Collapse of a protector species drives secondary endangerment in waterbird communities

Hannu Pöysä[a,], Esa Lammi[b], Silvo Pöysä[c], Veli-Matti Väänänen[d]

[a]Natural Resources Institute Finland, Natural Resources, Yliopistokatu 6, FI-80100 Joensuu, Finland
[b]Environmental Planning ENVIRO, Leilitie 1 B 12, FI-02230 Espoo, Finland
[c]Saviniementie 808, FI-52740 Tuustaipale, Finland
[d]University of Helsinki, Department of Forest Sciences, P.O. Box 27, FI-00014 Helsinki, Finland

Corresponding author:
Hannu Pöysä
Natural Resources Institute Finland, Natural Resources, Yliopistokatu 6, FI-80100 Joensuu, Finland
e-mail: hannu.poysa@luke.finland
Phone: +358 295 327 401

Abstract

Interactions and dependence between species can transmit the effects of species declines within and between trophic levels, resulting in secondary endangerments and, in some cases, extinctions. Many mixed-species avian breeding aggregations commonly have a protector species whose aggressive nest defense is used by other species to defend their nests. Disappearance of the protector species may have population demographic consequences on the dependent species. Aggressive nest defense behavior of small colonial gulls, such as the black-headed gull (*Chroicocephalus ridibundus*), is used by many waterbird species to gain protection against predators. We used data from 15 local waterbird communities in Finland to study long-term changes and dynamics of breeding numbers of other waterbirds as a response to long-term changes and dynamics of black-headed gull colonies. We found that breeding numbers of many species tracked long-term changes in the size of black-headed gull colonies. This was true even after controlling for a common trend in the size of the black-headed gull colony and the breeding numbers of the other species. The trend-controlled positive temporal association with black-headed gull was relatively stronger in species that nest in similar habitats of a lake as the black-headed gull, and in species that have a more critical conservation status due to drastic population decline. Our results suggest that the overall decline of black-headed gull colonies has resulted in secondary endangerment of many other species in waterbird communities.

Keywords
Conservation status; Gull colony; Population trend; Secondary endangerment; Species interaction; Threatened species

1. Introduction

Interactions and dependence between species can transmit the effects of primary extinctions within and between trophic levels, resulting in secondary extinctions and extinction cascades (Colwell et al., 2012). Such co-extinctions typically concern cases with direct causal links between extinctions such as a specialist herbivore going extinct along with its food plant (Colwell et al., 2012; Brodie et al., 2014). The loss of a predator species can also trigger secondary extinction cascades, as shown by Donohue et al. (2017) with a field experiment in a marine benthic system. Sanders et al. (2018) in turn demonstrated experimentally in a plant-insect community that harvesting one species of parasitoid wasp led to the secondary extinction of other, indirectly linked, species at the same trophic level. The risk of secondary extinctions may thus also concern systems in which the dependence between species is mediated via indirect links.

Many mixed-species avian breeding aggregations commonly have a protector species whose aggressive nest defense is used by other species to defend their nests (Groom, 1992; Haemig, 2001; Lima, 2009), with clear fitness consequences to the protected species (examples in Quinn and Ueta, 2008). Disappearance of the protector species may increase nest predation rates of the other species, with potentially drastic population demographic consequences. In such systems, where the dependence is not obligate, the loss or drastic decline of the protector species may not necessarily cause immediate secondary extinctions but secondary endangerments (sensu Brodie et al., 2014), probably causing unanticipated extinction debts (e.g., Kuussaari et al., 2009; Hylander and Ehrlén, 2013; Brodie et al., 2014).

Protective nesting associations occur in many avian orders (Quinn and Ueta, 2008) and have been recognized as potentially important for conservation, particularly for preserving avian biodiversity (Haemig, 2001). However, we still lack studies convincingly demonstrating the connection between the decrease or disappearance of a protector species and a consequent population decline of the protected species, although various numerical responses in the protected species have been documented. For example, Bogliani et al. (1999) studied the nesting association between the woodpigeon (*Columba palumbus*), the protected species, and the hobby (*Falco subbuteo*), the protector species. The authors found that predation rate of dummy woodpigeon nests was negatively correlated with the intensity of nest defense by the hobby pair. Interestingly, the number of real woodpigeon nests around the hobby nests was positively correlated with the number of fledglings produced by the hobby pair, the latter being associated with the intensity of nest defense by hobby pairs (Bogliani et al., 1999). Nesting associations between larids (protectors) and other waterbirds provide another example of widespread protective nesting associations in birds (Quinn and Ueta, 2008). In particular, aggressive nest defense behavior of small colonial gulls, such as the black-headed gull (*Chroicocephalus ridibundus*), is used by many waterbird species to gain protection against predators (Burger, 1984; Götmark, 1989; Väänänen, 2001; Väänänen et al., 2016). Breeding numbers and size of local black-headed gull colonies have decreased considerably during the last few decades Europe-wide, and the decrease of many other waterbird species is suggested to be associated with this decrease (e.g., Viksne et al., 2011; Fox et al., 2016a; Leito et al., 2016). For example, based on the IUCN criteria and categories, the threat assessment for Finnish birds in 2015 considered the black-headed gull as 'Vulnerable' and two diving duck species, known to be strongly associated with black-headed gull colonies, the common pochard (*Aythya ferina*) and tufted duck (*Aythya fuligula*) (Väänänen, 2001; Väänänen et al., 2016), as 'Endangered' (Tiainen et al., 2016). The status report by Tiainen et al. (2016) also considers several other waterbird species breeding in the same habitats as the black-headed gull as threatened or nearly threatened in Finland. The black-headed gull–other waterbirds system thus provides an excellent opportunity to study whether the decline of a protector species causes secondary endangerment of other species in the community. Indeed, Leito et al. (2016) studied long-term changes in breeding numbers of black-headed gulls and other waterbird species at Lake Endla, Estonia, and suggested that the loss of black-headed gulls resulted in lower diversity and abundance of breeding birds in the community. However, a potential problem with the analyses of Leito et al. (2016) is that the authors did not control for similar long-term trends in black-headed gulls and other species. This is important, because contemporary changes may not be directly inter-linked but rather responses to some common drivers, and therefore spurious with respect to presumed interspecific interactions (e.g., Lindström and Forchhammer, 2010; Iler et al., 2017; Pöysä and Väänänen, 2018). Clearly, further studies from other lakes and waterbird communities are urgently needed to assess the role of the black-headed gull in driving changes in breeding numbers of other waterbird species.

Here, we used data from 15 local waterbird communities in Finland to study long-term changes and dynamics of breeding numbers of other waterbirds as a response to long-term changes and dynamics of black-headed gull colonies. In these communities, black-headed gull colonies showed diverse dynamics, ranging from consistent long-term increase or decrease to abrupt local appearance/disappearance, making it possible to rule out common global drivers of population dynamics. We addressed three questions. First, using community-level data we asked: do other waterbird species show contemporary changes in breeding numbers along with the black-headed gull, after controlling for common long-term trends between them and the black-headed gull? Considering the protective function of gull colonies, we expected that similarity in nesting ecology between the black-headed gull and other species is potentially an important factor affecting the degree of interspecific dependence. To take an example, common pochard and tufted duck prefer nesting within or in the vicinity of gull colonies, whereas the mallard (*Anas platyrhynchos*) is highly flexible in nest sites and the common goldeneye (*Bucephala clangula*) is a cavity-nesting species. Both of the latter species typically nest far from gull colonies (Väänänen et al., 2016). The two first-mentioned species presumably benefit more from the protective function of black-headed gull colonies than the two last-mentioned species. Hence, our second question addressed the role of nesting ecology in the black-headed gull–other species interaction. We used trend-controlled temporal associations between the other species and the black-headed gull (i.e. the outcome from the first study question) and studied whether the risk of secondary endangerment due to the decline of black-headed gulls is associated with nesting ecology of the other species. Specifically, we hypothesized that the trend-controlled temporal association of the other species with the black-headed gull is stronger in species that nest in similar habitats as the black-headed gull than in species that nest on the ground or in tree cavities far away from gull colonies. Finally, we studied whether the trend-controlled temporal association of the other species with the black-headed gull correlated with the current conservation (threatened) status of the species.

2. Material and methods

2.1. Bird data

Our data of lake-specific breeding numbers of black-headed gull and other waterbird species are from five regions in southern and central Finland and cover the period of 1977–2017, with the length of the lake-specific time series of breeding numbers varying from 22 to 41 years (Supplementary material, Table A1; additional details for four of the study regions can be found in Pöysä et al., 2016). The lakes in the study regions represent typical lakes in boreal Northern Europe, ranging from oligotrophic lakes surrounded by forest and peat shores to eutrophic lakes surrounded by arable lands. As the black-headed gull prefers eutrophic lakes, most of the study lakes are eutrophic. In the respective study regions, the waterbird surveys were carried out by one of us (and the late Jukka Kauppinen) for each lake and during each year, using the standard methods for monitoring breeding waterbird numbers in Finland (census methods described in detail in Koskimies and Väisänen, 1991). In brief, to take into account differences in the timing of spring migration between species, 2–6 censuses were carried out in late April–May in each study region; pair numbers for a species were interpreted using field observations from the census within the recommended species-specific time window (Kauppinen, 1983; Koskimies and Väisänen, 1991; Pöysä, 1996). In other words, an annual pair number for each species was derived from one census, except in Parikkala, where waterbird surveys were conducted more frequently (4–6 surveys per year, approximately once per week; see also Pöysä, 1996). For each species, we used the average pair number of two consecutive surveys within the species-specific time window. All in all, our data included time series of breeding numbers for 17 waterbird species (in addition to the black-headed gull). In general, a declining trend dominated in the time series of many species, in particular the black-headed gull, great crested grebe (*Podiceps cristatus*), northern pintail (*Anas acuta*), tufted duck, common pochard, and common coot (*Fulica atra*), while the whooper swan (*Cygnus cygnus*) is a notable exception with an increasing population trend in most local communities (Supplementary material, Table A2).

A colony of breeding black-headed gulls has been present for a varying number of years on 15 of our study lakes (see Supplementary material, Fig. A1; we use the term ‘colony’ to mean any number (> 0) of breeding pairs of black-headed gulls at a lake). The colony fluctuated or showed a monotonic increasing or decreasing trend on many of the lakes, whereas on other lakes the colony suddenly appeared and was present for a number of years and disappeared again. High spatiotemporal variation in the use of nesting sites has been documented earlier for the species (Virkkala, 2006). We used the longest possible time period for which we could obtain the most comprehensive data for all 15 lakes (1991–2009 for 14 lakes and 1996–2009 for one lake; see Supplementary material, Fig. A1) and calculated all possible pair-wise correlations between lake-specific colony time series. The correlations for many of the lakes ranged from significant negative to significant positive (Supplementary material, Table A3), suggesting that the dynamics of black-headed gull colonies was not driven by a common global factor, but was largely governed by local factors. The time series of the black-headed gull colony size, and of the breeding numbers of the other species from the 15 lakes, were used to study whether the other species showed contemporary changes in breeding numbers with the black-headed gull, after controlling for common long-term trends and fluctuations (see below).

2.2. Nest site and conservation status

The primary nest site of each species with respect to black-headed gull colonies was classified according to Cramp and Simmons (1977) and Väänänen et al. (2016), two categories: nest site typically situated within a black-headed gull colony or in its vicinity in open aquatic habitat; nest site far from a black-headed gull colony on the ground in a shore meadow or field or in a tree cavity in a forest (see Supplementary material, Table A4). The conservation status of each species in Finland was taken from Tiainen et al. (2016; IUCN criteria) and coded for the test as follows: ‘Least Concern’ = 0; ‘Vulnerable’ or ‘Near Threatened’ = 1; ‘Endangered’ = 2 (see Supplementary material, Table A4).

2.3. Statistical analyses

The time series data included runs of zeros (i.e., years with no breeding pairs) and did not meet the assumptions of parametric correlation and regression. Therefore, we used Kendall rank correlation and Kendall partial rank correlation (Siegel and Castellan, 1988) to study whether the other species showed contemporary changes in breeding numbers with the black-headed gull, after controlling for common long-term trends. Rank-based correlations are a robust and widely used method to detect trends in nonnormally distributed time series data, and allow simultaneous control of confounding co-variates (e.g., Hamed and Rao, 1998; McCarthy, 1998; Libiseller and Grimvall, 2002; Gocic and Trajkovic, 2013). In our data, zeros are not structural, nor can they be considered purely sampling zeros; in other words, a lake was basically suitable for a species, but zeros occurred due to intermittent occupancy or local extirpation. Nevertheless, to minimize the effects of chance in affecting population trends, and to be able to detect a trend if there was any, we only included species-specific time series that had > 5 non-zero observations (years), resulting in sample sizes of 17 species and 1–15 time series per species (length range of the time series 22–41 years). There were 15 lakes in all (see Fig. A1), and each lake only produced one time series for a species (i.e., maximum 15 time series per species). All correlations were done at lake level; for example, the black-headed gull time series from the lake Kutajärvi was correlated with the time series of the other species from the same lake but not with time series from the other lakes. [Note, however, that the pair-wise Kendall rank correlations for the black-headed gull breeding numbers presented in Table A3, and discussed above, were calculated between all the 15 lakes.] Because the black-headed gull and the other species typically showed a similar long-term trend, we calculated partial Kendall rank correlation coefficients for the association between the black-headed gull and the other species by controlling for the effect of the common trend (i.e., year; hereafter, trend-controlled temporal association). In other words, we aimed to produce a measure of the relation between the black-headed gull and the other species in which the effect of year upon the relation is eliminated. Note that this procedure does not affect the numerical result if the species do not share a common trend (i.e., in those cases ordinary zero-order and partial correlation coefficients are identical; for a demonstration of how the Kendall partial rank correlation works see Appendix 1). As site fidelity or life history characteristics, such as age at first breeding, may cause response delays of the other species to the change in gull colony size, we repeated the analysis by taking into account a one-year time lag in responses, i.e. black-headed gull colony size was taken from year t-1 (the previous year) while all the other data were from year t, and the correlations were re-calculated. Kendall partial rank correlations were calculated and their significance tested according to Siegel and Castellan (1988).

We calculated the average of the lake-specific trend-controlled temporal associations with the black-headed gull for each species (13 species, 4–15 time series per species to calculate the mean; black-throated diver (*Gavia arctica*), red-necked grebe (*Podiceps grisegena*), gadwall (*Mareca strepera*), and goosander (*Mergus merganser*) were excluded because of insufficient data, only one time series each). We used these species-specific average values and the Mann-Whitney U-test to study whether the trend-controlled temporal association of the other species with the black-headed gull (without time lag) was associated with similarity in nest site between the black-headed gull and the other species. Finally, we used the same species-specific average values and Kendall rank correlation to study whether the trend-controlled temporal association of the other species with the black-headed gull (without time lag) was associated with the current conservation status of the species. Note that primary nest site with respect to black-headed gull colony and threatened status were not inter-correlated; i.e., no difference existed in terms of the conservation status between species that nest within black-headed gull colonies or in their vicinity (n = 6 species) and species that nest far away from black-headed gull colonies (n = 7 species) (Mann-Whitney U-test, U = 30.5, p = 0.140).

All statistical analyses were performed in SYSTAT 13.

3. Results

All in all, 58 (37.4%) of the 155 zero-order pair-wise Kendall correlations between black-headed gull and other species were significant, the corresponding number being 32 (20.6%) for partial Kendall correlations, i.e., after controlling for the common trend (year) effect (Table 1). Considering species for which we had more than one time series, the mean of the partial correlation was somewhat lower than that of the zero-order correlation for most species (Table 1). Partial Kendall correlations based on data with a one-year time lag (i.e., size of black-headed gull colony was from year t-1) did not reveal a response lag for any of the species (Table 1). After controlling for common trends, differences were still found amongst the species in the strength of the temporal association with black-headed gulls (i.e., trend-controlled temporal association); for example, tufted duck, common pochard, Slavonian grebe (*Podiceps auritus*), and common coot showed a relatively strong positive trend-controlled temporal association with the black-headed gull, whereas whooper swan, mallard, and common goldeneye did not (Table 1).

In general, species that nest within black-headed gull colonies or in their vicinity (n = 6 species) had relatively stronger positive trend-controlled temporal associations with the black-headed gull than species that nest far away from gull colonies (n = 7 species) (Fig. 1a; Mann-Whitney U-test, U = 36.0, p = 0.032), the whooper swan (included in the statistical test) being a clear exception to this general pattern (the lowest value in the group ‘Similar nest site’ in Fig. 1a). Finally, the trend-controlled temporal association of the other species with black-headed gull correlated with the conservation status of the species (Fig. 1b; Kendall rank correlation, $\tau = 0.691$, $p < 0.01$, n = 13 species); species with a relatively stronger positive trend-controlled temporal association with black-headed gulls had a more critical conservation status.

4. Discussion

We found that breeding numbers of many species tracked long-term changes in the size of black-headed gull colonies. This was true even after controlling for a common trend in the size of the black-headed gull colony and the breeding numbers of the other species. Furthermore, the trend-controlled positive temporal association with black-headed gull was relatively stronger in species nesting in similar habitats within a lake as the black-headed gull, and in species with more critical conservation statuses. Hence, given the protective function of black-headed gull colonies in waterbird communities, with clear fitness benefits being documented for at least certain species (e.g., Väänänen, 2001; Liordos and Lauder, 2015), and considering that breeding numbers of many waterbird species show a contemporary decline with black-headed gull colonies (Viksne et al., 2011; Fox et al., 2016a; Leito et al., 2016; this study), we suggest that the overall decline of black-headed gull colonies has resulted in secondary endangerment of many other species in waterbird communities.

In general, our findings support the suggestion by Brodie et al. (2014) that we particularly need to know which traits affect the relative vulnerability of species to secondary endangerment and, finally, secondary extinctions. In our case, and speaking of secondary endangerment, nest site similarity between the protector species and other species appeared important. Contrary to most of the other species, the whooper swan showed consistent population increase and no temporal association with black-headed gull colonies. The latter finding was interesting especially because the whooper swan shares the open nesting habitat with black-headed gulls, providing an exception to the general relationship between nest site similarity and positive temporal association with the black-headed gull (cf. Fig. 1a). The whooper swan is a large territorial species able to defend its nest (and young) against most nest predators; we suggest that this explains the exception. The consistent increase of whooper swans in our data is in line with the overall trend of the species in Northern Europe (e.g., Pöysä et al., 2018 and references therein).

Although the black-headed gull is globally considered a 'Least Concern' species (BirdLife International, 2018), its breeding numbers have declined locally in several European countries (e.g., Neil, 1990; Heldbjerg, 2001; Viksne et al., 2011; Poprach et al., 2016). Reasons for these declines are not known, but food shortage due to changes in agriculture, poisoning by chemicals, and increased predation of eggs and chicks are often mentioned as possible reasons. On the other hand, new colonies have appeared on islets and human-built breakwaters on certain large lakes (E. Lammi, unpubl. data); however, these sites are unsuitable for breeding for other waterbird species. We urgently need more research to uncover reasons for the decline of black-headed gull colonies to stop this decline and maintain the globally favorable conservation status of the species. Notwithstanding the fact that we do not know the reasons for overall black-headed gull declines, we consider it unlikely that the other declining waterbird species have simply responded to the same local or global factors as the black-headed gull, except perhaps predation and disturbance. We already showed that the dynamics of the black-headed gull colonies could not be driven by a common global factor (see Material and methods, Bird data). It is also unlikely that changes in agriculture could explain the highly variable patterns in the lake level dynamics of the black-headed gull colonies (see Fig. A1). Also variations in water level between years are relatively small in the study lakes, and so we do not believe it has importantly affected the dynamics of the black-headed gull colonies. For example, Virkkala (2006) studied spatiotemporal dynamics in the use of breeding sites in four gull species breeding in a stable lake complex, Lake Kukkia, in southern Finland. The author found that the spatial turnover of the breeding black-headed gulls was extremely high, while the other three species, the common gull (*Larus canus*), herring gull (*Larus argentatus*) and lesser black-backed gull (*Larus f. fuscus*) showed low spatial turnover. Because the water level in the Lake Kukkia complex was stable and the habitat of the gull colonies did not change during the study, other local factors such as changes in predation risk or disturbance by humans probably affected the high spatiotemporal dynamics of the black-headed gull colonies in the lake complex (Virkkala, 2006).

It is important to recognize that not all the species studied here tracked the local dynamics of black-headed gull colonies. The species that did have a relatively strong trend-controlled temporal association with black-headed gull were the tufted duck, common pochard, Slavonian grebe and common coot. What might be a common local factor, not related to predation risk per se, that explains why these species tracked the local dynamics of the black-headed gull colonies? For example, the feeding ecology of black-headed gulls differs in many respects from that of the tracking species. Black-headed gulls prey on earthworms and insects flying over water or fields, and their foraging areas reach distances of up to 5–20 km from the nesting colony (Götmark, 1984; see also Väänänen et al., 2016), while the other species associated with black-headed gulls mainly forage near their nest sites (i.e., near black-headed gull colonies). Similarly, because the other species represent different diets and foraging strategies (Slavonian grebes mainly feed on free-swimming insects and fish, whereas tufted ducks and pochards forage on stationary or slow-moving prey and plant material collected from the bottom, and the common coot is largely omnivorous with divergent feeding methods; Cramp and Simmons, 1977), we argue that the main common reason for their similar temporal association with the black-headed gull is not their foraging ecology but the protective function of black-headed gull colonies (see also Leito et al., 2016). The hooded crow (*Corvus corone cornix*) and marsh harrier (*Circus aeruginosus*) are common avian nest and chick predators of black-headed gulls and other waterbird species that share nesting habitat with it, and based on our own observations, black-headed gulls are often successful at defending the colony area against these predator species. In addition, the American mink (*Neovison vison*), an alien species, has efficiently colonized lakes in Finland and other European countries, and is currently considered an important depredator not only of waterbird eggs and chicks but also of incubating females (Nordström et al., 2002; Brzeziński et al., 2012; Fox et al., 2016a). Other mammalian predators that may take eggs, chicks and even adults of waterbirds in our study areas include the raggoon dog (*Nyctereutes progyonoides)*, another alien species, red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) (Kauhala, 2004; Väänänen et al., 2007), the latter two being less frequent predators at gull colonies. Unfortunately, there are no studies of the relative importance of different predator species in affecting nest losses and mortality in the black-headed gull and other waterbirds, although the American mink is generally considered an important predator at wetlands. Nevertheless, because the black-headed gull colonies typically were among emergent vegetation or on floating vegetation rafts relatively near the shore line, basically all the above-mentioned predator species, except perhaps the pine marten and red fox, can be considered equally dangerous for both the black-headed gull and the associated species and ground nesting waterbirds in general. The American mink and raggoon dog started to increase in numbers in Finland in 1970s (Helle and Kauhala, 1991; Kauhala, 1996). Their overall increase may have affected the long-term decline of the black-headed gull and other species but we do not have data to assess their importance in the year to year local dynamics of waterbirds.

The sudden disappearance of a black-headed gull colony from a site and the high spatiotemporal dynamics of black-headed gull colonies in general may reflect avoidance of American mink predation by the species, as suggested by Virkkala (2006). The disappearance of a protector species most likely affects the dynamics of the dependent species, as we have demonstrated here. Because the other species tracked without a time lag changes in the size of black-headed gull colonies, it is probable that, in addition to direct fitness consequences (see below), at least some individuals responded by emigrating from the lakes after the disappearance of black-headed gulls. Furthermore, because our study deals with declining species, and hence small populations, local dynamics may also have been affected by stochastic events (e.g., Beletsky and Orians, 1994; Haila et al., 1996); for example, a local population of a species associated with the black-headed gull may have vanished due to demographic stochasticity before the gull colony disappeared. Our data are not suitable to study in more detail the response of the other species to a sudden and severe change in the black-headed gull colony. A proper test for such a response would require time series with the black-headed gull staying at a high level for a long period before the crash, ensuring that the response of other species is not confounded by the colony dynamics prior to the crash. The black-headed gull colony studied by Leito et al. (2016) met this requirement, and the authors found that populations of many species, including the pochard and tufted duck, decreased sharply after the disappearance of the black-headed gull colony in their study lake. This observation is in line with the idea that species associated with black-headed gull may respond behaviorally to the crash of black-headed gull colonies.

Our findings have relevance to the conservation of waterbird species and to the maintenance of species richness in waterbird communities in general. First, most of the species studied here have a wide breeding distribution in Europe (Hagemeijer and Blair, 1997) and co-occur with black-headed gulls in local waterbird communities all over their range. Moreover, waterbirds breeding in Finland encompass a high proportion of the total European population for many of the species studied here (Hagemeijer and Blair, 1997). Therefore, the drastic decline of many species in Finland (e.g., Pöysä et al., 2013; Lehikoinen et al., 2016) contributes strongly to the overall conservation status of the species in Europe.

The common pochard in particular has shown rapid declines in breeding numbers across much of its breeding territory in Europe (reviewed in Fox et al., 2016a), and is currently globally assessed as 'Vulnerable' (BirdLife International, 2018). Several explanations for this decline have been suggested, the loss of black-headed gull colonies being mentioned as one possible explanation for nine of the 17 countries included in the review by Fox et al. (2016a). Väänänen (2001) specifically studied the protective function of black-headed gull colonies in terms of nest predation risk for the common pochard and the tufted duck, another diving duck species preferring nesting within gull colonies (the gull colonies were on the same lakes (region 5) that we studied). He found that nest predation was significantly higher outside than within gull colonies for both species (common pochard, 48% vs. 8%; tufted duck, 40% vs. 10%). Such differences in nest depredation rates obviously have important consequences to population demography and dynamics. It should be added that there is no evidence that ducklings or chicks of other waterbirds would suffer predation from the black-headed gulls like it has been found for ducks breeding in association with California (*Larus californicus*) and ring-billed gulls (*Larus delawarensis*) in Canada (Dwernychuk and Boag, 1972).

Our study provides evidence for the hypothesis that the loss of black-headed gull colonies can result in the declines of common pochard and other waterbird species in local communities (see also Leito et al., 2016). We acknowledge that the evidence presented in this study is correlational. Field experiments would be most welcome to confirm our findings, although such experiments would be difficult to do, given that we are dealing with species of conservation concern. In the meantime, the bad news here is that, if breeding numbers of the common pochard and the other threatened species are strongly dependent on the presence of black-headed gull colonies, as our results and those of Leito et al. (2016) indicate, conservation and habitat management actions that do not directly enhance black-headed gull numbers may not be efficient enough to increase breeding numbers of the other species either (for success of management actions used in Finnish wetlands, see Lehikoinen et al., 2017). This being the case, conservation measures and management activities on wetlands and lakes should always take into account nest-site requirements of black-headed gulls and other colonial larids (see also Väänänen et al., 2016). Furthermore, the high temporal (this study) and spatiotemporal (Virkkala, 2006) dynamics of the black-headed gull colonies makes the protection of breeding sites (lakes) for waterbirds challenging, because the protective gull colony may disappear from a protected site and a new colony may be established at a site not protected (see also Virkkala, 2006).

Other factors besides the decline of black-headed gull colonies have obviously also affected the decline and endangerment of other species in waterbird communities. For example, both the garganey (*Spatula querquedula*) and northern pintail are classified as 'Endangered' in Finland while the Eurasian wigeon (*Mareca penelope*) is considered 'Vulnerable'; these species did not show a strong temporal association with the black-headed gull. It is important to note, however, that these species do not nest within or in the vicinity of gull colonies, a factor that possibly explains the weak temporal association with black-headed gull. The garganey is a long-distant trans-Saharan migrant, and inter-annual variation in its breeding numbers is affected by rainfall in the wintering areas and weather conditions during spring migration (Pöysä and Väänänen, 2014). Part of the northern pintail population breeding in northwest Europe also winters south of the equator in Africa (Scott and Rose, 1996), but very little is known about factors that drive the population dynamics of this species. It is possible that conditions in the wintering areas have become worse, negatively affecting the breeding numbers of both species. Factors affecting the population decline of Eurasian wigeon are not known, but are currently under active research (e.g., Fox et al., 2016b; Pöysä et al., 2017; Pöysä and Väänänen, 2018).

In conclusion, our study provides a strong candidate for secondary endangerment, in which the effect is mediated via an indirect interaction between species. Black-headed gulls provide overall protection against nest and chick predators for several other species that share its nesting habitat preference. We suggest that the decline of the black-headed gull has caused secondary endangerment in these species. Conservation actions aimed to stop the decline of black-headed gulls and increase its breeding numbers on lakes used by other declining waterbird species are vitally important to reverse the declining trends of the dependent species. Such protective associations between species may be widespread, not only in birds (Quinn and Ueta, 2008), but in many other species groups, a phenomenon that has not been fully appreciated in the research fields of extinction risk and biodiversity conservation. We encourage further research to recognize such associations and to study their possible importance in biodiversity conservation in local communities worldwide.

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Figure legends

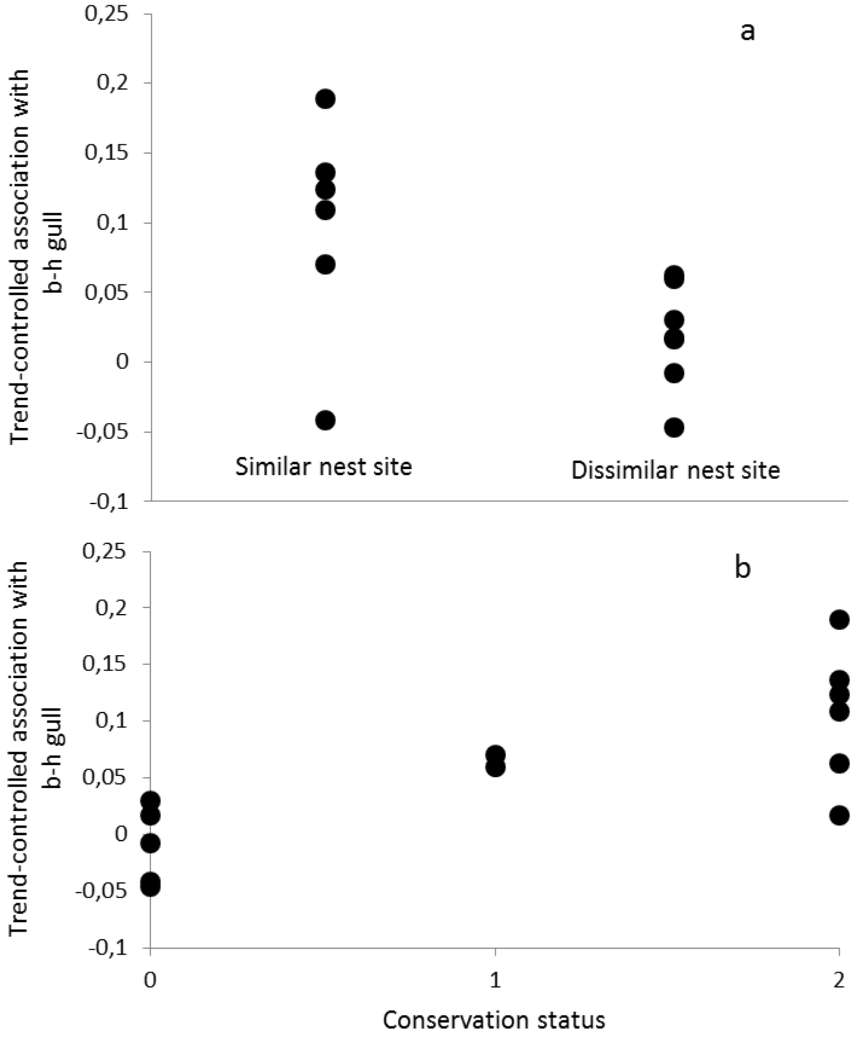
Fig. 1. Trend-controlled temporal association of other waterbird species with black-headed gull in relation to (a) primary nest site and (b) conservation status of the species. The species-specific trend-controlled temporal association values are from Table 1 (column ‘Partial correlation’; i.e., the means of the Kendall partial rank correlation coefficients). Primary nest site of each species with respect to black-headed gull colony was classified as ‘Similar nest site’ (n = 6 species; nest typically within a colony or in its vicinity in an open aquatic habitat) or ‘Dissimilar nest site’ (n = 7 species; nest typically far from a colony on the ground or in a cavity in a shore meadow, field, or forest). Conservation status was classified as 0 (‘Least Concern’; n = 5 species), 1 (‘Vulnerable’ or ‘Near Threatened’; n = 2 species), and 2 (‘Endangered’; n = 6 species). For more details, see Material and methods.

Table 1. Means of Kendall zero-order, partial, and partial with a 1-year time lag correlation coefficients between black-headed gull colony size and pair numbers of other species (correlations based on only one time series are in parentheses). In partial correlations, the effect of a common trend (year) has been controlled for; partial correlations with a 1-year time lag have been calculated using a black-headed gull colony size from year t-1 (for further information, see Material and methods). n = number of correlation coefficients (i.e. lake-specific time series; maximum n = 15 lakes) used for calculating the mean; number of significant ($p < 0.05$) correlations (positive or negative) are given for each species and correlation type.

Species	Zero-order correlation		Partial correlation		Partial correlation with 1-year time lag	
	Mean	Significant	Mean	Significant	Mean	Significant
Black-throated diver, *Gavia arctica* (n = 1)	(0.190)	0	(-0.040)	0	(0.270)	1
Great crested grebe, *Podiceps cristatus* (n = 10)	0.208	5	0.071	2	0.001	2
Red-necked grebe, *Podiceps grisegena* (n = 1)	(0.550)	1	(0.290)	1	(0.077)	0
Slavonian grebe, *Podiceps auritus* (n = 4)	0.216	1	0.124	0	0.184	0
Whooper swan, *Cygnus cygnys* (n = 13)	-0.175	7	-0.042	1	-0.070	2
Eurasian wigeon, *Mareca penelope* (n = 13)	-0.123	5	0.060	3	0.080	2
Gadwall, *Mareca strepera* (n = 1)	(-0.133)	0	(-0.144)	0	(-0.177)	0
Common teal, *Anas* crecca (n = 15)	0.029	4	0.017	5	-0.013	3
Mallard, *Anas platyrhynchos*	-0.040	1	-0.046	0	-0.020	0

(n = 15)						
Northern pintail, *Anas acuta* (n = 10)	0.142	3	0.062	3	0.016	1
Garganey, *Spatula querquedula* (n = 10)	0.141	3	0.017	2	0.026	2
Shoveler, *Spatula clypeata* (n = 11)	0.087	4	0.030	2	-0.020	2
Common pochard, *Aythya ferina* (n = 12)	0.326	7	0.136	2	0.141	4
Tufted duck, *Aythya fuligula* (n = 14)	0.327	9	0.189	7	0.117	4
Common goldeneye, *Bucephala clangula* (n = 15)	-0.101	5	-0.008	3	-0.017	3
Goosander, *Mergus merganser* (n = 1)	(0.008)	0	(0.008)	0	(0.095)	0
Common coot, *Fulica atra* (n = 7)	0.258	3	0.109	1	0.141	1

Fig 1.


a
Trend-controlled association with b-h gull
0,25
0,2
0,15
0,1
0,05
0
-0,05
-0,1
Similar nest site
Dissimilar nest site
b
Trend-controlled association with b-h gull
0,25
0,2
0,15
0,1
0,05
0
-0,05
-0,1
0
1
2
Conservation status