Black-headed Gull (*Larus ridibundus* L.) as a Keystone Species in the Lake Bird Community in Primary Forest-Mire-Lake Ecosystem

AIVAR LEITO [1,] *, MEELIS LEIVITS [2], AGU LEIVITS [3], JANAR RAET [1], RAYMOND WARD [1,4], INGMAR OTT [1], HARDI TULLUS [5], RAUL ROSENVALD [5], KAI KIMMEL [6] AND KALEV SEPP [1,]**

[1] *Institute of Agriculture and Environmental Sciences, Estonian University of Life Sciences, 5 Kreutzwaldi Str., 51014 Tartu, Estonia*

[2] *Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, 46 Vanemuise Str., 51014 Tartu, Estonia*

[3] *Environmental Board, 7a Narva St., 15172 Tallinn, Estonia*

[4] *School of Environment and Technology, University of Brighton, Cockcroft Building, Lewes Road, 11 Brighton, BN2 4GJ, United Kingdom*

[5] *Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, 5 Kreutzwaldi St., 13 51014 Tartu, Estonia*

[6] *Environmental Board, Jõgeva-Tartu Region, 2 Aia Str., 48306 Jõgeva, Estonia*

** Corresponding author: Tel: +3725153995; E-mail: aivar.leito@emu.ee*

*** Corresponding author: Tel: +3727313777; E-mail: kalev.sepp@emu.ee*

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Abstract

Within animal communities the loss of a single keystone species can lead to substantial change, or in extreme cases, community collapse. This phenomenon has been documented in different communities and habitats but has not been widely investigated in bird communities. We studied the long-term dynamics of breeding birds in a medium-sized hemiboreal lake that is situated within a large primary forest-mire-lake ecosystem in central-east of Estonia. The aim of this 25 year study was to determine whether the black-headed gull, *Larus ridibundus*, acts as a keystone species in the bird community and what was the effect of the loss of this species. Results revealed large changes in the bird community similar to those that would occur in a fragile system in response to keystone species loss, confirming our theory. Mallard *Anas platyrhynchos*, common pochard *Aythya ferina*, tufted duck *Aythya fuligula*, great crested grebe *Podiceps cristatus*, red-necked grebe *Podiceps grisegena*, Eurasian marsh harrier *Circus aeruginosus*, spotted crake *Porzana porzana*, coot *Fulica atra*, and common tern *Sterna hirundo* were most closely related to the abundance of black-headed gull. During the study period there was little change in habitat quality or extent. It is unclear as to the causes of the gull colony collapse; however, landscape-level changes in feeding areas and agricultural land could be a reason. We conclude that further study of keystone species and fragile communities in different habitats and ecosystems is important to ascertain which species and communities are most likely to be affected in the event of the loss of a keystone bird species.

Key words: Keystone species, bird community, forest-mire-lake ecosystem, fragile system, species richness.

Introduction

Lake bird communities are affected by the properties of the lake and its surroundings as well as by the regional species pool (Sala et al. 2000, Dawson et al. 2011, Hilli-Lukkarinen et al. 2011, Vīksne et al. 2011, Kajzer et al. 2012, Saurola et al. 2013, Skorka et al. 2014, Arzel et al. 2015). Natural fluctuations in those factors are usually long-term (Belleau et al. 2011), although human influence can accelerate these processes (Long et al. 2007) and can directly or indirectly, positively or negatively affect lake bird communities (Robledano et al. 2010, Hilli-Lukkarinen et al. 2011). Several studies have predicted population decreases and localised extinctions in a wide variety of habitats and animal species as a result of climate change, the overexploitation of natural resources, and habitat fragmentation (including woodland) (Hanski 2000, Myers and Worm 2003, Thomas et al. 2004, Seppälä et al. 2009, Dawson et al. 2011, Cahill et al. 2012). The mechanisms that enable the coexistence of interacting species can break down when a species is lost from a community, which leads to a sequence of secondary extinctions (Ebenman and Jonsson 2005). Such secondary extinctions or coextinctions have been previously observed in several natural communities, and, in the worst case, the loss of a single species can lead to the collapse of the community (Paine 1966, Estes and Palmisano 1974, Koh et al. 2004, Ebenman and Jonsson 2005). A question is thus posed 'are there particular types of species (keystone species) whose loss is likely to have serious effects on the continued existence of other species and hence on the long-term persistence of the community?' Furthermore, to what extent is the keystone status and vulnerability of a species context-dependent? The answers to these questions are crucial to the prediction of the response of ecological communities to species loss (Ebenman and Jonsson 2005). It is therefore of great importance to ascertain which species and communities are most likely to be threatened.

The focus of this study was on the relationships between different bird species, particularly protective nesting associations, between the black-headed gull *Larus ridibundus* and the waterfowl that have a crucial role in the determination of the species composition, diversity, and abundance of the breeding bird community in boreal and sub-boreal eutrophic lakes (Väänänen 2000, 2011, Quinn and Ueta 2008, Vīksne et al. 2010, 2011, Nummi et al. 2012). Most "protected" associates on this type of lakes are found in the *Anseriformes*, particularly ducks, and most "protective" associates originate from the *Charadriiformes*, particularly gulls and terns (Quinn and Ueta 2008, Vīksne et al. 2011, Väänänen 2011). In addition to lakes, protective nesting associations in birds have been described in many other habitats, such as forest, farmland, island, and tundra, with different protected and protective species (reviewed in Quinn and Ueta 2008). Although various nesting associations in birds and other animals have long been recognised, these associations continue to provide many novel research opportunities because it is a complicated field with a great diversity of strategies to limit predation (Popham 1897, Durango 1954, Haemig 2001, Vīksne et al. 2011).

This study took place in the Endla forest-mire-lake ecosystem, in Estonia. Predominant environmental variables affecting the wider study area are precipitation/evaporation and their impacts on lake, wetland and forest water levels influencing plant communities, tree growth and peat deposition (Valk 1988, Robroek et al. 2007, Kimmel 2009, Smiljanić et al. 2014). The aim of the present study was to analyse the response of the black-headed gull on breeding bird community species composition, richness, diversity, dissimilarity, turnover rate, and abundance to determine whether the black-headed gull acts as a keystone species and whether the crash of the gull colony would cause the collapse of the bird community in a hemiboreal lake. For this purpose, we used the total counts of breeding birds at natural mesotrophic Lake Endla in Estonia due to the availability of a long term dataset recorded between 1987 and 2012. A limited number of case studies have analysed the effect of black-headed gull colonies on the bird community based on valid long-term total counts of all breeding bird species in a lake (e. g. Vīksne et al. 2005, 2011).

We hypothesised that clear differences in community parameters would be detected during periods characterised by the presence and absence of the black-headed gull colony. We predicted the greatest differences in total abundance and fewer changes in abundance and the relative share of some bird species following the disappearance of black-headed gull colony. The confirmation of these predicted changes indicates that this type of community is in fact a fragile system that can break down or markedly change as a result of the loss of a keystone species, such as the black-headed gull, which triggers a cascade of shifts in the community, as described before in different ecosystems (Koh et al. 2004, Ebenman and Jonsson 2005, Woodward et al. 2005, Quinn and Ueta 2008). The total population of black-headed gull, as well as common pochard *Aythya ferina*, tufted duck *Aythya fuligula*, and several surface-feeding ducks that are closely associated with gull colonies, have declined in Estonia, Finland, Latvia, Lithuania, over recent decades (Elts et al. 2009, 2013, Vīksne et al. 2010, 2011, Väänänen 2011, Pöysä et al. 2013, Estonian State Environmental Monitoring Programme 2015). In addition, due to this simultaneous decline, it is important to understand the relationships of these species in the community and identify the most likely associated reasons for their local decline and extinction.

Material and methods

There are two main approaches that can be used to perform a community viability analysis, dynamic or static analysis, each of which has advantages and disadvantages and require different types of community data (Ebenman and Jonsson 2005). In a dynamic analysis, selected for use in this study, changes in species population over time and the indirect effects that these changes have on the abundance of other species are taken into account. A dynamic community analysis can be applied to natural communities if a method can be found to estimate the intrinsic growth rates of species and the strength of the interactions among species. Two possible methods to estimate these parameters are to infer these from the body size of species using allometric scaling relationships and to estimate the parameter using numerical abundance data and the equilibrium assumption (Yodzis and Innes 1992, Jonsson and Ebenman 1998, Emmerson and Rafaelli 2004, Woodward et al. 2005).

Study area

Lake Endla is located in the central-east of Estonia (central coordinates: 58°51'N and 26°11'E) in a hemiboreal mixed forest zone (Hämet-Ahti 1981). The lake is situated in the southern margin of the Endla Mire System, the majority of which is composed of open and semi-open pool rich pine bogs, pine forest and wooded mires forming a large forest-mire-lake ecosystem. The total area of Lake Endla is 482 ha and the catchment area is 43,300 ha, 42% of which is covered by forests and 21% both by bogs and arable land (EELIS 2015). The area of open water of the Lake Endla is 287 ha and the total area of quagmire and water-growing reed bed 153 ha. The lake is edged with a 10–150 m wide belt of emergent vegetation and quagmire (Fig. 1). There are six mineral islets (area 0.7–29.2 ha) in the lake, which exhibit a total area of 42 ha. There are also floating vegetation "islets" covered with reeds and other aquatic macrophytes and single willow shrubs. The main colony was situated on one of these floating islets "Gulls islet", with an area of 14 ha. The lake is shallow with an average depth of 1.6 m and a maximum depth of 2.4 m. Lake Endla is a mixotrophic (dyseutrophic) lake with moderate nutrient content, medium water hardness and high organic content (Mäemets 1977). Lake Endla freezes over from December to April and is colonised anew each spring by migrating birds.

Altogether 84 species of vascular macrophytes have been recorded in Endla Lake (Viljasoo 1959, Mäemets 1968, Ott 2011, I. Ott, H. Mäemets and K. Palmik pers. comm.). The most abundant and important aquatic macrophytes for nesting birds were *Phragmites australis*, *Equisetum fluviatile*, *Carex* spp., *Schoenoplectus lacustris*, *Menyanthes trifoliata* and *Nymphaea* sp. The lake has a high fish productivity (10 kg/ha) and contains nine species, providing an important food resource for the bird population. The most abundant fish species is *Rutilus*

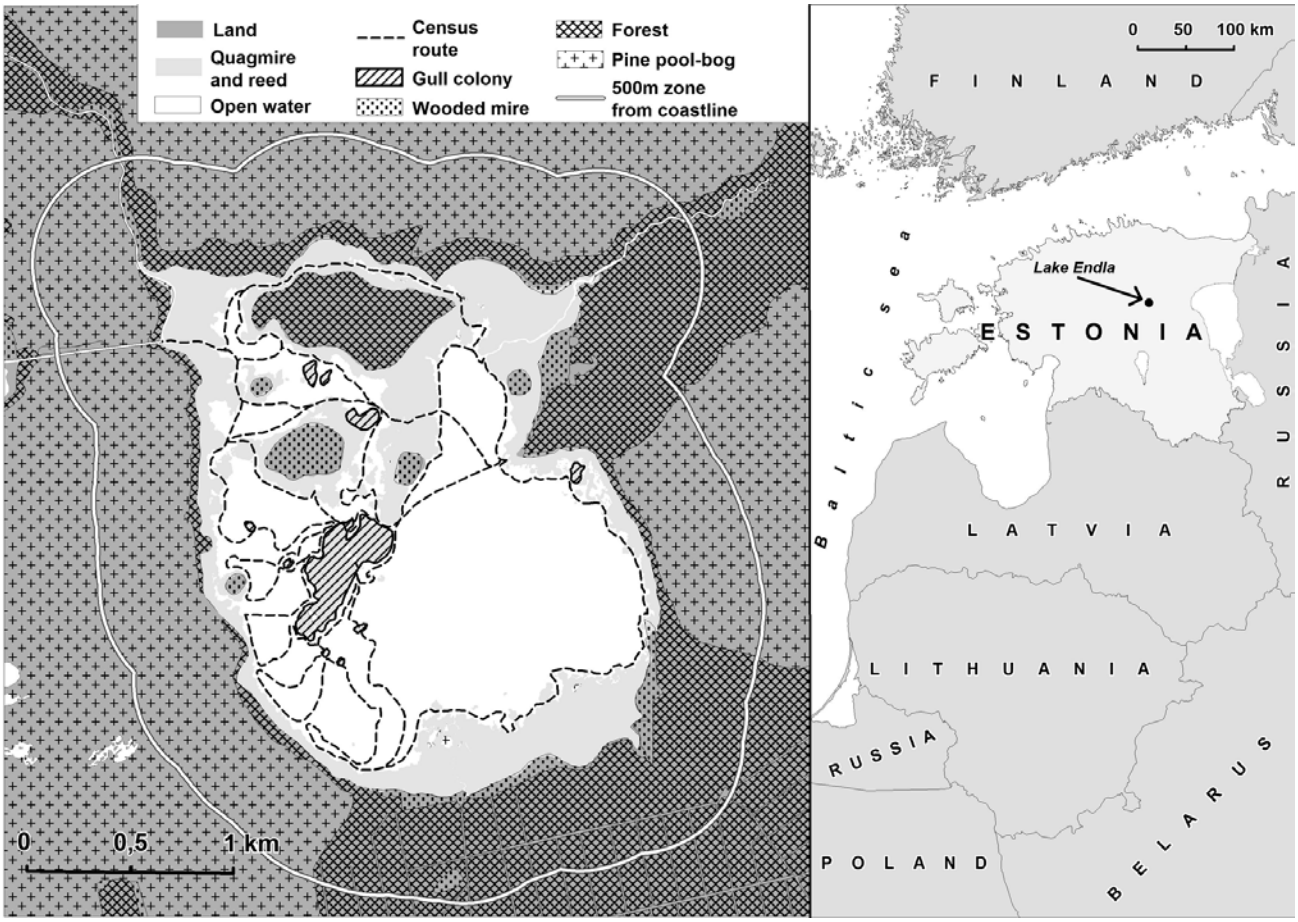

Figure 1. Location of the study area, main habitats, and black-headed gull colonies

rutilus, followed by *Perca fluviatilis* and *Tinca tinca* (Mäemets 1968). In Lake Endla fish species abundance and diversity has undergone minimal change during the study period (Ott 2011). In addition to fish inhabiting Lake Endla amphibian prey species are *Rana arvalis* (the most numerous), *Rana temporaria*, *Bufo bufo* and *Rana* kl. *esculenta* (Rannap 2012). The Eurasian marsh harrier *Circus aeruginosus*, white-tailed eagle *Haliaeetus albicilla*, and hooded crow *Corvus cornix* are the most common birds of prey in the lake. The Eurasian marsh harrier nests in reed beds at the lake, hooded crow in trees on the lake shore and islands. One pair of white-tailed eagles nests in the forest close to the lake. In addition, a single common raven *Corvus corax* preys on duck and gull eggs and chicks within the area. *Nyctereutes procyonides* and *Mustela vison* are the most important predator mammals of ground-breeding bird's nests in the lake.

Lake Endla is predominantly surrounded by pine pool-bogs, pine forests and paludified forests (Fig. 1 and Table 1). The nearest inhabited farm is situated 3 km southeast of the lake. Extensive drainage of peatland and forest at the edges of the Endla mire system was carried out between the 1950s and 1980s influencing water levels in the lake during these periods (Masing 1957, Valk 1988, Kimmel 2009). Lake Endla is one of the core areas of the Endla Nature Reserve (area 10,161 ha), which was established in 1985 and is a part of the Endla Ramsar Site and the Natura 2000 area (EELIS 2015, Ramsar Secretariat 2015).

Table 1. Main biotopes in hectares within 500 m of Lake Endla between 1989 and 2006

Biotope	1989	2006	Change
Forest	254	213	-41
Pine pool-bog	278	319	+41
Wooded mire	15	16	+1
Stream	3	2	-1
Other	7	7	
Total area	557	557	0

Bird counts

Breeding birds were counted in the last days of May in 20 of the years over the 25-year period between 1987 and 2012. No surveys were conducted during 1990, 1992, 1993, 1995, 2010 and 2012 due to financial constraints. The end of May is an optimal time for single counts as the lake is no longer frozen and the vegetation canopy is still quite open facilitating visibility. Additionally, all of the bird species have started to nest by late May. Breeding pairs were mapped (scale = 1:10,000) by boat using a permanent census transect covering the whole lake, with the exception of the mineral islets (Fig. 1). Nest findings, records of singing birds, and records of non-singing birds that displayed behaviour consistent with probable or confirmed nesting according to the instructions of the Estonian Bird Atlas (Renno 1993) were located on a map. Specifically, breeding pairs of duck were defined by identifying a nest, small chicks or sessile pair (a female and male acting together). Based on these data, breeding pairs were defined and marked on the survey map. More specifically, gull colonies were counted based on single birds at the moment of take-off from nests, and the number of pairs calculated by halving the count. Large colonies were partially counted and totals estimated. Nocturnal birds were counted passively by song and other voices. All counts were recorded between 15:00 to 24:00 and were continued the following morning from 5:00 to 11:00. As a result, the peak activity periods of both diurnal and nocturnal bird species were recorded. All surveys were performed by the same observer, Aivar Leito. The single mapping method was used in place of the two-time censuses that are usually currently recommended in northern Europe (Koskimies and Väisänen 1991, Vesilintujen laskentaohjeet 2013) as this study commenced prior to the publication and wide application of this methodology. The census method was not changed during this study to ensure uniform and compatible data from all of the censuses. The census data and the number of species are provided in the Appendix.

Data analysis

Mean numbers (M), standard deviations (SD), coefficients of variation (CV %), and trends in the numbers of breeding bird species were calculated using the census data recorded between 1987 and 2012 (Appendix 1). The Mann-Kendall trend test (McLeod 2011) was used to assess the existence and significance of monotonic trends in the time series. TRIM, as a widely used and accepted loglinear Poisson regression method was used for the time series analysis of count data (Pannekoek and van Strien 2001). The overall trend estimates between 1987 and 2012 was calculated using the TRIM type 2 software and provided in the multiplicative slope and according to the trend class (Table 2). All possible changepoints were used to estimate the model. The first year of the time series was chosen as the base-year for all species, except those with zero-abundance during that year. For species with zero counts in the first year, the first year in the time series with positive counts was chosen as the base-year. Margalef's evenness index (MG) and Shannon-Wiener's diversity index (H') were then calculated. Margalef's index was calculated using the following function:

$$MG = (S_i-1) / \ln N_i,$$

where S_i is the number of species and N_i is the number of species i (Magurran 1988, Oksanen et al. 2011).

Table 2. Multiplicative slope estimates of TRIM type 2 models with changepoints 1 and 14 (years 1987 and 2000) and the Wald test for the significance of the changepoint at year 2000. Z = Wald test statistic; sl8799 = multiplicative slope for the period 1987–1999 (gull colony was present); sl0012 = multiplicative slope for the period 2000–2012 (gull colony was absent). The bird species are shown as 3+3 first letter acronyms of the full Latin name and in alphabetical order. Significance (*P*) levels: *** < 0.001, ** < 0.01, * < 0.05, and · < 0.1. The species without any values (empty spaces) were too occasional for the estimation of the trend slopes

Species	sl8799	se8799	sl0012	se0012	Z	*P*-value	*P*-level
Acraru	0.99	0.02	0.96	0.03	0.3	0.581	
Acrsch	1.11	0.05	1.01	0.03	1.7	0.188	
Acrsci	1.26	0.09	1.02	0.04	5.5	0.019	*
Acthyp	0.71	0.07	1.27	0.17	7.3	0.007	**
Anacre	0.84	0.04	0.95	0.10	0.9	0.354	
Anapen	0.92	0.05	0.95	0.09	0.1	0.761	
Anapla	0.90	0.02	0.78	0.06	2.3	0.127	
Anaque	1.03	0.06	0.77	0.09	3.7	0.055	·
Aytfer	1.10	0.05	0.45	0.13	8.5	0.004	**
Aytful	1.10	0.06	0.49	0.15	6.5	0.011	*
Botste	0.94	0.03	1.06	0.04	3.5	0.060	·
Buccla	0.98	0.04	0.92	0.06	0.3	0.569	
Chlnig	1.10	0.06	0.80	0.07	6.2	0.013	*
Ciraer	1.06	0.01	0.93	0.01	41.9	0.000	***
Cygcyg	1.20	0.32	1.27	0.11	0.0	0.857	
Cygolo	1.31	0.09	1.08	0.03	5.4	0.020	*
Embsch	1.14	0.03	1.03	0.02	7.7	0.006	**
Fulatr	0.98	0.04	0.78	0.08	3.7	0.055	·
Galchl	1.22	0.14	0.64	0.13	5.9	0.015	*
Galgal	1.01	0.04	0.90	0.06	1.5	0.222	
Gavarc	1.07	0.11	0.98	0.10	0.2	0.631	
Grugru	1.05	0.02	1.06	0.02	0.1	0.831	
Lararg	0.95	0.05	0.75	0.12	1.6	0.207	
Larcan	0.98	0.03	1.00	0.05	0.1	0.792	
Larmin	1.10	0.13	0.48	0.30	1.6	0.210	
Larrid	0.93	0.03	0.45	0.16	4.0	0.045	*
Loclus	1.32	0.08	0.97	0.03	16.7	0.000	***
Motalb	1.04	0.12	0.94	0.13	0.2	0.654	
Motfla	0.86	0.04	1.08	0.08	3.8	0.053	·
Podcri	0.99	0.03	0.71	0.06	10.0	0.002	**
Porpar	1.13	0.17	1.22	0.09	0.2	0.687	
Porpor	1.06	0.04	0.73	0.06	13.6	0.000	***
Ralaqu	0.96	0.03	1.11	0.04	6.2	0.013	*
Stehir	0.94	0.04	0.86	0.07	0.8	0.363	
Trigla	1.05	0.03	0.98	0.04	1.1	0.293	

The species turnover rate (STO) was then estimated (Table 2) using the following function:

$$STO = 0.5\ (I + E),$$

where I is the number of new species and E is the number of extinct species (Schoener 1988, Hilli-Lukkarinen 2011). If the dataset has missing counts, the imputed counts given by TRIM were used to calculate the values of E and I. Community turnover rate was calculated as the percentage of dissimilarity. The dissimilarity of the communities in different years was measured using the percentage dissimilarity index (PDI):

$$PDI = 1 - PS,$$

where $PS = \sum \min (p_{i1}, p_{i2}, \ldots, p_{in})$ and p is the proportion of pairs of species i in the previous and the following years (Suhonen et al. 2009, Hilli-Lukkarinen 2011) (Table 3). The Mann-Whitney *U* test was used to estimate the presence-absence effect of the black-headed gull colony on the numbers of different bird species (Table 4). In addition to the comparison of species abundance related to the presence/ absence of the gull colony, species population trends were analysed at different periods. Trends in the numbers of breeding pairs in the periods characterised by the presence/absence of the gull colony were calculated with TRIM using a two changepoint model. The first changepoint was the initial year of the data series, and the second changepoint the year 2000, as this year marked the period without the gull colony (Table 2). All of basic analyses (S, SD, CV, H', MG, STO, and PDI) were made using R (R Development Core Team 2010).

Biotopes were described for Lake Endla and a 500 m buffer zone from the shoreline to describe the surrounding area. Estonian Basic map and state forest database from 2006 were used for habitat characterising (Figure 1). To identify changes in biotope during the study period another geographic dataset was created and used based on the Estonian Cadastral map from the 1980's. To characterize the changes in the agricultural land, we used FAOSTAT (2014) database.

Results

Changes in landscape

According to our measurements the area and relative share of the pine pool-bog and wooded mire together (+41 ha; 7.4 % of total area 557 ha) has increased and the area and relative share of the forest (–41 ha; 7.4 % of total area 557 ha) has decreased in the 500 m zone around the Lake Endla from 1989 to 2006 (Table 1). The main process leading to the decrease in forest area in the Endla forest-mire-lake ecosystem has most likely been the natu-

Table 3. Relative change in the breeding bird community at Lake Endla between 1987 and 2012.
E = number of extinct species; I = number of new species; STO = species turnover rate; PDI = percentage dissimilarity of the bird community; H' = Shannon-Wiener's index; MG = Margalef's index. The calculations are based on the imputed counts (TRIM)

Year	E	I	STO	PDI	H'	MG
1987					0.18	3.38
1988	3	2	2.5	0.01	0.23	3.32
1989	3	2	2.5	0.01	0.19	3.11
1990	0	4	2.0	0.01	0.21	3.55
1991	5	2	3.5	0.01	0.25	3.21
1992	3	6	4.5	0.01	0.28	3.56
1993	1	0	0.5	0.01	0.33	3.46
1994	3	1	2.0	0.02	0.41	3.25
1995	1	5	3.0	0.01	0.43	3.73
1996	4	2	3.0	0.01	0.48	3.53
1997	3	4	3.5	0.01	0.44	3.61
1998	5	1	3.0	0.01	0.40	3.19
1999	5	6	5.5	0.07	0.72	3.64
2000	6	4	5.0	0.57	2.15	4.27
2001	5	1	3.0	0.42	1.95	3.96
2002	2	6	4.0	0.65	1.53	4.06
2003	10	2	6.0	0.51	1.89	3.06
2004	1	9	5.0	0.26	1.90	4.56
2005	11	0	5.5	0.12	1.49	2.67
2006	4	8	6.0	0.10	1.50	3.15
2007	5	11	8.0	0.14	1.51	4.17
2008	7	4	5.5	0.08	1.41	3.71
2009	4	3	3.5	0.04	1.44	3.61
2010	4	2	3.0	0.04	1.42	3.36
2011	1	0	0.5	0.03	1.41	3.26
2012	1	2	1.5	0.04	1.52	3.50

ral growth of bogs due to a positive water balance leading to forest paludification. Despite the general change in the surrounding area the extent, distribution and relative importance of the main biotopes (open water, quagmire, reed, floating islets and mineral islets) and potential food resources (vertebrate and invertebrate fauna and vegetation) for birds were not substantially altered in Lake Endla during the study period (Estonian State Environmental Monitoring Programme 2015). Agricultural land is of importance as a feeding area for gulls and considerable alterations in agricultural land use took place during the study period, the greatest changes occurring at the same time as the gull colony crash (Figure 2).

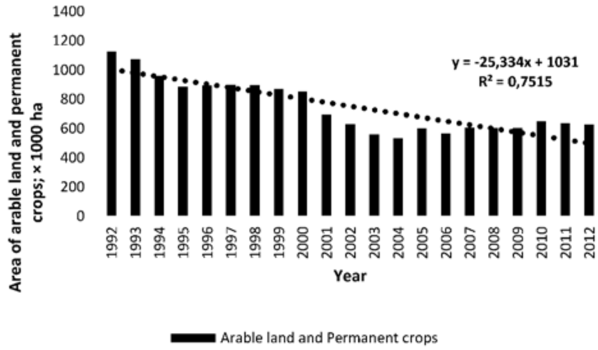

Figure 2. Area of arable land and permanent crops in Estonia in 1992–2012

Trends and community structure

At Lake Endla, 46 bird species from eight orders bred between 1987 and 2012 (Appendix 1). In any given year, 17–32 species (mean ± *SD* = 26.75 ± 4.22; *CV* = 16 %; *n* = 20 years) were observed to breed. There was a significant negative linear trend in the number of species during the study period (Mann-Kendall trend test, τ = –0.625, $P < 0.001$, $n = 20$).

At the beginning of the census period, the turnover rate was $STO_{1987} = 0.86 \pm 0.94$ (E ± SE), and, at the end of the census period, $STO_{2009} = 5.72 \pm 0.94$ (E ± SE). Thus, there was a substantial increase in the turnover rate between 1987 and 2009 ($\Delta STO = 4.87 \pm 1.87$). Assuming a linear increase in the turnover rate, we calculated a yearly increase in the turnover rate of 0.21 ± 0.08 %/year ($P < 0.01$, Wald χ^2 test) during this period. The community turnover, which was measured by the dissimilarity (PDI), varied from 0.001 to 0.65 (Table 3). The maximum dissimilarity was observed between 2000 and 2004, when the dissimilarity was approximately fivefold higher than that observed in other years during the study period. Shannon-Wiener's index (H') varied from 0.18 (in 1987) to 2.15 (in 2000), and Margalef's index (MG) varied from 2.67 (in 2005) to 4.56 (in 2004) (Table 3). In general, all of the main community characteristics (STO, PDI, H', and MG) exhibited a positive trend over the study period, but their variability rate and dynamics were different. The variability, instability, and species compositional change of the community increased considerably in the 2000s after the disappearance of the black-headed gull colony, and these processes have been coherent (Tables 2, 3 and 4; Figures 2 and 3; Appendix 1). The first recorded breeding of mute swan *Cygnus olor* was observed in 1991, whooper swan *Cygnus cygnus* in 1998, and the species pintail *Anas acuta*, northern shoveler *Anas clypeata*, common pochard *Aythya ferina*, and great crested grebe *Podiceps cristatus* disappeared as breeding bird species during the study period (Appendix 1). Of the identified breeding bird species 5 belong to Category II protected species in Estonia, 12 to Category III of protected species and 13 are listed in Annex I of the EC Bird Directive.

Table 4. Mean numbers of single bird species in the years characterised by the presence of the black-headed gull colony and in the years characterised with the absence of the colony. The bird species are shown as 3+3 first letter acronyms of the full Latin name and in alphabetical order. N1 = mean numbers in the years without the colony; N2 = mean numbers in the years with the colony; W = statistic of the Mann-Whitney *U* test; *P* = significance value. Significance (*P*) levels: *** < 0.001, ** < 0.01, * < 0.05, and · < 0.1

Species	N1	N2	W	*P-value*	*P-level*
Acraru	11.4	17.3	14	0.012	*
Acrsch	216.8	88.4	87	0.001	***
Acrsci	5	1.1	86	0.001	***
Acthyp	0	0.8	20	0.010	**
Anacly	0.1	2.4	17	0.009	**
Anacre	0.5	3.4	17.5	0.021	*
Anapen	0.6	1.9	14	0.008	**
Anapla	1.9	17.1	1.5	0.000	***
Anaque	0.8	2.3	25	0.100	·
Aytfer	4.2	33.2	9	0.003	**
Aytful	7.4	48.6	10.5	0.005	**
Buccla	0.5	1.3	20	0.028	*
Cygolo	5.4	1.1	86	0.001	***
Embsch	96.5	40.2	84	0.001	***
Fulatr	6.7	23.8	2	0.000	***
Galgal	1.1	2.1	24	0.083	·
Grugru	6.6	3.9	75	0.014	*
Lancol	0.6	0	58.5	0.093	·
Lararg	0.2	1.1	8	0.001	***
Larmin	0.1	3	13	0.004	**
Loclus	20	6	84	0.002	**
Motalb	0	1.1	20	0.010	**
Podcri	2.6	7.2	14.5	0.013	*
Podgri	0	1.2	15	0.003	**
Stehir	2.4	10.1	4.5	0.001	***

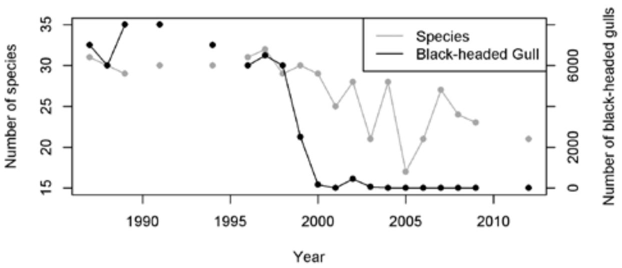

Figure 3. Annual number of breeding bird species and numbers of the black-headed gull colony at Lake Endla in 1987–2012

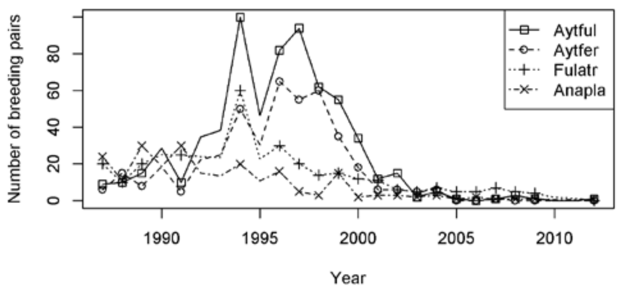

Figure 4. Counts of mallard, pochard, tufted duck, and coot at Lake Endla in 1987–2012

The role of black-headed gull

The total number of breeding pairs recorded between 1987 and 2012, including the black-headed gull colony, varied between 305 and 8,301 pairs (mean ± *SD* = 3,276 ± 3,341; *n* = 20 years), and the year on year variation (CV) was 102% (Appendix 1). The total number of breeding pairs discounting black-headed gull varied between 175 (in 1987) and 571 (in 2006) pairs (average ± *SD* = 392.2 ± 115.8; *n* = 20 years), and the CV was 29%. In the years when the black-headed gull colony was present and dominated, the relative share of this species was 58–97 % of the total breeding pairs of all species. In the years when the black-headed gull colony was absent, sedge warbler *Acrocephalus schoenobaenus* dominated. In the time period in which the black-headed gull colony was present, the CV of the total breeding pairs was 11%, whereas, in the time period in which this colony was absent, the CV was 25 %. The total number of breeding pairs was strongly related to the presence/absence and size of the black-headed gull colony, which varied between 0 and 8,000 pairs (average ± *SD* = 2,884 ± 3,375; *n* = 20 years; Figure 3 and Appendix 1). In the period in which the colony was at its peak (1987–1998), the total number of breeding pairs of all species was 10–15 fold higher than that observed during the period in which this colony disappeared and was absent (the 2000s). The long term population dynamics of the black-headed gull colony can be divided into three different periods: a steady peak period between 1987 and 1998 (11 years), a rapid decrease (colony collapse) between 1999 and 2000 (2 years), and a period characterised by very low numbers or absence between 2001 and 2012 (Figure 3 and Appendix 1). This latter period could be characterised as post-collapse fluctuation.

The two changepoint trend model suggested that the presence of the gull colony has a positive significant effect ($P < 0.05$) on the trends of common pochard, tufted duck, great crested grebe, Eurasian marsh harrier, spotted crake *Porzana porzana*, and black tern *Chlidonias niger* and a significant negative effect ($P < 0.05$) on the trends of mute swan, water rail *Rallus aquaticus*, Savi's warbler *Locustella luscinoides*, sedge warbler, reed warbler *Acrocephalus*

Appendix 1. Bird counts in pairs and their basic statistics at Lake Endla, Estonia, between 1987 and 2012

Bird species	1987	1988	1989	1991	1994	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2012	Mean	SD	CV%
Cygnus olor				1		2	1	4	2	2	4	3	4	5	6	5	11	7	7	6	3.5	3	86
Cygnus cygnus [1,2]								1								1	2	1	1	2	0.4	0.7	175
Anas penelope	1	2	2	5	2	1	1	2	1			1				1	1	2	1		1.1	1.2	109
Anas crecca	5	4	5	10	4		1	2				1		1		1		1	1		1.8	2.6	144
Anas platyrhynchos	24	11	30	30	20	16	5	3	15	2	3	3	2	3	1	2	1	1	1	1	8.7	10.1	120
Anas acuta			1	3																	0.2	0.7	350
Anas querquedula	1	2	1	3		6	5		3	1	1		2	2	1		1				1.4	1.7	121
Anas clypeata	1		10		3	2	4	2		1											1.1	2.4	218
Aythya ferina	6	15	8	5	50	65	55	60	35	18	6	6	5	6			1				17.1	22.4	131
Aythya fuligula	9	10	15	10	100	82	94	62	55	34	12	15	2	5	1		1	3	1	1	25.6	33.6	131
Bucephala clangula	1	1	1	1	2	1	3		2		1			1			1	1	1		0.8	0.8	100
Gavia arctica [1,2]				1	1					1		1				1		1			0.3	0.5	167
Podiceps cristatus	5	7	10	10	5	14	9	3	2	7	8	2	3	3		3					4.5	4.1	91
Podiceps grisegena	1			2	2	1	3		2												0.6	0.9	150
Botaurus stellaris [1,2]	1	1	2	3	2	2	1	1	1	1	1	1		1	1	1	1	1	3	2	1.4	0.7	50
Circus aeruginosus [1,3]	3	3	3	3	3	5	6	6	5	5	5	5	6	3	6	4	4	3	3	2	4.2	1.3	31
Circus pygargus [1,3]	1																				0	0.2	0
Rallus aquaticus [3]	3	2	2	2	2	5	1	2	1	2	3	1	2	2	3	1	1	6	6	6	2.6	1.7	65
Porzana porzana [1,3]	4	8	2		4	13	10	6	10	11	7	1		8			4			1	4.5	4.4	98
Porzana parva [1,2]							1							1	1		2		1	2	0.4	0.7	175
Crex crex [1,3]										1							1				0.1	0.3	150
Gallinula chloropus [3]		2							3	3	3	2		1							0.7	1.2	171
Fulica atra	20	10	20	25	60	30	20	14	15	12	11	6	5	7	5	5	7	5	4		14.1	13.4	95
Grus grus [1,3]	2	3	3	3	4	4	4	6	6	5	4	3	6	6	6	9	8	9	10	9	5.5	2.4	44
Gallinago gallinago	2	2	1	2	3	1	3	3	2	3	2	1		3					2	2	1.6	1.1	69
Tringa glareola [3]	1	1	1	1	1	3	2	1	3	1	1	1	2	3	2		2	1	3	1	1.6	0.9	56
Actitis hypoleuca	2	2	1	1		1														1	0.4	0.7	175
Vanellus vanellus									1												0	0.2	0
Larus minutus [1,2]	1	1	1	1	2		5	16									1				1.4	3.6	257
Larus ridibundus	7000	6000	8000	8000	7000	6000	6500	6000	2500	170	1	450	55				8		1		2884	3375	117
Larus canus	1	2	4	4	2	1	3	1	3	1	2	3		2	1	3	5	2	2		2.1	1.3	62
Larus argentatus	1	1	1	2	1	1	1	1	1				1	1							0.6	0.6	100
Sterna hirundo [1,3]	10	10	7	15	20	3	13	8	5	2	2	7	1	2			4	4	2	1	5.8	5.5	95
Chlidonias niger [1,3]	5	8	13	15	50	40	30	25		43		45	55	5		35		1			18.5	19.8	107
Clidonias leucopterus										1											0	0.2	0
Motacilla flava [3]	1	3	2	3		2						1		2		1	1	1			0.8	1	200
Motacilla alba					3	2	1	1	3											2	0.6	1	167
Saxicola rubetra											1										0	0.2	0
Luscinia luscinoides	2	1			2	10	11	14	14	14	19	12	30	14	27	26	25	20	13	7	13.1	9.3	71
Acrocephalus schoenobaenus	40	60	40	75	87	135	154	111	94	137	153	139	187	185	210	308	306	286	257	160	156.2	83.3	53
Acrocephalus scirpaceus		1			2	2	1	2	2	2	5	2	6	6	7	8	4	4	6	2	3.1	2.5	81
Acrocephalus palustris													2								0.1	0.4	400
Acrocephalus arundinaceus	11	19	13	20	20	27	13	12	21	10	8	9	8	18	20	16	8	8	9	11	14.1	5.6	38
Panurus biarmicus									1	1											0.1	0.3	300
Lanius collurio [1,3]												2				2		2		1	0.4	0.7	175
Emberiza schoeniclus	10	5	14	45	40	58	62	53	75	71	72	48	118	76	105	138	102	124	111	85	70.6	38.1	54
Pairs total	7175	6197	8213	8301	7497	6535	7023	6422	2883	562	335	771	502	372	403	571	513	494	446	305	3276	3341	102
Number of species	31	30	29	29	30	31	32	29	30	29	25	28	21	28	17	21	27	24	23	21	26.75	4.22	16

[1]Annex I species of the Bird Directive (n=13). [2] Category II protected species in Estonia (n=5). [3] Category III protected species in Estonia (n=12)

scirpaceus, and reed bunting *Emberiza scoeniclus* (Table 2). The comparison of the mean numbers of breeding pairs through the Mann-Whitney *U* test suggested that the presence of the gull colony had a significant ($P < 0.05$) positive effect on the abundance of northern shoveler, wigeon *Anas penelope*, mallard, common pochard, tufted duck, great crested grebe, red-necked grebe *Podiceps grisegena*, coot *Fulica atra*, little gull *Larus minutus*, herring gull *Larus argentatus*, and common tern *Sterna hirundo*, and the absence of the gull colony had a significant positive effect to the abundance of mute swan, Savi's warbler, sedge warbler, reed warbler, and reed bunting (Table 4). After the crash of the black-headed gull colony, northern shoveler, common pochard, great crested grebe and red-necked grebe disappeared (Appendix 1). The long-term dynamics of pochard and tufted duck, which are species that are highly associated with the black-headed gull colony, were very similar (Figure 4 and Appendix 1). The abundance of these species can be classified into four different periods: a steady growth period between 1987 and 1994 (7 years), a peak period between 1994 and 1999 (5 years), a strong decrease (population crash) between 1999 and 2001 (3 years), and steady a decrease up to their disappearance or very low numbers between 2001 and 2012 (11 years).

Discussion and conclusions

According to our results, system-wide changes took place in the bird community at Lake Endla during the study period. There was a large variation and an overall decreasing trend in the number of species and the total abundance of birds. As expected, species richness and diversity decreased during the study period, and the variation in the species richness, diversity, and dissimilarity exhibited the greatest fluctuations during the 5 to 7 years following the collapse of the black-headed gull colony (Figure 3, Table 3 and Appendix 1). The importance of the black-headed gull colony on the bird community was evident: it had a strong positive effect during the peak period of the colony. After black-headed gull die out from the study wetland populations of many duck species decreased sharply. According to Ebenman and Jonsson (2005), the loss of keystone species can cause the loss of one or more additional species or trigger a cascade of secondary extinctions with potentially dramatic effects on the function and stability of the community. In our case, the loss of the black-headed gull colony did cause the disappearance of four waterfowl species, and the stability of the community was strongly affected. All of the basic parameters of the community, such as the species richness, diversity, and dominance, were changed.

Based on these indicators, we conclude that the initially rich bird community at Lake Endla broke down and was restructured after the collapse of the black-headed gull colony. Thus, it is possible that the temporal "peak" period with extremely high total abundance and species richness that was detected during the first ten years of the study period (1987–1999) was an "abnormal" fluctuation in the bird community and that a less rich and less diverse community is the more "normal" community because the occurrence of a large black-headed gull colony on this type of lake in a large wild mire system is atypical. The existence of bird communities with limited species richness has been confirmed by bird surveys in other similar lakes in Estonia, which usually found 10–15 bird species with approximately 100-500 total breeding pairs annually on this type of lake in the absence of the black-headed gull (Onno 1958, Estonian State Environmental Monitoring Programme 2015).

The black-headed gull had the strongest positive effect on waterfowl species, particularly pochard and tufted duck. The main benefit for waterfowl and other species breeding inside or close to the gull colony was likely predation protection (Hildén 1964, Väänänen 2000, Quinn and Ueta 2008, Väänänen 2011, Skorka et al. 2014). At Lake Endla, the main raptors are Eurasian marsh harrier, white-tailed eagle, and hooded crow, and the protection benefit of the gull colony for waterfowl against these raptors was likely considerable. It is notable that pochard and tufted duck reached their peak abundance approximately five years after the peak of the black-headed gull colony, but their rapid and strong decrease coincided with the crash of the black-headed gull colony (Figure 3 and 4 and Appendix 1). This finding indicates a steady step-by-step immigration and adaptation to the gull colony at the beginning of the study period and a fast and coherent disappearance after the colony crash due to markedly increased nest predation by harriers and ravens and additional predation pressure by eagles and harriers on adult waterfowl, the numbers of which had already markedly decreased. Eurasian marsh harrier was found to have an evident positive relationship with the abundance of the black-headed gull, presumably through the trophic link, as gulls, in addition to waterfowl, amphibians, and small mammals, are an important food for harriers (von Blotzheim et al. 1971, Tornberg and Haapala 2013). It is interesting that marsh harrier reached their peak numbers of 5-6 pairs approximately five years after the peak of the black-headed gull colony, stayed at this maximum level for approximately ten years, and then steadily declined to an absolute minimum of 2 pairs over ten years. The comparison of the long-term dynamics of these two species revealed certain parallel but shifted trends among the species: the abundance of the marsh harrier follows the abundance of the black-headed gull with a delay of approximately ten years (Figure 3 and Appendix 1). In addition, this association is different from that found with common pochard and tufted duck, which exhibited a similar population growth period but a different rapid decline period that coincided directly with the crash of the black-headed gull colony and the following disappearance process. Potentially, the food source particularly of fish may play leading role in duck populations in lakes (Vīksne et al. 2010, 2011, Nummi et al. 2012) but in Lake Endla there has not found any considerable changes in fish species composition and abundance of different species and in total during the last decades (Mäemets 1968, 1977, Ott 2011).

A case study at Lake Engure in Latvia revealed similar findings regarding the relationship between black-headed gull colonies and waterfowl species to those found in our study (Vīksne et al. 2005, 2011). According to Väänänen (2000, 2011), the breeding of tufted duck and common pochard in eutrophic inland lakes in Finland is strongly related to colonial larids, particularly black-headed gull, and the main benefit that has been found is the protection against predators. As in our study, other waterfowl, ducks, and coots exhibited a weaker association with larid colonies. In addition, quite similar general results have been obtained in other studies on different bird communities in Europe and America (Quinn and Ueta 2008, Vīksne et al. 2010).

It has been recognised that anthropogenic stress increases the short-term variability of ecological communities (Angeler and Moreno 2007, Hillebrand et al. 2010). However, there has been limited human activity in Lake Endla, therefore there must be other factors that caused the rapid shifts in the bird community. The most considerable shifts in the community were associated with the abundance of the black-headed gull. Concurrently, other unrelated community changes took place. Both mute and whooper swan colonised the lake for the first time during our study period, and their population growth was likely mainly caused by the expansion and population increase of species over a larger surrounding area connected with climate-dependent changes in the distribution range (von Haartman 1973, Renno 1993, Väisänen et al. 1998, Saurola et al. 2013). The same reasoning could be applied to the population growth of the Eurasian crane and Savi's warbler at Lake Endla (Elts et al. 2009, 2013).

The reasons for the crash of the black-headed gull colony at Lake Endla are unknown. No external signs, including viral infection or toxic poisoning causing high mortality, increased nest predation, or habitat loss, were observed. Although this type of obscure disappearance of black-headed gull colonies is not rare and has been documented several times in different areas, and for which there is still no explanation (Kumari 1978, von Blotzheim and Bauer 1982, Ilitchev and Zubakin 1988, Vīksne et al. 2011). According to Vīksne et al. (2011), the reduction in the population size of the black-headed gull and waterfowls at Lake Engure was associated with the increase in American mink population size in the surrounding farms. However, this can be discounted as a factor at Lake Endla as there have never been American mink or other fur farms in this area.

Potentially, one cause of collapse of the colony at Lake Endla and the decrease in numbers of black-headed gull throughout Estonia (Elts et al. 2013) could be a decrease in feeding habitat and food resources. One of the main feeding habitats for black-headed gull during the breeding season are arable lands and meadows where they feed on invertebrates (predominantly earthworms, spiders and insects) and young shoots of different crops particularly of cabbage and turnip (von Blotzheim and Bauer 1982, Ilichev and Zubakin 1988). The area of agricultural land in Estonia decreased by almost fifty percent (Figure 2) and the crop type changed unfavourably for gulls between 1992 and 2012: the planting of summer and winter rape has increased dramatically (FAOSTAT 2014). Generally, agricultural intensification is harmful for farmland birds (Donald et al. 2006, Herzon et al. 2008). As elsewhere in Europe, agricultural intensification has taken place in Estonia (wheat yields per hectare have doubled and rapeseed tripled between 1992 and 2012) (FAOSTAT 2014), potentially another negative impact for black-headed gull. We don't have enough data to prove the connection between gull abundance and changes in agriculture, this is a question for a future study.

This study provides an important insight into the impacts of gull colony collapse on a lake bird community based on long-term observations, although further study is required including a greater number of lakes to identify if this is indicative of a wide ranging or local association. The reasons behind the gull colony crash are unknown, although it is possible that an unknown factor could also have been the cause for the changes in abundance of other bird species. However, other studies have shown shifts in bird communities following loss of the gull colony (e.g. Vīksne et al. 2011, Estonian State Environmental Monitoring Programme 2015).

In conclusion, our results show that the black-headed gull is a keystone species and that the bird community at Lake Endla has reacted to the loss of this species in a manner similar to that observed in a typical fragile system. In this case, the loss of a keystone species did not result in community collapse, but the post-extinction community is characterised by a significantly lower diversity and abundance of breeding birds. The main beneficial effect of the gull colony on waterbirds is likely to be the protection against predators, and the main reason for the strong decline and secondary extinction of several waterfowl species is likely closely related to the loss of the black-headed gull. We conclude that a large black-headed gull colony significantly enriches the bird community and the whole ecosystem, even though such a colony-dependent assembly is potentially fragile and may be short-lived.

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