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The impact of weather and the phase of the rodent cycle on breeding populations of waterbirds in Finnish Lapland

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Climate change may affect bird populations both directly by changing the weather conditions, and indirectly through changes in the food chain. While both theoretical and empirical studies have shown climate change having drastic impacts on polar areas, its consequences on Arctic bird species are still poorly known. Here we investigated how weather and changes in predator–prey interactions affected the annual growth rates of sub-Arctic birds by monitoring the breeding numbers of three duck and seven wader species in the alpine tundra of Finnish Lapland during 2005–2015 (except for 2006). We hypothesized that growth rates of waterbirds would be positively associated with warm and dry weather due to improved reproductive success. Furthermore, we tested the hypothesis that waterbirds have a higher reproductive success during the cyclic rodent peaks, when predators mainly prey on rodents, than during the decline and low phases of the cycle, when predation pressure towards waterbirds increases. Results showed that population growth rates of breeding ducks were negatively associated with the sum of rainfall in the previous year. In waders, growth rates were positively associated with the phase of the rodent cycle in the same year. Our results emphasize the importance of monitoring Arctic bird populations on their breeding areas to explore what the consequences of climate change might be for breeding waterbirds by linking the effects of both weather and rodent abundance.

1. Introduction

The Arctic region has been identified as being particularly vulnerable to the effects of climate change because temperatures have been predicted to increase more rapidly than elsewhere, especially during winter (Gonzalez *et al.* 2010, IPCC 2014). The latest climatic predictions also point towards increased rainfall in higher latitudes because of milder winters increasing the levels of water vapour (EEA 2012, Pearce-Higgins & Green 2014). As a potential example of the effect of climate change on Arctic wildlife, common alpine tundra bird species in Fennoscandia have already declined in recent years along with increasing temperature and rainfall (Lehikoinen *et al.* 2014).

Although climate change may affect populations directly, it may also have indirect effects on species, for example through food chains (Martin 2007). Breeding success of several Arctic birds, including ducks and waders but also passerines, is often dependent on the local rodent cycle. During the rodent peak years, predators, such as foxes and small mustelids, mainly prey on rodents leading to low predation pressure on birds. On the other hand, during the low rodent years predators use birds as alternative prey, and predation pressure is especially high on nests and young birds (Järvinen 1985, Pehrsson 1986, Sutherland 1988, Underhill *et al.* 1993, Summers *et al.* 1998, Hario *et al.* 2009). Peak years in rodent cycles have dampened in several areas in Europe (Cornulier *et al.* 2013), which has been suggested to be linked to climate change (Kausrud *et al.* 2008). However, strong cycles in our study area in northern Fennoscandia show at least short-term signs of recovery since clear peaks in rodent numbers have been identified in 2007, 2011 and 2015 (the present study).

Arctic areas are key breeding areas for many waterbird species such as waders and ducks (Wetlands International 2006). However, populations of many European duck species have been declining since 1990s (Fox *et al.* 2015). For instance, two duck species breeding at high latitudes, Long-tailed Duck (*Clangula hyemalis*) and Velvet Scoter (*Melanitta fusca*), became globally threatened in 2012 due to a very rapid population decline (BirdLife International 2015, see also Bellebaum *et al.* 2014). Furthermore, Fox *et al.* (2015) argued in their recent review that climate change and changes in predator–prey interactions may be one of the major threats for Nordic duck populations. Therefore, it is particularly important to study species' ability to cope with environmental changes in these areas and to investigate the factors affecting their population sizes during the breeding season.

Our aim was to study how environmental factors affected the population growth rate of three sub-Arctic (hereafter Arctic) duck and seven wader species in their breeding grounds. For this purpose, we investigated the joint impact of weather and predator–prey interactions (measured as the phase of the small rodent cycle). We hypothesized that the population growth rate of ducks and waders would increase in higher phases of the rodent cycle, when the rodent abundance is high (Summers *et al*. 1998), and also with increasing temperature (Syroechkovski *et al.* 1991) and decreasing rainfall (Newton 1998). To the best of our knowledge, this is the first study investigating the impacts of predator–prey interactions and weather conditions on multiple Arctic waterbird species. Furthermore, the impact of the rodent cycle on Arctic breeding waterbirds has rarely been investigated in an area where small rodents are characteristically fluctuating in 4–5-year cycles (Henttonen *et al.* 1977, Henttonen & Kaikusalo 1993, Hansen *et al.* 1999, Sundell *et al.* 2004).

2. Material and methods

2.1. Study area and bird monitoring data

We conducted the study in northwesternmost Finnish Lapland near Kilpisjärvi (68°59' N, 21° 17' E). The area is dominated by sub-Arctic alpine tundra (hereafter alpine tundra) at the altitude of 600–900 m.a.s.l. and it is characterized by alpine grasslands, shrubs and mires with tens of small ponds and lakes. The study area is approximately 43 km^2, and all the wetlands in the area were surveyed once a year during early July in 2005–2015 (excluding 2006 when the survey was not conducted). Although we visited the sites only once, and therefore not all the breeding pairs were found, the survey effort has been the same each year, which makes the annual values comparable.

Table 1. Annual observed breeding population sizes (transformed into pairs; see Koskimies &Väisänen 1991) of Anatidae and waders in the monitoring area in Northwest Finland near Kilpisjärvi. The phase of the rodent cycle and the associated rodent densities can be found at the end of the table. Species with sufficient data included in the analyses are marked with an asterisk (no data for 2006). Note that in 2011 the rodent peak was still observable in the alpine area (see methods).

Scientific name	2005	2007	2008	2009	2010	2011	2012	2013	2014	2015
Anser fabalis	0	0	0	0	1	0	0	0	0	0
Anas penelope	0	0	0	0	1	2	3	2	0	3
*Anas crecca**	5	10	11	7	4	5	8	5	2	7
Anas acuta	0	0	0	0	0	2	0	0	0	0
Aythya fuligula	0	0	0	0	0	1	0	1	0	0
*Aythya marila**	11	6	4	5	9	6	5	4	8	8
*Clangula hyemalis**	11	19	24	9	12	14	28	21	10	16
Mergus serrator	4	3	0	0	1	0	0	2	1	3
Mergus merganser	0	0	1	0	1	0	4	0	0	0
Anatidae total	31	38	40	21	29	30	48	35	21	37
*Charadrius hiaticula**	13	22	12	22	14	19	11	14	21	19
*Charadrius morinellus**	1	1	3	4	4	3	1	8	8	8
*Tringa glareola**	2	3	4	0	3	6	5	3	7	13
Tringa totanus	0	1	1	0	1	1	0	0	0	2
Tringa erythropus	1	1	0	1	0	2	0	1	0	1
Actitis hypoleucos	0	2	0	0	0	0	0	0	0	0
*Calidris pugnax**	3	7	4	5	1	7	3	8	11	27
*Calidris temminckii**	7	8	5	4	5	6	2	3	13	17
Calidris minuta	0	0	0	0	0	0	0	0	1	1
*Calidris alpina**	14	16	7	8	12	22	5	12	16	42
Calidris maritima	4	2	2	1	1	3	0	0	3	1
Gallinago gallinago	0	2	1	0	2	0	1	0	3	8
Lymnocryptes minimus	0	0	0	0	0	0	0	0	3	4
*Phalaropus lobatus**	27	34	18	39	37	43	14	37	24	43
Waders total	72	99	57	84	80	112	42	86	110	186
Rodent densities (Kilpisj.)	4	5.5	2.3	1	10.9	2.5	0.7	0.7	5.7	17.5
Phase of rodent cycle	2	4	1	2	3	4	1	2	3	4

We located the Anatidae and wader territories and marked them on a map. An exception was Eurasian Golden Plover (*Pluvialis apricaria*), for which territory mapping requires considerably more effort than what we could allocate. The selected method is a modified version of "Mapping census of breeding land birds" described by Koskimies & Väisänen (1991). We used the annual totals of each species as an estimate of the annual breeding population.

We collected the yearly data soon after the hatching of many wader species, when the successfully breeding adults are actively alarming. Adult waders with unsuccessful breeding attempts typically leave the area after failure (Cramp & Simmons 1983). Thus, we were unable to monitor non-breeding birds or individuals whose breeding attempts had failed during incubation or early chick development. Our wader count numbers (hereafter *post-hatching numbers*) were influenced by a combination of breeding propensity, breeding success (loss of clutch/brood or/and breeding adult) and overall population abundance. As for ducks, the breeding phase varies between species, and during the monitoring period Common Teal (*Anas crecca;* hereafter Teal) usually had ducklings, whereas Long-tailed Duck and Greater Scaup (*Aythya marila;* hereafter Scaup) females were usually incubating or laying eggs. In the latter case, females often left their nests when we visited the ponds, and we used the maximum number of the more abundant sex seen in each

pond as a measure of the number of breeding pairs (Koskimies & Väisänen 1991). Because we assume that the number of observed ducks reflects the number of breeding pairs, we hereafter refer to duck numbers as *breeding numbers*. All wader and duck numbers are shown in Table 1.

2.2. Rodent data, predator–prey interactions and expected effects

We monitored the annual abundance of small rodents at Kilpisjärvi using standardized trappings during June and September (Henttonen & Wallgren 2001, Cornulier *et al.* 2013). The rodent density was estimated by using snap traps in the same sites each year and it was scaled into the number of rodents per 100 trap nights. We used the June rodent density to explain the growth rates of waterbirds, since it describes the situation during the breeding season. As rodent data were collected from a mountain birch forest area approximately 15 kilometres from our waterbird study site, it does not fully represent the small rodent situation in the alpine tundra. This is because in Fennoscandian alpine tundra the Norway lemming (*Lemmus lemmus*) is often the main rodent species, whereas at lower altitudes dominated by birch forests several vole species are more common than lemmings. However, the phase of the small rodent cycle in the study area (Kilpisjärvi) is well represented by the rodent abundance data except for 2011, when vole numbers declined in lower altitudes already in June. We observed more lemmings in higher altitudes during 2011 than in any other year. This observation, together with other trappings in the Kilpisjärvi alpine region and visible autumn migration down to lower altitudes in autumn (H. Henttonen, unpublished work), indicates that the lemming peak still continued in the region that summer. The small rodent populations at Kilpisjärvi have been following a four- to five-year cycle at least since the late 1940s (Henttonen *et al.* 1977, Hanski *et al.* 2001, Henttonen & Wallgren 2001, Sundell *et al.* 2004, Cornulier *et al.* 2013). Although the cycle weakened in the 1990s and early 2000s, a proper four-year cycle seems to have returned in the area since the peak in 2007 (Cornulier *et al.* 2013).

Using the June rodent density indices, we classified the years of the small rodent cycle into four phases from highest to lowest predation pressure on waterbirds: 1) year with low rodent density after the peak characterized by the high number of mammal predators due to the delayed effect of the high rodent density in the previous year (hereafter the decline phase); 2) second year of low rodent density, when rodent numbers may have slightly increased in late summer, but the mammal predation pressure is lower than the year before due to the decline of mammal predators (hereafter the low phase); 3) year with a considerable increase in rodent numbers and therefore food availability for predators (hereafter the increase phase); and 4) peak in rodent density when food availability for predators is at its highest (hereafter the peak phase; e.g., Hanski *et al.* 1991, Turchin *et al.* 2000).

The predator community in the area influenced by rodent cycles includes both mammal and bird predators. Among mammal predators, Red Fox (*Vulpes vulpes*) and Arctic Fox (*Vulpes lagopus*; nowadays a rare visitor in the area with the last breeding documented in 1994; Henttonen *et al.* 2007 and our further monitoring, are regarded as generalist species, while Stoat (*Mustela erminea*) and Least Weasel (*Mustela nivalis*) are rodent specialists. As for bird predators, generalist species include Merlin (*Falco columbarius*), whereas Rough-legged Buzzard (*Buteo lagopus*), Short-eared Owl (*Asio flammeus*) and Long-tailed Skua (*Stercorarius longicaudus*) are all considered specialists (Hanski *et al.* 1991, Pokrovsky *et al.* 2015). Although we have no data on species-specific predation rates, we assume that the main predation effect on waterbirds is caused by the functional response of the resident mammalian predators, which switch to feed on birds when rodents are not available. Avian predators are more likely nomadic and do not settle down in the area if the rodent abundance is low (Hanski *et al.* 1991). The abundance of mammalian predators in the study area has not been monitored. However, it has been earlier shown in the nearby birch forest zone that during the decline phase of the rodent cycle the predation of passerines breeding in nest boxes is high. This suggests that rodent specialists (Least Weasel and/or Stoat; Hanski *et al.* 1991) that can access nest boxes are probably the main predators in this particular case (Järvinen 1985, Hansen *et al.* 1999). Nonetheless, Red Fox is nowadays also rather common in the low alpine tundra and may

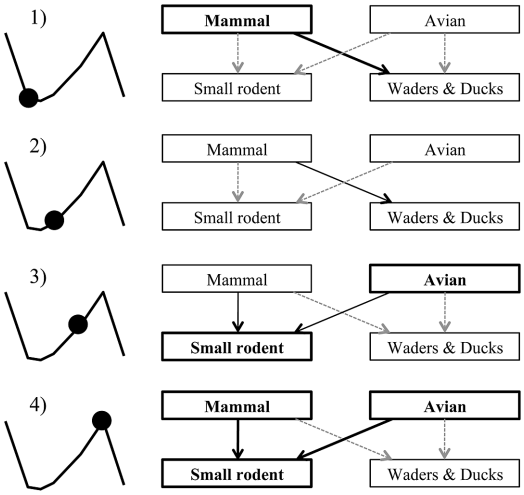

Fig. 1. Hypothetical illustration of predator–prey interactions during a four-year rodent cycle in the study area. Years of high mammal or bird abundances are denoted by boxes with thick lines and bolded text. Years of high predation are denoted by thick arrows (three different levels). On the left hand side of the diagram, the different phases of the rodent cycle are presented: 1) decline phase, 2) low phase, 3) increase phase, and 4) peak phase. Low productivity of waders and ducks is expected to occur during the decline phase. Note that some of the interactions are based on observations that have not been tested. This diagram has been adapted from Pearce-Higgins and Green (2014).

switch to alternative prey when rodents become scarce (Erlinge *et al*. 1983, Berryman 2002). For a graphical explanation of the predator–prey interactions in the study area, see Fig. 1.

Based on these observations, the predation risk of ducks and waders would be at its highest during the decline phase, when there are still many predators but low prey availability, and progressively decrease towards the peak phase of the cycle. For waders, this implies that the lowest growth rates of the post-hatching numbers would occur during the decline phase, and correspondingly the highest population growth rates would be found during the peak phase. In contrast to waders, adult ducks stay longer in the area even if their breeding fails (Cramp & Simmons 1977). Following the logic of this argument, we would expect to observe the impact of rodent abundance with a one-year time lag. Thus, the highest growth rates of ducks would occur one year after the peak phase (i.e., decline phase) due to a large number of recruits after a successful breeding. Because ducks often show relatively high natal philopatry (Andersson *et al.* 1992), their numbers would start to decline one year after the decline phase given the low productivity and increased mortality of breeding adults during the decline and low rodent phases.

2.3. Weather data

Weather data, covering the study area with a 10 × 10 km grid, was obtained from the Finnish Meteorological Institute (Venäläinen *et al.* 2005). We used the average temperature and the sum of rainfall ca one month before our monitoring counts (10^{th} June–9^{th} July). We presumed that high growth rates of post-hatching wader numbers would occur during warm and dry early summers, with a one-year lag effect in the increase of ducks' growth rates.

2.4. Study species, variables and statistical analyses

We observed altogether nine breeding duck and 14 breeding wader species during the study period (all of them adult individuals), but only three duck and seven wader species were included in the analyses (all the species with an average annual number of at least four pairs; see Table 1).

First, we tested whether any of these species had a significant population trend in breeding numbers (ducks) or post-hatching numbers (waders) over the study years using linear regression models, where the log-transformed population size was a dependent variable and year was the explanatory variable. In order to deal with multiple testing (10 tests being considered), we applied the sequential Bonferroni correction to adjust the level of significance α (Simes 1986).

Second, in order to test the factors responsible for fluctuations in breeding population sizes, we first defined a set of explanatory variables describing the effects of both the phase of the rodent cycle and weather. We used the phase of the rodent cycle as a continuous variable and assumed that the breeding success of waterbirds would improve from the decline phase (1) to the peak phase (4). Because of the different behaviour of the study

species (see section 2.1.), we made predictions about potential time lags separately for ducks and waders. For ducks and waders, we considered two measures of the rodent abundance (i.e., rodent abundance the same year and rodent abundance the year before, defined as "Rodent$_t$" and "Rodent$_{t-1}$", respectively). We accounted for the prior-rodent abundance since in some cases a correlation between rodent abundance and breeding success of birds has been demonstrated (e.g., Järvinen 1985, Royer-Boutin *et al*. 2014). Since population growth rates of ducks were expected to increase after a high rodent abundance year and *vice versa*, growth rates of ducks should be positively associated with the rodent abundance the year before. Weather was accounted for by including the current and previous year's average temperature and sum of rainfall ("Rain$_t$", "Rain$_{t-1}$", "Temp$_t$" and "Temp$_{t-1}$", respectively). The number of juveniles hatched may rise with an increase in temperature, which can be seen as a positive connection between growth rates of post-hatching wader numbers and the same-year temperature (World Conservation Monitoring Centre 2000, Boere *et al*. 2006). However, high summer temperatures may also have a negative effect on the abundance of crane flies, main source of food of several wader species (Pielou 1994), and consequently on the survival of chicks (Pearce-Higgins *et al*. 2010) leading to a negative connection between growth rates of post-hatching breeding numbers and temperature. Although high early summer rainfall is sometimes positively related to nesting success, mainly due to a reduction in egg predation (Dickey *et al*. 2008), changes in water levels caused by heavy rainfall in early summer may result in lower nest success because of flooding (McAuley & Longcore 1988). In such case, growth rates of ducks would be negatively connected with rainfall the year before, and growth rates of post-hatching wader numbers would be negatively associated with the same-year rainfall. All continuous explanatory variables were standardized to reduce differences in the scales of parameters and improve the model fit.

We employed a slightly modified version of the Ricker model (Ricker 1954, Brännström & Sumpter 2005), a classic discrete population model describing the expected population size/density in a focal year (N_t) as a function of the population size/density in the previous year (N_{t-1}) (see Eq. 1). Being so, our response variable was defined as the natural logarithm of the rate of change in bird numbers (i.e., growth rate; see Eq. 2), while the explanatory variables were N_{t-1} and several multiplicative environmental covariates (Lindén 2010) (see Eq. 3). The original form of the Ricker model where r is the intrinsic growth rate and K the carrying capacity is

$$N_t = N_{t-1} \exp[r\,(1 - N_{t-1} / K)] \quad (1)$$

and can be rewritten as follows

$$\ln(N_t / N_{t-1}) = r + (-r / K) \times N_{t-1} \quad (2)$$

If we call $a = r$, and $b = -r / K$, we obtain the same expression as in multiple regression models

$$\ln(N_t / N_{t-1}) = a + b \times N_{t-1} + c \times R_t + \varepsilon_t \quad (3)$$

with an additional variable (R_t) describing a particular environmental covariate at time t, c being its effect size and ε_t the unexplained variation.

We built different models to investigate which of them had the largest impact on waterbird growth rates. The competing models had all the possible subsets of explanatory variables whose maximum Pearson's correlation coefficients were below 0.5. We used this procedure/value to avoid problems with collinearity (for details see Booth *et al.* 1994). We finally obtained a total of 11 different models for ducks and waders (including rodent abundance, weather variables or a combination of these; see Tables 2–3). We did not consider other potential time lags (e.g., temperature two years before) due to limitations imposed by low sample size, which restricted the number of candidate models (Burnham & Anderson 2002). Measures of rodent abundance and rainfall were never evaluated in the same model because of a strong negative correlation (Rodent$_t$ / Rain$_t$: –0.68; Rodent$_{t-1}$ / Rain$_{t-1}$: –0.57).

In all models, we included "Year" as a random intercept to account for similarities in the unexplained random variation in population fluctuations (i.e., pseudoreplication; Hurlbert 1984). We assumed that both the common and the species-specific unexplained annual variations were temporally uncorrelated by modelling the autocorre-

Table 2. Results of the 11 candidate models explaining fluctuations in the adult duck population evaluated based on their AICc values: k is the number of explanatory variables, Δ_i the AICc differences compared to the most parsimonious model, and w_i the AICc weights. The base model is bolded.

Model explaining $\ln(N_t / N_{t-1})$	k	Δ_i	w_i
N_{t-1} × Species-ID + Rain_{t-1} + (1 | Year)	7	0.00	0.422
N_{t-1} × Species-ID + Rain_{t-1} + Temp_{t-1} + (1 | Year)	8	1.53	0.197
N_{t-1} × Species-ID + Rodent_{t-1} + (1 | Year)	7	2.35	0.130
N_{t-1} × Species-ID + Rodent_{t-1} + Temp_{t-1} + (1 | Year)	8	3.08	0.090
N_{t-1} × Species-ID + (1 | Year)	**6**	**4.51**	**0.044**
N_{t-1} × Species-ID + Rain_t + (1 | Year)	7	4.99	0.035
N_{t-1} × Species-ID + Temp_t + (1 | Year)	7	5.80	0.023
N_{t-1} × Species-ID + Rodent_t + (1 | Year)	7	6.35	0.018
N_{t-1} × Species-ID + Temp_{t-1} + (1 | Year)	7	6.46	0.017
N_{t-1} × Species-ID + Rain_t + Temp_t + (1 | Year)	8	6.49	0.016
N_{t-1} × Species-ID + Rodent_t + Temp_t + (1 | Year)	8	7.77	0.009

Table 3. Results of the 11 candidate models explaining fluctuations in the adult wader population evaluated based on their AICc values: k is the number of explanatory variables, Δ_i the AICc differences compared to the most parsimonious model, and w_i the AICc weights. The base model is bolded.

Model explaining $\ln(N_t / N_{t-1})$	k	Δ_i	w_i
N_{t-1} × Species-ID + Rodent_t + (1 | Year)	15	0.00	0.625
N_{t-1} × Species-ID + Rodent_t + Temp_t + (1 | Year)	16	1.93	0.238
N_{t-1} × Species-ID + Rain_t + (1 | Year)	15	5.41	0.042
N_{t-1} × Species-ID + (1 | Year)	**14**	**6.64**	**0.023**
N_{t-1} × Species-ID + Rain_t + Temp_t + (1 | Year)	16	7.04	0.019
N_{t-1} × Species-ID + Temp_{t-1} + (1 | Year)	15	7.98	0.012
N_{t-1} × Species-ID + Temp_t + (1 | Year)	15	8.06	0.011
N_{t-1} × Species-ID + Rain_{t-1} + (1 | Year)	15	8.22	0.010
N_{t-1} × Species-ID + Rodent_{t-1} + (1 | Year)	15	8.36	0.010
N_{t-1} × Species-ID + Rodent_{t-1} + Temp_{t-1} + (1 | Year)	16	9.13	0.007
N_{t-1} × Species-ID + Rain_{t-1} + Temp_{t-1} + (1 | Year)	16	9.73	0.005

lative pattern of each species using a type of AR(1)-model (i.e., an autoregressive model with previous time step N_{t-1} as explanatory; Bullmore *et al*. 1996, Lindén 2010). By including the interaction between species identity ("Species-ID"; set as a factor variable) and N_{t-1}, we allowed each species to respond differently according to its own density dependence. The interaction was placed in the fixed effects part of the model to see how much species density dependence varied between species. We defined our base model as the one including only the interaction described above and N_{t-1} as predictors of the log-transformed rate of change in population size at time t. For ducks, Teal was selected as the reference species (intercept) for the models, while Common Ringed Plover (*Charadrius hiaticula*; hereafter Ringed Plover) was defined as the intercept in the wader model set.

We fitted Linear Mixed Models (LMMs) to each of the candidate models using the "lme4" R package (Bates *et al*. 2015) and controlled for the mixed model fitting using the "lmerControl" function with optimizer BOBYQA (Powell 2009). Estimates were defined to optimize the log-likelihood function. In order to obtain the parameter-specific p-values from "lmer", we used the Kenward–Roger approximation to get approximate degrees of freedom and the t-distribution to get p-values. This approximation (implemented in the "pbkrtest" package; Halekoh & Højsgaard 2014) is more conservative than the Satterthwaite or the normal approximation, and its choice may

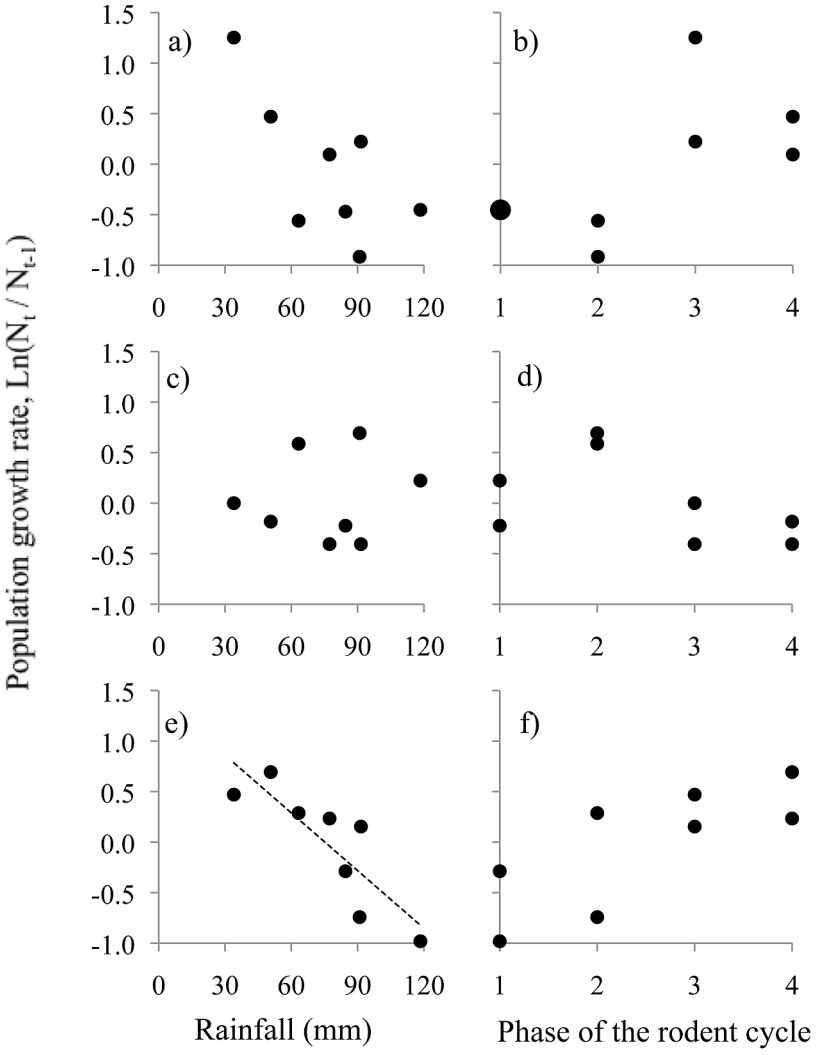

Fig. 2. Population growth rates of duck species in relation to previous years' rainfall (panels a, c and e) and the phase of the rodent cycle the year before (1 = decline phase, 4 = peak phase; panels b, d and f). Figures represent the following species: a–b) Common Teal (*Anas crecca*), c–d) Greater Scaup (*Aythya marila*), and e–f) Long-tailed Duck (*Clangula hyemalis*). The dashed regression line represents a nearly significant (*p*-value ≤ 0.1) relationship between the variables based on the regression analyses (see results section). The large dot in panel b represents two data records with the same values.

be of relevance in this case given our small sample size (Halekoh & Højsgaard 2014). In addition, we calculated the marginal (hereafter *marg*) and conditional (hereafter *cond*) R^2 describing the proportion of variance explained by the fixed factors alone and the proportion of variance explained by both the fixed and random factors, respectively, as a test of absolute model fit (Nakagawa & Schielzeth 2013). In this case, we used the "sem.model.fits" function inside the package "piecewiseSEM" (Lefcheck 2016).

The candidate models were evaluated according to their parsimony based on their AICc values (the corrected version of Akaike's Information Criterion, AIC, for small sample size), assuming normally-distributed residuals (Burnham & Anderson 2002). These values were calculated employing the formula proposed by Burnham and Anderson (2002).

Finally, we performed species-specific post hoc analyses for the most parsimonious models, also considering combinations (only when the difference in AIC of the model including weather and/or rodent variables was $\Delta_i > 2$ better than the base model) that could potentially provide additional information than the one given by the most parsimonious model (i.e., different variables evaluated). This was done to find out which species were especially influenced by the weather and/or rodent variables. In this case, the random effect

Table 4. Coefficients and test values of the top ranked linear mixed model explaining changes in ducks' growth rates. Species-ID2 is Greater Scaup (*Aythya marila*) and Species-ID3 Long-tailed Duck (*Clangula hyemalis*). Species-ID1 (Common Teal; *Anas crecca*) was defined as the intercept in the models (see section 2.4.). Statistically significant (p-value ≤ 0.05) coefficients and associated test statistics are bolded.

Parameter	Estimate	SE	t-value	p-value
Intercept	0.323	0.362	0.892	0.379
N_{t-1}	–0.067	0.050	1.329	0.194
Species-ID2	0.907	0.639	1.419	0.166
Species-ID3	0.209	0.492	0.425	0.674
Rain_{t-1}	**–0.276**	**0.101**	**2.734**	**0.010**
N_{t-1} × Species-ID2	–0.148	0.101	1.446	0.153
N_{t-1} × Species-ID3	0.031	0.051	0.597	0.555
SD (Year)	0.000	–	–	–

Table 5. Coefficients and test values of the top ranked linear mixed models ($\Delta_i < 2$) explaining changes in waders' growth rates. Species-ID2 is Eurasian Dotterel (*Charadrius morinellus*), Species-ID3 Wood Sandpiper (*Tringa glareola*), Species-ID4 Ruff (*Calidris pugnax*), Species-ID5 Temminck's Stint (*Calidris temminckii*), Species-ID6 Dunlin (*Calidris alpina*), and Species-ID7 Red-necked Phalarope (*Phalaropus lobatus*). Species-ID1 (Common Ringed Plover; *Charadrius hiatecula*) was defined as the intercept in the models (see section 2.4.). Statistically significant (p-value ≤ 0.05) coefficients and associated test statistics are bolded.

Parameter	Estimate	SE	t-value	p-value
Intercept	0.483	0.823	0.587	0.559
N_{t-1}	–0.081	0.045	1.797	0.076
Species-ID2	0.046	0.864	0.053	0.958
Species-ID3	–0.258	0.937	0.276	0.784
Species-ID4	–0.451	0.879	0.513	0.609
Species-ID5	–0.697	0.867	0.805	0.424
Species-ID6	–0.172	0.911	0.189	0.851
Species-ID7	0.338	0.989	0.341	0.734
Rodent_t	**0.348**	**0.088**	**3.950**	**0.000**
N_{t-1} × Species-ID2	**–0.204**	**0.090**	**2.265**	**0.026**
N_{t-1} × Species-ID3	–0.111	0.106	1.045	0.299
N_{t-1} × Species-ID4	–0.046	0.079	0.590	0.557
N_{t-1} × Species-ID5	–0.016	0.074	0.223	0.824
N_{t-1} × Species-ID6	–0.005	0.057	0.093	0.927
N_{t-1} × Species-ID7	0.027	0.049	0.561	0.576
SD (Year)	0.183	–	–	–

and the interaction were removed from the individual models (only one data point per year). Given the simplicity of the species-specific models, we fitted Linear Models (LMs) using the "lm" function with the same response variable ($\ln[N_t / N_{t-1}]$) and the population size in the previous year (N_{t-1}) and the variable or variables of interest (R_t) as explanatory (see Eq. 3). All statistical analyses were carried out in R version 3.2.3 (R Development Core Team 2013). Note that year 2005 was not used in the second part of the analyses, since our response variable was the population growth rate and therefore required two consequent years of data.

3. Results

None of the ten studied species showed any statistically significant directional trend in population size during the study period (Linear regression, sequential Bonferroni correction, all p-values larger than 0.005).

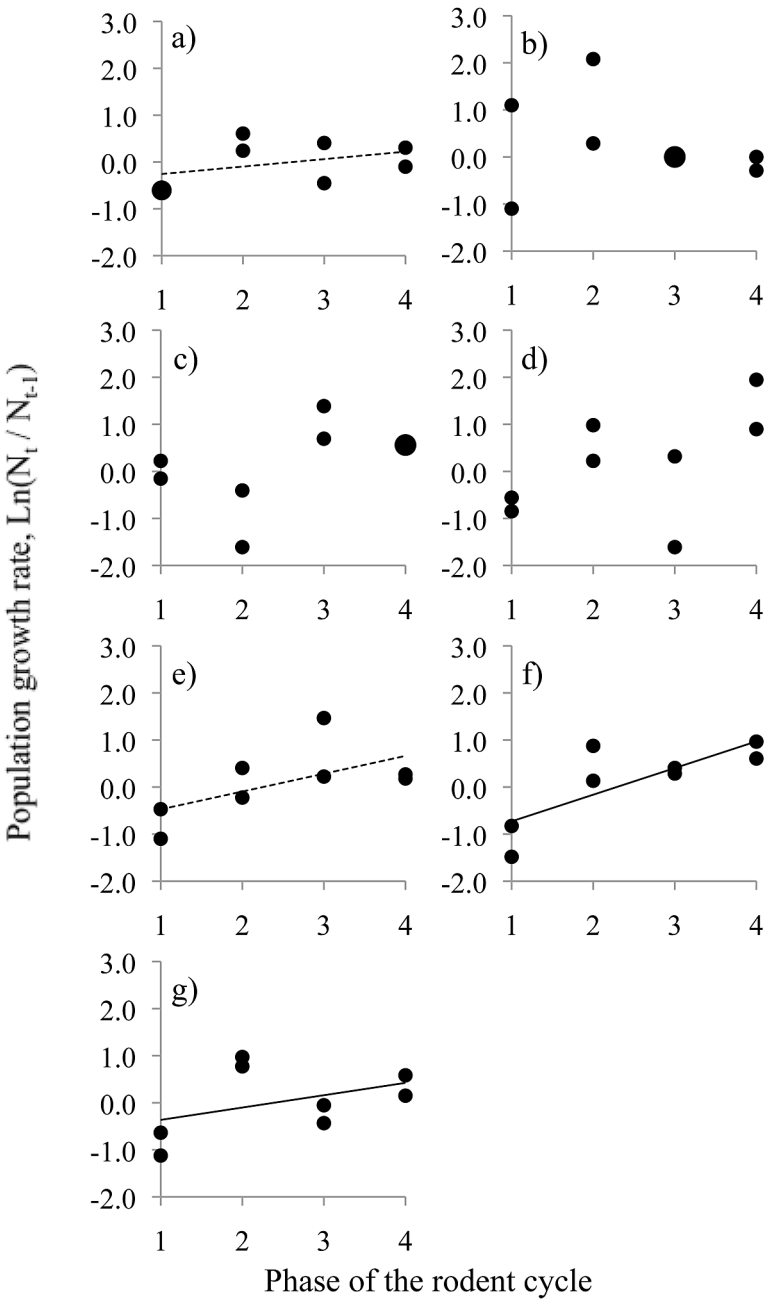

Fig. 3. Population growth rates of adult wader species in relation to the phase of the rodent cycle the same year (1 = decline phase, 4 = peak phase). Figures represent the following species: a) Common Ringed Plover (*Charadrius hiaticula*), b) Eurasian Dotterel (*Charadrius morinellus*), c) Wood Sandpiper (*Tringa glareola*), d) Ruff (*Calidris pugnax*), e) Temminck's Stint (*Calidris temminckii*), f) Dunlin (*Calidris alpina*), and g) Red-necked Phalarope (*Phalaropus lobatus*). Solid regression lines represent a significant (p-value ≤ 0.05) and dashed lines a nearly significant (p-value ≤ 0.1) relationship between the variables based on the regression analyses (see results section). Large dots in panels a–c represent two data records with the same values.

Among ducks, one-year time lag combinations including rainfall alone, rainfall and temperature, and the phase of the rodent cycle alone were better than the base model (difference in AICc for these models $\Delta_i > 2$ as compared to the base model) (Table 2). The rainfall-only model and the model including both rainfall and temperature in the previous year were the top ranked models ($w_i = 0.422$ and $w_i = 0.197$, respectively). We did not consider the second best model, as the additional temperature in the model can be recognized as an uninformative parameter (*sensu* Arnold 2010). The rodent-only model was ranked as the third best model. Although it also differed from the base

model ($\Delta_i > 2$), the difference in AICc compared to the best model was greater than 2 (Table 2; Fig. 2). In the top ranked model, previous years' rainfall was negatively associated with the log-transformed growth rate of the duck population (b = –0.276 ± 0.101 SE, t = 2.734, p = 0.010; Table 4). None of the species-specific density dependencies differed significantly from Teal (the intercept in Table 4). In the top model, the ducks' growth rate was not explained by the between-year variation (*marg* R^2 = 0.551, *cond* R^2 = 0.551).

Previous year's rainfall was nearly significantly associated with the rate of change of Long-tailed Duck (Linear regression, b = –0.391 ± 0.169 SE, t = 2.316, p = 0.068; Fig. 2e), but not with Teal (Linear regression, b = –0.419 ± 0.290 SE, t = 1.444, p = 0.208; Fig. 2a) or Scaup (Linear regression, b = –0.092 ± 0.162 SE, t = 0.568, p = 0.594; Fig. 2c). Density dependence did not have any effect on the population growth rate in the individual species models (Supplementary Table 1). No effect of the phase of the rodent cycle the year before (third best model) was observed for any of the duck species (Figs 2b, d and f; Supplementary Table 1). Neither was the density dependence significant (Supplementary Table 1).

For waders, there were two best supported models, one of them being the phase of the rodent cycle-only model (Rodent$_t$), and the other one including also temperature (w_i = 0.522 and w_i = 0.199, respectively; Table 3). However, like in the case of ducks, temperature seemed to be an uninformative parameter (*sensu* Arnold 2010), and we only considered the top ranked model later on. The top model was also better than the base model (difference in AICc $\Delta_i > 6$; Table 3).

Thus, the growth rate of post-hatching wader numbers increased linearly with the phase of the rodent cycle from the decline to the peak phase (b = 0.348 ± 0.088 SE, t = 3.950, $p < 0.001$; Table 5; Fig. 3). In addition, the post-hatching population size in the previous year (N_{t-1}) of Eurasian Dotterel (*Charadrius morinellus*; hereafter Dotterel) differed significantly from Ringed Plover (the intercept in Table 5) and was negatively associated with the response variable (b = –0.204 ± 0.090 SE, t = 2.265, p = 0.026; Table 5).

The percentage variance in wader population growth rate explained by year was around 11% (*marg* R^2 = 0.519, *cond* R^2 = 0.569). None of the weather variable-only models were better than the base model.

Among waders, the phase of the rodent cycle was nearly significantly associated with the growth rate of post-hatching numbers of Ringed Plover (Linear regression, b = 0.137 ± 0.058 SE, t = 2.377, p = 0.063; Fig. 3a) and Temminck's Stint (*Calidris temminckii*; Linear regression, b = 0.435 ± 0.190 SE, t = 2.289, p = 0.071; Fig. 3e), and significantly associated with Dunlin (*Calidris alpina*; Linear regression, b = 0.478 ± 0.108 SE, t = 4.410, p = 0.007; Fig. 3f) and Red-necked Phalarope (*Phalaropus lobatus*; Linear regression, b = 0.250 ± 0.066 SE, t = 3.778, p = 0.013; Fig. 3g). No significant association was found for Dotterel, Wood Sandpiper (*Tringa glareola*) or Ruff (*Calidris pugnax*; Supplementary Table 1, Fig. 3b–d). Density dependence had a negative effect on the growth rates of Ringed Plover, Dunlin and Red-necked Phalarope, but not on Temminck's Stint, Dotterel, Wood Sandpiper or Ruff (Supplementary Table 1).

4. Discussion

Population growth rates of ducks and post-hatching numbers of waders were affected by different variables. In waders, growth rates were positively influenced by the phase of the rodent cycle the same year, with values increasing towards the peak phase of the rodent cycle. This first result supports the hypothesis that predators tend to focus on rodents at high densities, which leads to decreased predation pressure on waterbirds (previously shown in ducks and waders by e.g., Pehrsson 1986, Sutherland 1988, Summers *et al.* 1998 and Hario *et al.* 2009). On the other hand, we failed to find any significant relationship between waders' growth rates and weather variables. Similarly, Robinson *et al.* (2014) demonstrated that the abundance of lemmings in the Canadian Arctic led to a growing number of breeding waders and gulls, but none of the groups were affected by the weather conditions. However, and despite the pitfalls of our census method, with which we could only account for the number of post-hatching pairs, these results suggest that the wader populations in the alpine tundra seem to be particularly sensitive to changes in the small rodent cycle.

Several studies have suggested that climate change may cause nonlinearly temporal loss and amplitude-dampening of small rodent cycles (Gilg *et al.* 2009, Cornulier *et al.* 2013, Korpela *et al.* 2013), which may have a strong influence on the populations of alternative prey (Zydelis *et al.* 2006, Hario *et al.* 2009, Guillemain *et al.* 2013, Fox *et al.* 2015, but see Korpela *et al.* 2014). Flattened population cycles of lemmings in the Russian Arctic have already been suggested to reduce the productivity and the population size of Dark-bellied Brent Goose (*Branta bernicla bernicla*) wintering in Europe, as well as waders along the East Asian-Australasian Flyway (Nolet *et al.* 2013, Aharon-Rotman *et al.* 2015). In Tawny Owls (*Strix aluco*), the dampening of the prey cycle has been suggested to override the positive impact of climate change on owl populations (Millon *et al.* 2014). The decline in amplitude of the rodent cycle may cause drastic reductions in the breeding success of specialist predators, even if the response of generalist predators may not always be negative (Schmidt *et al.* 2012). It is still unknown how the predator community and predation pressure would develop in case of dampened rodent cycles. Potentially continuous low rodent levels could lead to loss of high production years of waterbirds in the short-term, and to population declines in the long-term (Zydelis *et al.* 2006, Hario *et al.* 2009, Guillemain *et al.* 2013, Fox *et al.* 2015).

In the case of ducks, growth rates were negatively affected by previous year's rainfall, suggesting that a) increased rainfall may have caused nest and brood loss, e.g., due to poor incubation and brood-rearing conditions (found for instance in several birds of prey and passerines; Kostrzewa & Kostrzewa 1990, Lehikoinen *et al.* 2009, Mero *et al.* 2014, Öberg *et al.* 2015), and b) drier conditions in the previous breeding season could possibly lead to positive growth rates. However, opposite results have been found in Common Eider (*Somateria mollissima*), whose breeding success improved during warm and wet late springs (Iles *et al.* 2015). Fox *et al.* (2016) have also recently shown that climatic conditions during the breeding season can influence breeding success of Eurasian Wigeon (*Anas penelope*) on a flyway level, the latter being measured by age ratios in Danish hunter wing surveys. Although rainfall and the phase of the rodent cycle could not be evaluated in the same model because of strong collinearity, our findings suggest that rainfall can be even more important than the phase of the rodent cycle. In any case, both rainfall and the phase of the rodent cycle seem to have a strong influence on the breeding productivity of ducks and waders, respectively.

Along these lines, the role of density dependence was minimal, given that it only had a significant negative effect on Dotterel's breeding population (all wader species evaluated at the same time). Negative density dependence effects indicate that for this particular species, its growth rate decreases as density increases (i.e., the species is dependent on the population size). Likewise, temperature had no effect on any of the bird groups. However, we should note that although our time series is longer than the ones used in similar works on the same topic (e.g., Pehrsson 1986, Syroechovski *et al.* 1991, Underhill *et al.* 1993, Robinson *et al.* 2014), it is still rather short, with only ten years corresponding to eight data points. Therefore, our data do not allow us to assess the impact of extreme weather events upon bird populations, such as very cold summers, or comprehensively assess whether rainfall is more important than the phase of the rodent cycle for ducks. Lastly, the unexplained random variation in population fluctuations was only apparent in the wader set, with a small percentage variance explained by year.

At species-specific level, a total of four species (Ringed Plover, Temminck's Stint, Dunlin and Red-necked Phalarope) were positively influenced by the phase of the rodent cycle. In addition, the same species were limited by density dependence, except for Temminck's Stint. These were also the most abundant study species in the area, which could suggest that our sample sizes were too small to detect the effect in rare species. As for ducks, rainfall had only a negative effect on Long-tailed Duck. One potential explanation for the lack of any effect upon Scaup could be that this species has a longer maturation age than Long-tailed Duck and Teal (Cramp & Simmons 1977), and thus the recruitment process is likely to be delayed (Gardarsson & Einarsson 1994).

Populations of European and Asian waterbirds breeding in the Arctic and sub-Arctic regions have traditionally been monitored using mid-winter counts (the International Waterbird Census, IWC;

Wetlands International 2014). Whilst the IWC monitoring scheme has a relatively good coverage in European coastal and inland wetlands, it is scarce for species that are wintering in the offshore areas and in wetlands outside Europe (Wetlands International 2014) and thus the monitoring of pelagic species like Long-tailed Duck and Scaup cannot be well covered on an annual basis. In addition, different wintering areas of sex and age classes can further complicate studies examining factors that affect the breeding populations of Arctic species, even if the calculation of long-term population trends is feasible. Although in the Nordic countries bird monitoring schemes enable the analysis of national population trends also for some Arctic wader species, local changes in population dynamics/size are difficult to investigate given that the same sites are seldom covered every year (Lindström *et al.* 2015). We emphasize that counts from the breeding areas are rather rare compared to winter counts.

To conclude, several studies have shown that the effects of climate change are going to be particularly severe in the Arctic region, causing detrimental impacts upon breeding Arctic waterbird species. Changes in weather, as for instance increased summer rainfall, together with altered rodent cycles (e.g., flattened peaks) can lead to unstable dynamics which may translate into population declines of Arctic waterbirds in the future. In view of our findings and with these considerations in mind, future research should be carried out to further investigate the consequences of these and other changes, such as the spread of generalist predators, for breeding waterbird populations.

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Sääolojen ja pikkunisäkässyklin vaiheen vaikutus sorsien ja kahlaajien pesimäkantoihin Suomen tunturialueella

Ilmaston on ennustettu muuttuvan voimakkaimmin arktisilla alueilla, mutta muutosten vaikutukset arktisiin lintukantoihin tunnetaan huonosti. Ilmastonmuutos voi vaikuttaa lintukantoihin suoraan muuttamalla sääolosuhteita tai epäsuorasti ravintoverkon kautta. Tutkimme pitkäaikaisaineiston avulla miten vuosittaiset sääolosuhteet ja pikkunisäkässyklin vaihe vaikuttavat kolmen arktisen sorsalinnun ja seitsemän kahlaajalajin pesimämääriin. Aineisto kerättiin Suomen Käsivarren tunturipaljakalta läheltä Kilpisjärveä vuosina 2005–2015 (poislukien 2006). Oletuksemme oli, että pikkunisäkäshuipun aikaan pedot käyttävät ravintonaan pikkunisäkkäitä, paljakalla etenkin tunturisopulia, jolloin sorsien ja kahlaajien pesimämenestys on suurempi kuin pikkunisäkässyklin pohjavuosina. Lisäksi oletimme pesintöjen onnistuvan paremmin lämpiminä ja kuivina kesinä verrattuna kylmiin ja sateisiin.

Tutkimuslajien kannankehityksissä ei ollut merkitseviä pitkäaikaissuuntauksia. Poikasia hoitavien kahlaajien lukumäärät olivat suurimmillaan pikkunisäkäshuipun aikaan, jolloin saalistuspaine on alhainen. Pesivien sorsien lukumäärät kasvoivat edellisen kesän oltua kuiva, mutta olivat runsaimmillaan pikkunisäkäshuippua seuraavana vuonna. Sadanta ja myyräsyklin vaihe korreloivat keskenään, jonka takia niitä ei voitu tarkastella mallissa samanaikaisesti. Tutkimustuloksemme painottavat, että lintukantojen muutokset ovat alttiita pikkunisäkäskannan vaihtelulle, mutta sadannallakin on merkitystä. Ilmastonmuutoksella voi olla kohtalokkaita seurauksia arktisille lajeille, mikäli se lisää pesimäaikaista sadantaa ja heikentää pikkunisäkässyklien voimakkuutta.

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