s09) and the European Regional Development Fund (Centre of Excellence FIBIR).

REFERENCES

Anonymous 1902. Die Thätigkeit des Estländischen Vereins von Liebhabern der Jagd. *Baltische Waidmannsblätter*, **2**, 424.

Anonymous 1907. Raubzeugprämierung des Estl. Vereins. von Liebhabern der Jagd im 12 jährigen Zeitabschnitt 1895-1906. *Neue Baltische Waidmannsblätter*, **3**, 191.

Anonymous 1909. Uebersicht über die Anzahl des vom Estländischen Verein vom Liebhabern der Jagd in den letzten 5 Jahren vertilgten Raubzeuges. *Neue Baltische Waidmannsblätter*, **5**, 168.

Anrep, A. v. 1914. Streckenbericht 1904-1914 aus Lauenhof. *Neue Baltische Waidmannsblätter*, **10**, 226–227.

Bijleveld, M. 1974. *Birds of Prey in Europe*. MacMillan Press.

Elton, C. 1924. Fluctuations in the numbers of animals: their causes and effects. *Brit. J. Exp. Biol.*, **2**, 119–163.

Engelhardt, E. 1904. Abschuss-Liste von Raubzeug der Forstverwaltung Techelfer, Kerrafer und Laiwa (Livland) von 1894 bis 1904. *Baltische Waidmannsblätter*, **4**, 218.

Erkamo, V. 1990. Raptor persecution history in Finland. *Lintumies*, **25**, 90–92.

F., A. v. 1908. Eine Raubvogelfalle. *Neue Baltische Waidmannsblätter*, **4**, 566–567.

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. *Fauna (Oslo)*, **22**, 73–126.

Hanski, I., Hansson, L. & Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.*, **60**, 353–367.

Henden, J.-A., Ims, R. A. & Yoccoz, N. G. 2009. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *J. Anim. Ecol.*, **78**, 636–645.

Hermann, K. 1910. Abschussliste für das Gut Adsel-Koiküll, Livland vom 1. Mai 1909-1. Mai 1910. *Neue Baltische Waidmannsblätter*, **6**, 250.

Jõgi, J. & Tarand, A. 1995. Climate. In *Estonia. Nature* (Raukas, A., ed.), pp. 183–216. Valgus & Eesti Entsüklopeediakirjastus, Tallinn.

Karing, P. 1992. *Air Temperature in Estonia.* Valgus, Tallinn.

Kivisikk, A. 1939. Raudkullist Puurmanni metskonnas [The Sparrowhawk in Puurmanni forest district]. *Eesti Looduskaitse*, **4**, 150 (in Estonian).

Kolga, E. 1933. How to kill Goshawks? *Eesti Mets*, **1933**, 157–159.

Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? *J. Anim. Ecol.*, **63**, 619–628.

Leibak, E., Lilleleht, V. & Veromann, H. (eds) 1994. *Birds of Estonia. Status, Distribution and Numbers*. Estonian Academy Publishers, Tallinn.

Lõhmus, A. 1997. Röövlindude arvukuse muutustest Loode-Tartumaal. [Population changes of raptors and owls in northwestern Tartumaa]. *Hirundo*, **10**, 4–16 (in Estonian with English summary).

Lõhmus, A. 1999. Vole-induced regular fluctuations in Estonian owl populations. *Ann. Zool. Fenn.*, **36**, 167–178.

Lõhmus, A. 2004. Eesti röövlinnuseire 1999–2003: kanakulli kadu ja hiiretsüklite kellavärk [Monitoring of raptors and owls in Estonia, 1999–2003: decline of the Goshawk and the clockwork of vole-cycles]. *Hirundo*, **17**, 3–18 (in Estonian with English summary).

Lõhmus, A. & Väli, Ü. 2004. The effects of habitat quality and female size on the productivity of the Lesser Spotted Eagle *Aquila pomarina* in the light of the alternative prey hypothesis. *J. Avian Biol.*, **35**, 455–464.

Mander, Ü. & Palang, H. 1999. Landscape changes in Estonia: reasons, processes, consequences. In *Land-use Changes and Their Environmental Impact in Rural Areas in Europe* (Krönert, R., Baudry, J., Bowler, I. R. & Reenberg, A., eds), pp. 165–187. Parthenon.

Martenson, A. 1908. Der Abschuss von Raubvögeln. *Neue Baltische Waidmannsblätter*, **4**, 228–229.

Middendorff, M. v. 1910. Ein neues Verzeichnis der Vögel Estlands. *Neue Baltische Waidmannsblätter*, **6**, 145–151.

Newton, I. 1979. *Population Ecology of Raptors*. Poyser, Berkhamsted.

Newton, I. 2002. Population limitation in Holarctic owls. In *Ecology and Conservation of Owls* (Newton, I., Kavanagh, R., Olsen, J. & Taylor, I., eds), pp. 3–29. CSIRO Publishing, Collingwood.

Randla, T. 1976. *Eesti röövlinnud* [*Estonian Birds of Prey*]. Valgus, Tallinn (in Estonian with English summary).

Rootsmäe, I. & Rootsmäe, L. 1983. *Die Ornitologische Literatur Estlands*. Tartu.

R. V. 1921. Hävitagem röövloomi ja -linde [Extirpate carnivores and raptorial birds!] *Eesti Kütt*, **3**, 29–30 (in Estonian).

Sass, F. 1901. Raubvogeljagd am Horst. *Baltische Waidmannsblätter*, **1**, 328–329.

Schönfeldt, v. 1909. Abschussliste von Könhof und Charlottenthal in Livland, vom 1. Febr. 1908 bis 1. Februar 1909. *Neue Baltische Waidmannsblätter*, **5**, 135–136.

Selås, V. & Steel, C. 1998. Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis. *Oecologia*, **116**, 449–455.

Sivers, E. v. 1914. Abschuss-Tabelle Gut Euseküll vom 1. März 1908 bis zum 1. März 1914. *Neue Baltische Waidmannsblätter*, **10**, 345.

Steen, H., Yoccoz, N. G. & Ims, R. A. 1990. Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations. *Oikos*, **59**, 115–120.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *J. Anim. Ecol.*, **73**, 167–178.

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton.

Tuule, E., Tuule, A. & Lõhmus, A. 2011. Fifty-year dynamics in a temperate raptor assemblage. *Est. J. Ecol.*, **60**, 132–142.

Vietinghoff, O. & Engelhardt, E. 1901. Livländischer Verein von Liebhabern der Jagd. Protokoll der Generalversammlung am 26. Januar 1901. *Baltische Waidmannsblätter*, **1**, 108–112.

Vietinghoff, O. & Engelhardt, E. 1902. Livländischer Verein von Liebhabern der Jagd. Protokoll der Generalversammlung vom 25. Januar 1902. *Baltische Waidmannsblätter*, **2**, 103–106.

Viksne, J. (ed.) 1983. *Birds of Latvia. Territorial Distribution and Number*. Zinatne, Riga.

Wasmuth, P. 1909. Aufzählung aller bisher für Estland festgestellten Vogelarten. *Korrespondenzblatt des Naturforscher-Vereins zu Riga*, **52**, 29–72.

Kolmeaastased tsüklid “kullisõdade” andmestikus: pisinäriliste arvukustsüklite peegeldus?

Asko Lõhmus

Röövlindude sigivuses ja arvukuses on Eestis vähemalt 1970. aastatest teada pisiimetajate (eeskätt uruhiirte) arvukustsüklitest tulenev 3–4-aastase sammuga perioodilisus. Käesolevas töös uuriti, kas niisugust tsüklilist dünaamikat on võimalik

tuvastada ka märksa varasema aja kohta, kasutades selleks röövlindude süstemaatilise tapmise (nn kullisõdade) andmeid Eesti- ja Liivimaa kohta aastatest 1890–1908. Mõlema kubermangu kohta käivas andmestikus ilmnes kolmeaastane perioodilisus ja selle miinimumaastad langesid kokku. Uruhiirlastest toituvad liigid moodustasid materjalist küll suhteliselt väikese osa, aga teistegi liikide arvukus fluktueerus sarnaselt (sh tavalisima liigi, raudkulli arvukus sarnaselt hiireviu omaga). Tõenäoliselt on leitud mustri põhjuseks röövlindude sigivuse muutused, mis seega järgisid samasugust kolmeaastast uruhiiretsüklit 19/20. sajandi vahetusel, nagu on teada ka kahest viimasest aastakümnest. Tsüklite rekonstruktsioon võimaldab seletada mõningaid ajalooliselt teadaolevaid röövlindude invasioone. Samuti viitab Liivimaa andmestik “kullisõdade” jooksul toimunud arvukuse vähenemisele kulliliste populatsioonides.