J Ornithol (2016) 157:419–425
DOI 10.1007/s10336-015-1306-2

ORIGINAL ARTICLE

Extracting historical population trends using archival ringing data—an example: the globally threatened Aquatic Warbler

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Received: 16 September 2015 / Accepted: 5 November 2015 / Published online: 8 December 2015

Abstract Understanding how animal population size changes over time is one of the key means to identify threats and facilitate the successful implementation of conservation measures. The globally endangered Aquatic Warbler has undergone a major decline throughout its range. While in the first half of the 20th century, it was still an abundant species across major parts of Central and Western Europe, over the last century the size of its European population is considered to have declined by more than 90 %. However, little is known of the historical changes in its population size. Here we model the past population size of the Aquatic Warbler using historical ringing records of European ringing schemes and population monitoring software (TRends for Indices and Monitoring). We found that during the short 30-year period between 1950 and 1980 the European Aquatic Warbler population underwent a dramatic 95 % decline. According to this model, the population has recently been stable, no further decline was observed between 1980 and the late 1990s.

Keywords *Acrocephalus paludicola* · Bird ringing · Population change · TRends for indices and monitoring

Zusammenfassung

Rekonstruktion früherer Populations-Trends anhand archivierter Beringungsdaten am Beispiel des weltweit bedrohten Seggenrohrsängers (*Acrocephalus paludicola*)

Zu wissen, wie sich die Größen von Populationen über die Zeit verändern, ist im Naturschutz entscheidend wichtig für das Verstehen zukünftiger Bedrohungen und für Entscheidungen, mit welchen Maßnahmen man erfolgreich gegen sie vorgehen kann. Die Bestände des weltweit bedrohten Seggenrohrsängers gehen auf breiter Front zurück. In der ersten Hälfte des 20. Jahrhunderts gab es noch Populationen in weiten Bereichen Zentral- und Westeuropas, aber im letzten Jahrhundert sind die Populationen um mehr als 90 % zurückgegangen, wobei über die früheren, historischen Veränderungen der Populationsgrößen jedoch nur sehr wenig bekannt ist. In unserer Untersuchung modellierten wir frühere Populationsgrößen des Seggenrohrsängers mit Hilfe alter Beringungsdaten europäischer Beringungsprojekte und einer für Populationsuntersuchungen erstellten Software (TRends for Indices and Moniotoring—TRIM). Wir haben festgestellt, dass die europäische Population des Seggenrohrsängers nur allein in den 30 Jahren von 1950 bis 1980 um dramatische 95 % zurückgegangen ist. Das Modell zeigt ferner, dass sich die Population in letzter Zeit stabilisiert hat; zwischen 1980 und den späten 1990er Jahren konnte kein weiterer Rückgang mehr beobachtet werden.

Communicated by F. Bairlein.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-015-1306-2) contains supplementary material, which is available to authorized users.

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Introduction

Many bird species have faced severe population declines during the past decades (BirdLife International 2004; Bonebrake et al. 2010). Among the most affected are wetland and farmland breeding species along with long-distance migrants (Böhning-Gaese 1992; Böhning-Gaese and Bauer 1996; Laaksonen and Lehikoinen 2013; Sanderson et al. 2006; Thaxter et al. 2010; Vickery et al. 2014). For wetland and farmland birds, the main causal factor for the decline has been the deterioration and loss of breeding habitats (Berthold 1993; Böhning-Gaese and Bauer 1996; Kozulin and Flade 1999). Declines in the density of breeding birds throughout the breeding range have also frequently been reported in long-distance migrants. Unfavourable conditions at non-breeding grounds, such as drought in Sahel and carry-over effects, have been mentioned as some of the main factors underlying these declines (Laaksonen and Lehikoinen 2013; Norris et al. 2004; Svensson 1985; Thaxter et al. 2010).

For most of these species detailed knowledge on large-scale population trends are available only for the last three to four decades. However, many species have experienced changes in population size due to large-scale habitat transformation in Europe during the second half of the 20th century and even earlier [for example, see Norris (1947) for the Corncrake (*Crex crex*)]. Historical ringing records for many species are the only available source of quantitative data for greater part of the 20th century. The number of birds captured and ringed over a long period of time can provide data on changes in population size and distribution (Hjort and Lindholm 1978; Österlöf and Stolt 1982; Žídková et al. 2007). Furthermore, ringing data are collected using standardized methods which allow for not only local country-wide analysis but also meta-analyses on a large geographic scale, i.e. pan-European. However, such data must be carefully controlled to avoid biases resulting from changes in ringing habits and intensity (Hochachka and Fiedler 2008).

In the study reported here we focussed on an iconic species which has experienced widespread decline in its distributional range and local breeding numbers—the Aquatic Warbler *Acrocephalus paludicola*. It is the only globally threatened Passerine species in continental Europe. It breeds in a very specific habitat that is restricted to particular types of fen mires in Europe and is a long-distance migrant (Kloskowski and Krogulec 1999; Kozulin and Flade 1999), spending the non-breeding period in sub-Saharan Africa (Baker 1997; Flade and Lachmann 2008). In the first half of the 20th century, the Aquatic Warbler was still an abundant species across major parts of Central and Western Europe (Schäffer et al. 2006), but over the last century the size of its European population is considered to have declined by more than 90 % (Flade et al. 2011; Kozulin and Flade 1999). The current European population size is estimated at 10,300–13,800 singing males (Flade et al. 2011), with a breeding area of <375 km^2 (Flade and Lachmann 2008). More than 80 % of the current breeding population is concentrated in only four sites in Belarus, Ukraine and Poland (Flade and Lachmann 2008). Three ringing expeditions carried out in 1999, 2000 and 2001 confirmed the existence of a West Siberian Aquatic Warbler population. However, the known size of this Siberian population was small (Flade 2001), and it is most likely now extinct. Unfortunately, there is no reliable data of population estimates before 1995 when the Belarusian and later Ukrainian populations were discovered (Kozulin and Flade 1999).

We used archival ringing records for the Aquatic Warbler to model its historical European population size by using the population monitoring software TRends for Indices and Monitoring (TRIM; Pannekoek and van Strien 2005). TRIM can calculate annual indices of population size even if the data set is incomplete. The aim of this study was to reconstruct the historical change in the size of the European population of the Aquatic Warbler. We hypothesized that during the 20th century (1) the size of this population declined by more than 90 % and (2) this decline took place in a stepwise manner consisting of a few but very rapid decreases that reflect habitat destruction—and not as a steady decline over time.

Materials and methods

For the greater part of the 20th century, the annual number of ringed individuals per country was the only available large-scale quantitative data source of information on the historical population status of the Aquatic Warbler to be collected in a standardized manner. Other data sources, such as skin and egg collections in museums and/or published observations, contain many gaps and are of variable temporal coverage. Therefore, for our model, we collected data on the total number of Aquatic Warblers ringed annually by 27 European ringing schemes and Morocco (see Electronic Supplementary Material Table S1). We considered only data on ringed adult and juvenile birds and excluded nestlings (pulli).

Since both the intensity and nature of bird ringing have changed over the last century we selected two species with known population sizes as a reference—the Reed Warbler *Acrocephalus scirpaceus* and the Sedge Warbler *A. schoenobaenus*. By indexing the number of ringed reference species to the number of ringed Aquatic Warblers, we were able to control for changes in ringing intensity. Up to very recent times, the majority of Aquatic Warblers were ringed during migration when they were captured as by-catch during the trapping of other migratory songbirds. The two reference species were selected because during migration they use similar habitats as the Aquatic Warbler and are more abundant than the Aquatic Warbler (and thus are captured much more frequently at the same capture sites). Our data analysis was based on the assumption that all Aquatic Warblers were ringed randomly—i.e. bird ringers used every opportunity to ring any bird captured and no selective ringing of Aquatic Warblers took place. Thus, the probability of encountering Aquatic Warblers should be higher when the population level is high and more birds are present. Consequently, we excluded the data collected by a Belgian ringing scheme from our analysis due to its use of playbacks to specifically attract, capture and ring Aquatic Warblers (N. Roothaert, personal communication). We also excluded data from a 1984 Bulgarian ringing scheme in which the ringing of 183 fully-grown Aquatic Warblers was reported (Nankinov 1984). This number was very contradictory to the Bulgarian data of other years during which zero to three annual captures of Aquatic Warblers were reported, suggesting that the 1984 data represented a clear case of species misidentification. We restricted our analyses to years prior to 1998, as in recent years there have been increased targeted efforts (by using playbacks) in the ringing of this species throughout Europe (Jiguet et al. 2011; Musseau et al. 2014; Provost et al. 2010).

We used the bird population monitoring data software TRIM v3.53 (Pannekoek and van Strien 2005) to analyse the ringing data. TRIM is designed for time-series analyses of counts with missing values, and it calculates annual indices of species by using data rows from various observation points (sample plots). For TRIM to work successfully, the data rows must overlap. TRIM is an application of loglinear models to the analysis of monitoring data, also referred to as “Poisson regression”. The model used takes into account the effects of each site and each time-point (Pannekoek and van Strien 2005):

$$\ln \mu_{ij} = \alpha_I + \gamma_j,$$

where α_I is the effect of site, and γ_j is the effect of the year on the natural logarithm of the expected count value of μ_{ij}.

Each ringing scheme was treated as a separate study site. TRIM indices were calculated using a time–effect model with overdispersion and serial correlation. Bird population monitoring programs usually express changes in population size as changes in an index relative to the reference year. In order to restore an unknown historical population size, backcalculation from a recent year with known population size was used.

To model the historical population size of the Aquatic Warbler, we first calculated the TRIM indices for this species and for the two reference species (Reed Warbler and Sedge Warbler) and then calculated population indices for the reference species from 1980 to 1997 [source: EBCC (European Bird Census Council) 2012]. Due to the lack of data, we made the assumption that EBCC population indices prior to 1980 were constant at the level calculated for 1980. Although by making this assumption we were not able to compensate for year-by-year variation before 1980, the major trend was still reliable. We then calculated annual quotients of the TRIM indices for the Aquatic Warbler and the two reference species, weighted by their EBCC indices. Next we determined the maximum and minimum population size of the Aquatic Warbler in 1997—the first year with a reliable population estimate (AWCT 1999). The calculated quotients were then used as population indices, with the 1997 value assigned to be the reference year. The historical population size was backcalculated from this reference year.

The final model was

$$AW_{pj} = R_{i(\mathrm{EBCC})j} \times AW_{i(\mathrm{TRIM})j} \times AW_{p1997} \times R_{i(\mathrm{TRIM})1997} \times AW^{-1}_{i(\mathrm{TRIM})1997} \times R^{-1}_{i(\mathrm{EBCC})1997} \times R^{-1}_{i(\mathrm{TRIM})j},$$

where AW_{pj} is the size of the Aquatic Warbler population p in the year j; $R_{i(\mathrm{EBCC})j}$is the EBCC population index of the reference species in the year j; $AW_{i(\mathrm{TRIM})j}$ is the TRIM index of the Aquatic Warbler in the year j; AW_{p1997} is the absolute size of the Aquatic Warbler population in 1997; $R_{i(\mathrm{TRIM})1997}$ is the TRIM index of reference species in 1997; $AW_{i(\mathrm{TRIM})1997}$ is the TRIM index of the Aquatic Warbler in 1997; $R_{i(\mathrm{EBCC})1997}$ is the EBCC population index of reference species in 1997; $R_{i(\mathrm{TRIM})j}$ is the TRIM index of reference species in the year j.

Pearson correlation analysis was used to determine the similarity of models derived from the Reed and Sedge Warblers.

Results

We collected data on 2263 Aquatic Warblers ringed during the period 1930–1997 (Table 1) and calculated TRIM indices of the number of ringed individuals for the period from 1947 to 1997. Our calculation of indices prior to 1947 failed due to the low number of ringed birds. The TRIM indices of the number of ringed Aquatic Warblers thus calculated showed a tenfold increase in the 1990s compared to the late 1940s (Fig. 1). During the same period, the TRIM indices of the numbers of the selected reference species, the Reed Warbler and Sedge Warbler, showed a 200- and 3000-fold increase, respectively.

Table 1 Number of ringed Aquatic Warblers *Acrocephalus paludicola* per ringing scheme and period of available data

Ringing scheme	Period	Total ringed	Source
Bulgaria (BGS)	1976–1983	10[a]	EURING Databank
Channel Islands (CIJ)	1975–1985	78	EURING Databank
Croatia (HRZ)	1947–1985; 1988; 1990–1997	52	EURING Databank
Czechoslovakia (CSP)	1934–1942; 1947–1948; 1951–1952; 1964–1980	77	EURING Databank
Denmark (DKC)	1909–1997	17	www.zmuc.dk
Estonia (ETM)	1909–1997	1	EURING Databank
Finland (SFH)	1909–1997	1	Finnish Ringing Scheme'; M. Piha, personal communication
France (FRP)	1975–1985	147	EURING Databank
Germany, Helgoland (DEW)	1957; 1962;1964; 1966–1997	106	EURING Databank
Germany, Hiddensee (DEH)	1975–1997	147	EURING Databank
Germany, Radolfzell (DER)	1957–1981; 1992–1997	219	EURING Databank
Hungary (HGB)	1908–1932; 1951–1997	30	EURING Databank
Italy (IAB)	1909–1997	13	EURING Databank
Latvia (LVR)	1924–1997	29	Latvian Ringing Scheme; J. Kazubiernis, personal communication
Lithuania (LIK)	1929–1997	40	Ž. Priekša, personal communication
Morocco (MAR)	1975–1984	7	EURING Databank
Netherlands (NLA)	1909–1997	297	EURING Databank
Norway (NOS)	1975–1982	1	EURING Databank
Poland (PLG)	1932–1962; 1975–1982	56	EURING Databank
Portugal (POL)	1976–1983	26	EURING Databank
Russia (RUM)	1909–1982; 1988–1995; 1997	6	EURING Databank
Slovenia (SLL)	1975–1984	13	EURING Databank
Spain, ICONA (ESI)	1973–1982	7	EURING Databank
Spain, San Sebastian (ESA)	1980–1997	97	EURING Databank
Spain, SEO (ESM)	1975–1982	4	EURING Databank
Sweden (SVS)	1909–1997	17	EURING Databank
Switzerland (HES)	1924–1997	78	E. Wiprächtiger, personal communication
United Kingdom & Ireland (GBT)	1909–1997	687	www.bto.com
Total		2263	

EURING, European Union for Bird Ringing, BGS, Bulgaria, Sofia; CIJ, Channel Islands, Jersey; HRZ, Hrvatska, Zagreb; CSP, Czechoslovakia, Prague; DKC, Denmark, Copenhagen; ETM, Estonia, Matsalu; SFH, Suomi/Finland, Helsinki; FRP, France, Paris; DEW, Deutschland, Wilhelmshaven; DEH, Deutschland, Hidensee; DER, Deutschland, Radolfzell; HGB, Hungary, Budapest; IAB, Italia, Bolonia; LVR, Latvia, Riga; LIK, Lithuania, Kaunas; MAR, Morocco, Rabat; NLA, Netherlands, Arnhem; NOS, Norway, Stavanger; PLG, Poland, Gdansk; POL, Portugal, Lisbon; RUM, Russia, Moscow; SLL, Slovenia, Ljubljana; ESI, Espana, ICONA; ESA, Espana, Aranzadi; ESM, Espana, Madrid; SVS, Sverige, Stockholm; HES, Helvetia, Sempach; GBT, Great Britain, Tring

[a] Data collected in 1984 were excluded from the analysis (see text for details)

The estimated population size for the Aquatic Warbler in 1948 ranged from 470,000 to 740,000 individuals when the Reed Warbler was used as the reference species and from 420,000 to 670 000 individuals when the Sedge Warbler was the reference species (Fig. 2). Both models show a rapid decrease in Aquatic Warbler population size in late 1940s and 1950s. From 1948 to 1963, the Aquatic Warbler population was estimated to have declined by more than five-fold—from approximately 500,000 to <100,000 individuals. The population size continued to decrease until 1980, but at a lower rate. Between 1980 and 1997, the population level was stable, and our analysis detected no further decline. Both models show a strong similarity in population estimates ($r = 0.965$; $p < 0.001$; $n = 51$).

Discussion

Ringing records have a great potential as a population monitoring tool to study changes in the abundance and distribution of bird species. Archival records can be of exceptional value as they provide quantitative, comparable

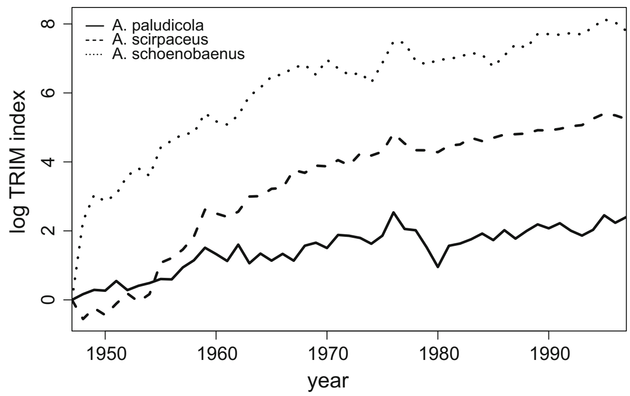


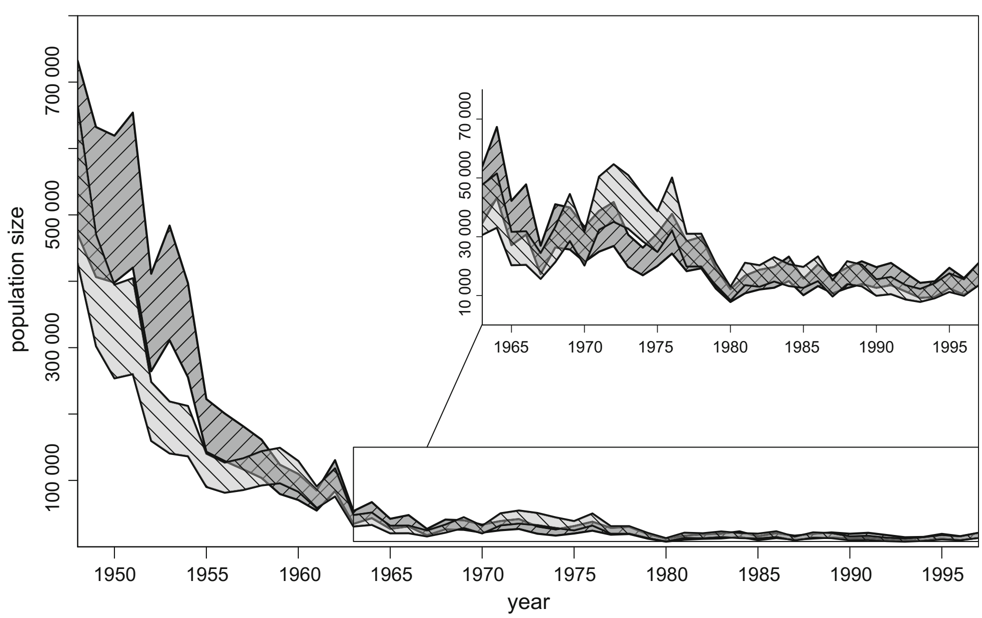
Fig. 1 TRends for Indices and Monitoring (TRIM) indices of the ringed Aquatic Warbler (*Acrocephalus paludicola*) (*solid line*), Reed Warbler (*A. scirpaceus*) (*dashed line*) and Sedge Warbler (*A. schoenobaenus*) (*dotted line*)

data from periods when standardized population monitoring techniques had not yet been developed. In the study reported here, we adopted a novel approach of using archival ringing data to study changes in population size using the population monitoring software TRIM. To date, TRIM has been used successfully to monitor populations using data collected by traditional bird censuses (EBCC 2012; Gregory et al. 2005). Keišs et al. (2007) adopted the quite simple approach of using archival ringing data and TRIM to reconstruct the population trends of Corncrakes. The TRIM indices thus calculated show changes in bird abundances compared to the reference year. By treating each ringing scheme across Europe as a bird census study site we were able to use TRIM analysis under the same conditions as those for regular bird counts. Raw TRIM indices for ringing data do not show changes in species abundance but rather changes in the number of birds ringed. Over the long term, they reflect changes in bird ringing intensity and habits (e.g. the introduction of mist-nets in the 1950s and 1960s; Hochachka and Fiedler 2008; Saurola 1987; Rintala et al. 2003). Consequently, a between-species comparison is needed to correct for this variation in ringing effort. In our study, we chose to compare the TRIM indices calculated for the Aquatic Warbler with those calculated for two species—Reed Warbler and Sedge Warbler—that use similar habitats during migration and for which the historical population status is known. These two species have also been impacted by the same advancement of ringing technologies and—most likely—the same catching effort by ringers.

When modelling the historical size of the Aquatic Warbler population, we used EBCC population indices (EBCC 2012) of the selected reference species from 1980 to 1997 to compensate for year-to-year population fluctuations. Unfortunately there are no annual data on species indices prior to 1980. Consequently, we lost information on annual population fluctuations, while preserving the major population trend. European populations of both the Reed Warbler and Sedge Warbler have remained relatively stable or even slightly increased since the mid-20th century, with the numbers of both species having declined in Western Europe and expanding further north (Hagemeijer and Blair 1997). Thus, while possible changes in the population sizes of the reference species could have had an effect on the modelled population size of the Aquatic Warbler, we suggest that the influence is minor due to the relatively stable population sizes of the reference species.

Our results suggest that the size of the European population of the Aquatic Warbler has declined by more than

Fig. 2 Modelled population size for the Aquatic warbler from 1948 to 1997. *Inset* Detailed estimates for 1963–1997. *Ranges* indicate estimated minimum and maximum population sizes. *Different shading* Models using different reference species: *dark grey* Reed Warbler, *light grey* Sedge Warbler



95 %—from approximately 500,000 individuals in the late 1940s to approximately 20,000 individuals in late 1990s. During the 20th century, the Aquatic Warbler became extinct in most parts of Western Europe (Flade 2008). Formerly it was known to breed in France, Belgium, the Netherlands, Italy, Austria, former West Germany, the former Czechoslovakia and former Yugoslavia (Cramp 1992). Studies from the core area of the current population show a 80–90 % decline during the last 30 years of the 20th century (AWCT 1999; Kozulin and Flade 1999). However, these estimates were based on the number of suitable breeding habitats lost due to degradation rather than on changes in Aquatic Warbler abundance. Population estimates before 1995 are unreliable because Belarusian and Ukrainian populations were still unknown then; currently they hold more than 50 % of the known global Aquatic Warbler population. Flousek and Cepák (2013) also reported a major decline in the ringed Aquatic Warbler/Reed Warbler ratio from 1960 to 2011 in the Czech Republic, with a relatively stable Reed Warbler population. These data suggest that the population size of the Aquatic Warbler has decreased accordingly.

Results from our study show two waves of decline in population size. A rapid decline took place from the late 1940s to the early 1960s, which we believe corresponds to the time when the population became extinct in Western Europe as large areas of wetlands were drained. It is estimated that in the former West Germany alone 30,000 km^2 or more of its 44,000 km^2 wetlands were drained after the World War II (van der Ploeg and Sieker 1999). The Aquatic Warbler population continues to decline after the 1960s, but at a more steady pace until 1980. This period of decline could correspond to the drainage of suitable habitats in Central and Eastern Europe, which took place considerably later than in Western Europe. In Belarus alone, 15,000 km^2 of suitable habitats have been drained since 1960 (Flade 2008). On the contrary, in late 1950s and early 1960s there was an increasing occurrence of Aquatic Warbler in West Siberia and along the eastern Mediterranean flyway (Aquatic Warbler Conservation Team 1999). One hypothesis for this phenomenon could be a large-scale relocation of breeding populations from Europe to West Siberia due to habitat destruction in Europe.

In our study we have shown how archival ringing data can be used to reconstruct the previously unknown historical population size of a currently endangered species. Our data suggest that the Aquatic Warbler population underwent a dramatic 95 % decline across Europe in just the 30-year period extending from 1950 to 1980. The present-day core breeding areas of this species are in Poland, Belarus and Ukraine and are under protection; no rapid declines have been observed for the last two decades. However, further identification and protection of non-breeding grounds are necessary, along with future research on this species' migratory connectivity.

Acknowledgements We gratefully acknowledge the Swiss Ornithological Institute in Sempach, Switzerland for support during the data collection, particularly Verena Keller and Christian Marti. We thank Peter Adamík, Nicholas Friedman and three anonymous referees for their comments on an earlier version of this manuscript. During the study Martins Briedis was supported by the ESF project to support MSc studies at the Faculty of Biology, University of Latvia. During the preparation of the manuscript Oskars Keišs was supported by the ESF project Nr. 2014/0009/1DP/1.1.1.2.0/13/APIA/VIAA/044 to the Institute of Biology, University of Latvia. The study complies with the current laws of the Republic of Latvia.

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