J Ornithol (2014) 155:679–687
DOI 10.1007/s10336-014-1051-y

ORIGINAL ARTICLE

Drivers of breeding numbers in a long-distance migrant, the Garganey (*Anas querquedula*): effects of climate and hunting pressure

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Received: 18 September 2013 / Revised: 9 December 2013 / Accepted: 28 January 2014 / Published online: 15 February 2014

Abstract A multitude of anthropogenic factors are threatening bird populations but their roles as drivers of population changes are generally poorly understood. Several duck species, for instance, have unfavorable conservation status at the Pan-European level but in most cases we do not know why the species have been declining, nor do we know actual drivers of their population dynamics. We studied population dynamics of the Garganey (*Anas querquedula*), a quarry species with unfavorable conservation status at the Pan-European level. As a trans-Saharan migrant, Garganey is potentially highly vulnerable to climate change impacts. We used long-term (1989–2012) data of breeding numbers from a study area in central Finland and assessed the relative importance of three climatic variables (representing conditions in wintering areas and during spring migration) and local hunting pressure in explaining the interannual variation in breeding numbers. Population size of Garganey showed a decreasing trend over the study period but also considerable interannual variation. Spring temperature in southern Finland was the most important factor in explaining interannual variation in breeding numbers. Rainfall in the wintering areas was also of importance, whereas the NAO (North Atlantic Oscillation) and local hunting pressure appeared not to be important. Our results suggest that weather conditions during spring migration largely drive interannual variation in Garganey breeding numbers at the NW edge of the species' range. However, positive effects of warm springs may be counteracted by negative effects of drought in the wintering areas.

Keywords Climate change · Hunting pressure · Population dynamics · Spring migration · Weather · Wintering conditions

Zusammenfassung

Einflussfaktoren auf Brutpaarzahlen bei einem Langstreckenzieher, der Knäkente (*Anas querquedula*): klimatische Effekte und Jagddruck

Eine Vielzahl anthropogener Einflussfaktoren bedrohen Vogelpopulationen. Ihre Rolle hinsichtlich Populationsveränderungen ist jedoch allgemein nur wenig verstanden. Verschiedene Entenarten beispielsweise besitzen einen unzureichenden Schutzstatus auf pan-europäischer Ebene. In den meisten Fällen sind weder die Gründe für die Rückgänge der Arten bekannt, noch sind die derzeitigen Auslöser für ihre Populationsdynamiken verstanden. Wir untersuchten die Populationsdynamik von Knäkenten (*Anas querquedula*), eine Zielart mit ungünstigem Erhaltungszustand auf pan-europäischer Ebene. Als Transsaharazieher sind Knäkenten potentiell stark gefährdet im Hinblick auf Auswirkungen des Klimawandels. Wir nutzten Langzeitdaten (1989–2012) zu Brutpaarzahlen aus einem Untersuchungsgebiet in Zentralfinnland und bewerteten die relative Bedeutung dreier klimatischer Faktoren (repräsentativ für die Bedingungen in den Überwinterungsgebieten und während des Frühjahrszuges) sowie den lokalen Jagddruck zur Erklärung von interannuellen Schwankungen im Brutbestand. Die Knäkenten-Population zeigt einen abnehmenden Trend während des Betrachtungszeitraumes, jedoch mit deutlichen

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Schwankungen zwischen den Jahren. Die Frühjahrstemperatur in Südfinnland war der wichtigste Faktor zur Erklärung der variierenden Brutpaarzahlen zwischen den Jahren. Außerdem war der Niederschlag in den Überwinterungsgebieten ebenfalls von Bedeutung, wohingegen die NAO (Nordatlantische Oszillation) und der lokale Jagddruck unerheblich zu sein schienen. Unsere Ergebnisse deuten daraufhin, dass die Wetterbedingungen während des Frühjahrszuges weitgehend die jährlichen Schwankungen der Brutpaarzahlen von Knäkenten an der nordwestlichen Grenze ihres Verbreitungsgebietes bewirken. Allerdings könnten die negativen Effekte von Dürren in den Wintergebieten den positiven Auswirkungen von warmen Frühjahren entgegenwirken.

Introduction

In the course of their annual cycle, individuals of migratory species are exposed to multiple environmental conditions in geographically separated areas. Depending on the season, changes in these environmental conditions affect the fundamental demographic processes of births, deaths, immigration, and emigration that determine the dynamics of populations (Fretwell 1972). For example, there is compelling evidence that weather conditions during both the breeding season and the non-breeding season affect the fluctuations in the size of bird populations (Sæther et al. 2004; Sæther and Engen 2010). Similarly, climate change has been found to affect long-term population trends of migratory species (Møller et al. 2008; Saino et al. 2011). On the other hand, population limitation by human-induced habitat alterations has been recognized as an important driver of the recent declines in the abundance of some farmland and forest species (Newton 2004a; Eglington and Pearce-Higgins 2012; Morrison et al. 2013). Clearly, recognition of season-dependent effects that drive population dynamics of migratory species is essential for efficient conservation and management of their populations (see also Calvert et al. 2009).

While factors driving the dynamics and long-term trends of populations are relatively well studied for farmland and forest species, for example, much less is known about the role of climate change impacts and other human-related factors in driving the dynamics of waterfowl populations (see e.g., Guillemain et al. 2013; Pöysä et al. 2013; Reif 2013). Garganey (*Anas querquedula*) is a Palearctic duck species, breeding at temperate latitudes across Europe and Asia, mainly between 42°N and 65°N (Scott and Rose 1996). The main wintering areas of Garganey breeding in western Europe are situated in West Africa from southern Mauritania, Senegal and Gambia to Chad (i.e., the Sahel zone; Scott and Rose 1996), the main wintering wetlands being the Lake Chad area, the Inner Niger Delta, and the Senegal Delta (Zwarts et al. 2009). Numbers of Garganey have declined in several European countries (e.g., Viksne et al. 2010; Pöysä et al. 2013), and the overall population trend in Europe is decreasing (Sanderson et al. 2006; Wetlands International 2013).

Factors driving changes in the breeding numbers of Garganey have not been analyzed. Hypothesized reasons for long-term declines include habitat loss due to drainage and transformation of wetlands into arable land in breeding areas in Europe and due to large-scale irrigation schemes in wintering areas in West Africa (Scott and Rose 1996; Schricke 2001; Viksne et al. 2010). The long-term decline of Garganey breeding numbers has also been attributed to high hunting pressure in some breeding areas in Europe (Schricke 2001; Kear 2005; Viksne et al. 2010) and in the West African wintering areas, especially in years of severe drought (Zwarts et al. 2009). Moreover, variation in the severity of drought in the West African wintering areas and in the condition of wetlands in Western Europe have been suggested to affect interannual variation in breeding numbers in Europe (Fouquet et al. 1992; cited in Schricke 2001). Indeed, population fluctuations especially at the edges of the species' range have been suggested to be due to variation in climatic conditions; for example, Cramp and Simmons (1977) suggested that warm springs may stimulate northern spring migration or dry years in the south may force birds further north (see also Schricke 2001). This phenomenon is also known as "prolonged spring migration" (sensu von Haartman 1973), and it is one of the early hypotheses put forward to play an important role in range expansion of migratory birds (see von Haartman 1973).

In this paper we focus on the factors that drive interannual fluctuations in the breeding numbers of Garganey in central Finland, i.e., at the northwestern edge of the species' distribution (see e.g., Scott and Rose 1996). Specifically, we determine the relative role of climatic factors (rainfall in wintering areas, winter NAO, and spring temperature in southern Finland, the latter two describing climatic conditions during spring migration; see "Materials and methods") and local hunting pressure in driving fluctuation in the annual breeding numbers of the species. In doing this, our study addresses recent calls to study simultaneously the effects of multiple climatic conditions and other human-related threats on bird populations (Møller et al. 2010a; Pautasso 2012; Møller 2013).

Materials and methods

Study area and duck censuses

Data on the breeding numbers of Garganey (1989–2012) and on the numbers of Garganey and Common Teal (*Anas*

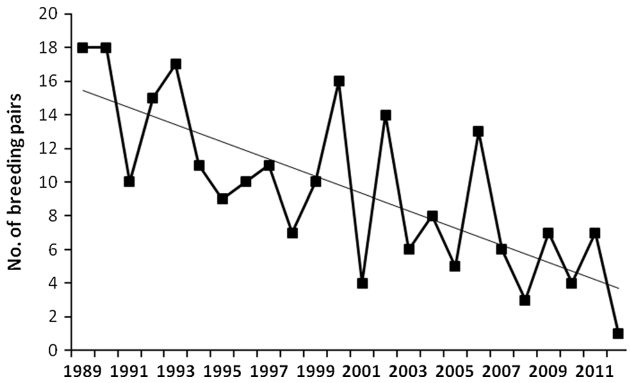

Fig. 1 Population time series (no. of breeding pairs) of the Garganey in a study area in central Finland, 1989–2012. Trend line is also given (for details, see "Results")

crecca) just before the start of the hunting season (1988–2011) were gathered from four adjacent eutrophic lakes (size 25–180 ha) in central Finland (63°N, 27°E) (lakes 1–4 in Fig. 1 of Väänänen 2001). Most (ca. 90 %) of the wing data (see below), obtained annually (1988–2011) from local hunters, were gathered from the same four lakes; the rest of the wing data were gathered from neighboring lakes in the same area (see the map in Fig. 1 in Väänänen 2001). The study lakes were eutrophic and emergent vegetation covered about 30 % of the total lake area (Väänänen 2001).

Numbers of breeding Garganey were surveyed in May using the standardized waterfowl "round count" method described by Kauppinen et al. (1991). Bird observations from the surveys were interpreted as breeding pairs after the criteria given in Koskimies and Väisänen (1991). Numbers of Garganey and Common Teal before the start of the hunting season were surveyed usually on 18 or 19 August (see Väänänen 2001); the duck hunting season in Finland opens on 20 August.

Climatic conditions and hunting pressure

A key climatic characteristic in the Sahel region, the main wintering areas of Garganey breeding in western Europe (see "Introduction"), is marked interannual variation in rainfall (e.g., Lebel and Ali 2009; Lélé and Lamb 2010). The rainfall during April–October has strong impacts on habitat conditions of wintering waterbirds in the area, in particular on the extent of inundation areas of main rivers and lakes (Zwarts et al. 2009). Moreover, Zwarts et al. (2009) found that fluctuations in Garganey numbers in Lake Engure, Latvia, were correlated with the surface of the flooded areas in the Inner Niger Delta and the Senegal Delta. We used average normalized (relative to the 1941–2000 mean) April–October rainfall departures 1988–2011 for the 20 stations of Lélé and Lamb (2010; data updated by M. Issa Lélé, unpublished), covering the main wintering sites of Garganey in the Sahel zone, to assess the role ecological conditions determined by rainfall in the wintering areas in driving breeding numbers of Garganey.

The North Atlantic Oscillation (NAO) has a strong influence on climate in Europe. High positive values of December–March (winter) NAO index (e.g., Hurrell et al. 2003) imply strong westerly winds over the North Atlantic, and are associated with mild and rainy winters in northern Europe, while low negative values are associated with opposite winter weather conditions in Europe (e.g., Kucharski et al. 2006; Hurrell and Deser 2010). The NAO has been found to affect numerous ecological systems and processes (e.g., Ottersen et al. 2001; Blenckner and Hillebrand 2002; Westgarth-Smith et al. 2012), including the migration behavior of birds (e.g., Hüppop and Hüppop 2003; Stervander et al. 2005; Rainio et al. 2006; Lehikoinen and Sparks 2010). For example, Rainio et al. (2006), see also Vähätalo et al. (2004), demonstrated that the timing of especially the early phase of spring migration in waterfowl is associated with the winter NAO; arrival was earlier after winters with high NAO index. We used the winter NAO (hereafter NAO) indices of 1989-2012 to measure climate conditions during the early spring migration period of Garganeys in West Europe (Schricke 2001). The annual NAO indices were obtained from the website of the Climatic Research Unit at the University of East Anglia (http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm).

Spring temperature (mid April–late May) has been found to be associated with fluctuations of duck breeding numbers, including Garganey, in Finland (Siira and Eskelinen 1983; Kauppinen and Väänänen 1999). Hence, to index weather conditions during the spring migration of Garganey in Finland (Lehikoinen and Vähätalo 2000), we used mean daily temperatures for the April 15 to May 31 periods of 1989–2012 for southern Finland (i.e., south of the study area). The original temperature data was provided by the Finnish Meteorological Institute and consisted of mean daily temperatures (based on eight records at intervals of 3 h) calculated for each of 10 × 10-km squares, so-called gridded HILA-data base (http://en.ilmatieteenlaitos.fi/observations).

Comparable and reliable long-term data on the annual numbers of bagged Garganey are not available for our study area. Therefore, we used annual (1988–2011) data on the numbers of wings of Garganey and Common Teal in the hunting bag (total number of wings per year, species combined: mean 63, range 10–258) and annual census data on the numbers of the two species in the study area in August just before the start of the hunting season (total number of birds per year, species combined: mean 310, range 114–574), and calculated an index of relative local hunting pressure as follows. We fitted the proportion of Garganey in the annual wing samples against the proportion of Garganey in the field (i.e., annual bird abundance data in August) and used residuals from this regression as an index of relative annual hunting pressure. This index should provide a reasonable measure of relative local hunting pressure for the Garganey in our study area, because both the wing data and the August bird abundance data are principally from the same lakes (see above) and because these two species are very similar in size and plumage during the hunting season making it practically impossible for hunters to separate them in the field. This view is also supported by Bregnballe et al. (2006, p. 859) who pointed out that, because of the "look-alike" problem, it is hardly practicable to protect the Garganey efficiently if an open season is maintained for the Common Teal. The hunting pressure index relies on the proportions of Garganey and Common Teal in the field and in the wing-samples but does not take into account the number of hunters or hunting days, aspects that potentially are important components when assessing hunting pressure. However, because the hunting pressure index we have used is based on the actual numbers of individuals available in the field and on the actual numbers of birds shot, we consider it appropriate for quantifying hunting impact even without considering hunting effort.

To consider the role of hunting impact more generally, we assessed in a separate analysis the impact of the annual total Garganey and Common Teal bag in Finland the previous year on the annual breeding numbers of Garganey in our study population. For this analysis, we used the annual bag statistics of Garganey and Common Teal (these two species are pooled in the Finnish bag statistics) for the period of 1996–2011 in Finland to index the overall annual hunting pressure on Garganey in Finland (estimated total annual bag for the two species varied between 109,500 and 162,000 birds; annual bag statistics are compiled by Finnish Game and Fisheries Research Institute; for an example, see Finnish Game and Fisheries Research Institute 2013). It is not possible to estimate the annual relative proportion of Garganey in the combined bag because national wing-survey data needed for that are available only from 2005–2007 (e.g., Guillemain et al. 2010). Hence, using the combined bag of the two species assumes that high combined take of Garganey and Common Teal means high take of Garganey and low combined take of Garganey and Common Teal means low take of Garganey.

Statistical analyses

Trends in time-series data may result in spurious correlations between time series as demonstrated by Lindström and Forchhammer (2010). The breeding numbers of Garganey (Fig. 1, see "Results") and the NAO index (Fig. 2b; linear regression, slope $= -0.086$, $r^2 = 0.179$, $F = 4.786$, $p < 0.05$) showed a statistically significant decreasing trend through the study period 1989-2012; no statistically significant trend over years was found in the other predictor variables ($p > 0.17$ in all cases; see Fig. 2). Hence, to eliminate possible over-riding effect of the trends and to avoid spurious correlations (Lindström and Forchhammer 2010), we detrended the time series of the breeding numbers and the NAO by fitting first-order polynomial to the original data and used residuals of those fits in the analyses (see Chatfield 2004). We used linear regression models to test how the annual breeding numbers of Garganey (year t) are associated with the variation in the annual spring temperature in southern Finland (year t), NAO (year t), Sahel rain (year $t-1$), and relative local hunting pressure (year $t-1$). There was no strong correlation between the predictor variables (pair-wise Pearson correlations, range of r: 0.063–0.367; range of p: 0.07–0.70). Our set of candidate models included all possible models without interactions (15 models in all, see Table 1), and we used Akaike's information criterion adjusted for small sample size (AIC_c) in model selection (Burnham and Anderson 2002; Burnham et al. 2011). We calculated AIC difference ($\Delta AIC_{ci} = AIC_{ci} - AIC_{cmin}$) and Akaike weight ($w_i$) for each model. The latter was used to assess the relative importance of the predictor variables. As there was uncertainty in model selection (see "Results"), and in order to make the number of models that contain a given predictor equal between the predictor variables, variable-specific weights were calculated using all models in which a given variable was included (see Burnham and Anderson 2002, p. 167). Parameter estimates (β_j) and their standard errors were calculated using model averaging (Burnham and Anderson 2002, p. 180). All analyses were run in SYSTAT 13.

Results

The numbers of breeding Garganey showed a decreasing trend over the study period (linear regression, slope $= -0.510$, $r^2 = 0.543$, $F = 26.136$, $df = 22$, $p < 0.001$) but also considerable interannual variation (Fig. 1).

According to current standards (Burnham et al. 2011), two models received considerable support from the data (i.e., $\Delta AIC_c < 2$; models 1 and 2 in Table 1) while seven additional models (i.e., ΔAIC_c in the 2–7 range; models 3–9 in Table 1) received some support. The two top models included the predictors Sahel rain and spring temperature in southern Finland (first-ranked model) or only the latter (second-ranked model).

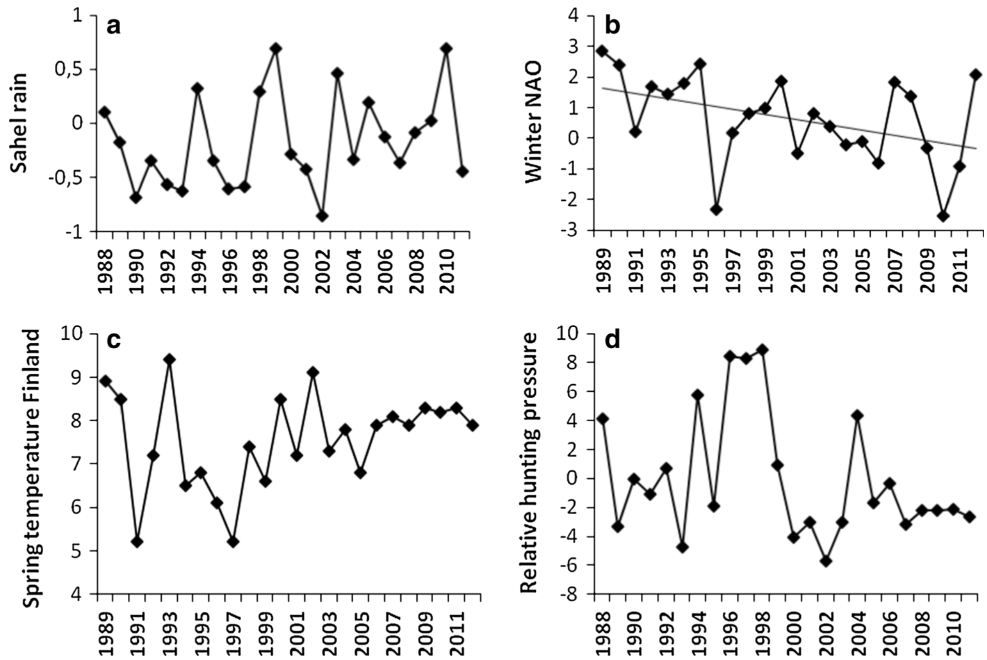

Fig. 2 Temporal variation of the predictor variables used in the analyses: **a** Sahel rainfall index (1988–2011), **b** the winter (December–March) NAO index (1988/89–2011/12), **c** the mean spring (15 April–31 May) temperature in southern Finland (1989–2012), and **d** the local hunting pressure index (1988–2011). Trend line for the NAO index is also given; no statistically significant trend was found for the other predictor variables (for data sources, see Materials and methods)

Table 1 Summary of models used to explain interannual variation in the breeding numbers of Garganey; models are ranked according to AIC_c. For explanation of the predictor variables, see "Materials and methods"

	Model	K[a]	AIC_c^b	ΔAIC_c^c	w_i^d
1	Spring temperature + Sahel rain	4	119.622	0.000	0.3057
2	Spring temperature	3	119.663	0.041	0.2995
3	Spring temperature + NAO	4	121.892	2.270	0.0983
4	Spring temperature + Local hunting	4	122.137	2.515	0.0869
5	Spring temperature + Sahel rain + NAO	5	122.275	2.653	0.0811
6	Spring temperature + Sahel rain + Local hunting	5	122.775	3.153	0.0632
7	Spring temperature + NAO + Local hunting	5	124.351	4.729	0.0287
8	Spring temperature + Sahel rain + NAO + Local hunting	6	125.621	5.999	0.0152
9	Sahel rain	3	126.150	6.528	0.0117
10	Sahel rain + Local hunting	4	128.358	8.736	0.0039
11	Sahel rain + NAO	4	128.850	9.228	0.0030
12	Sahel rain + NAO + Local hunting	5	131.309	11.687	0.0009
13	NAO	3	131.466	11.844	0.0008
14	Local hunting	3	131.538	11.916	0.0008
15	NAO + Local hunting	4	134.097	14.475	0.0002

[a] Number of parameters

[b] Akaike's information criterion corrected for small sample size

[c] AIC_c for model *i* minus the minimum AIC_c

[d] Akaike weight

The sums of the Akaike weights for the predictors revealed that spring temperature in southern Finland had substantial evidence of being the most important variable in explaining interannual variation in Garganey breeding numbers (sum of w_i 0.979). Sahel rain also received some support (sum of w_i 0.485) while support for the importance of the other predictors was considerably less: NAO (sum of w_i 0.228), local hunting pressure (sum of w_i 0.200). Breeding numbers of Garganey increased both with spring temperature in southern Finland ($\beta = 1.799$, SE $= 0.518$) and with Sahel rain ($\beta = 2.157$, SE $= 1.308$), while parameter estimates for the NAO index ($\beta = -0.337$, SE = 0.458) and local hunting pressure ($\beta = 0.064$, SE = 0.317) were highly un-precise (i.e., high SE in relation to β).

Considering the impact of the total Finnish Garganey and Common Teal bag on the breeding numbers of Garganey, there was no correlation between the two (detrended breeding numbers in year *t* vs. total bag in year *t*-1, Pearson correlation, $r = 0.091$, $df = 14$, $p = 0.738$).

Discussion

The breeding numbers of Garganey in our study population declined during the study period of 1989-2012, a pattern consistent with the recent decline of the breeding numbers of the species in Finland and in other European countries (see "Introduction"). We also found considerable interannual variation in the breeding numbers, and this variation was driven mainly by spring temperature in southern Finland but also by rainfall in the main wintering areas in the Sahel region the previous year. We found the NAO to be of minor importance in affecting the breeding numbers of Garganey in our study population, suggesting that climatic conditions during the end, but not during the early part of spring migration are important.

Numerous studies have demonstrated that spring temperature affects the timing of migration in birds (migrants arrive earlier in years of relatively higher spring temperature; reviews in Lehikoinen et al. 2004; Rubolini et al. 2007; Gordo 2007; Lehikoinen and Sparks 2010) but, to our knowledge, direct effects of temperature during spring migration on population numbers of migratory species have not been examined in the context of climate change impacts. We found that the breeding numbers of Garganey increased with higher spring temperatures in southern Finland. Similarly, Kjeldsen (2008) found a positive correlation between the average temperature in March and the breeding numbers of Garganey in Vejlerne, Denmark. This association is most probably explained by temperature-driven variation in the migratory behavior of Garganey rather than by weather-dependent mortality of birds (for the latter explanation see e.g., Sæther et al. 2004; Leech and Crick 2007). Specifically, high spring temperature probably stimulates prolonged (northern) spring migration, resulting in higher breeding numbers near the northern edge of the species' range. As found with the timing of spring arrival in long-distance migrants (e.g., Halkka et al. 2011), temperature over larger areas in Europe than just in southern Finland most probably affects the process. Our finding thus gives support to the early hypothesis that prolonged spring migration, stimulated by warm spring temperature, may directly affect population numbers (e.g., von Haartman 1973). It is important to note, however, that the positive short-term response to warmer spring temperatures has not translated into a positive long-term trend in the breeding numbers of the species; on the contrary, Garganey numbers have been decreasing despite the fact that especially spring temperatures in northern Europe have been increasing (e.g., Lehikoinen and Sparks 2010, fig. 9.5). Hence, we consider it unlikely that the mechanism revealed here will result in range expansion of the species, a process that could be alleviated by temperature-driven prolonged spring migration. Neither does the latest Finnish breeding bird atlas suggest any northward shift in the distribution of the species (Valkama et al. 2011). On the other hand, climate change-based simulations by Huntley et al. (2007) suggest that the future distribution of the species is shifted northward in Finland, Sweden, and NW Russia (see also below). Nevertheless, because a positive correlation between breeding numbers and spring temperature has also been found in other duck species breeding at northern latitudes (Siira and Eskelinen 1983; Kauppinen and Väänänen 1999), we suggest that this aspect of climate change impacts on migratory birds, especially on their population dynamics (Sæther and Engen 2010) and range shifts (Brommer and Møller 2010), deserves more attention.

Temperature-driven population dynamics has been documented for North American breeding ducks. When analyzing geographical gradients in the population dynamics of North American prairie ducks, Sæther et al. (2008) found that population increases at higher latitudes were generally associated with cold spring temperatures, i.e., a pattern contradicting our finding with the Garganey. However, the North American prairies are highly variable in terms of the availability of wetlands, the main driver of spatial and temporal variation in duck numbers (e.g., Johnson and Grier 1988; Bethke and Nudds 1995). Wetland availability, in turn, is affected positively by high precipitation and cool temperature (e.g., Withey and van Kooten 2011). A well-known phenomenon is the overflight (i.e., prolonged spring migration) of North American prairie ducks to the north or northwest in years of drought and low wetland availability in the prairies (e.g., Smith 1970; Johnson and Grier 1988). These characteristics make the system studied by Sæther et al. (2008) quite different from the breeding environments of ducks in northern Europe where the availability of wetlands (lakes and ponds) is stable year after year. Nevertheless, our results, and those from North American prairies together, demonstrate considerable flexibility of breeding ducks to respond to changing climatic and other environmental conditions (see also Oja and Pöysä 2007; Sjöberg et al. 2010; Drever et al. 2012).

The breeding numbers of Garganey also increased with the preceding year's rainfall in the Sahel region, implying that ecological conditions in the wintering areas in West

Africa affect annual fluctuations in the breeding numbers at northern latitudes. A similar connection between annual fluctuations in breeding numbers and annual fluctuations in the Sahel rainfall has been found for some European passerines (e.g., Peach et al. 1991; see also Newton 2004b). Several mechanisms may underlie this connection. First, poor ecological conditions in dry years may result in lower body condition and increase wintering mortality and/or mortality during spring migration, as suggested in many other trans-Saharan migratory species (e.g., Peach et al. 1991; Norman and Peach 2013; reviews in Newton 2004b; Leech and Crick 2007). Second, drought in West African wintering areas may induce movements to wintering areas in eastern Africa (Urban 1993; but see Zwarts et al. 2009), representing a different flyway with a more eastern breeding distribution (see Scott and Rose 1996). This could decrease breeding numbers at the northwestern edge of the species' range through increasing abmigration (switch between flyways), a phenomenon found to be frequent for both sexes in the Common Teal (Guillemain et al. 2005). Drought-induced movements between wintering areas may also increase mortality, affecting negatively subsequent breeding numbers in the north. Third, as suggested by Zwarts et al. (2009), local hunting pressure in the main wintering areas of the species may be particularly high in dry years, increasing total mortality. This explanation, however, may not apply to the present population (see below). Whatever the actual mechanism(s) behind the winter conditions-driven breeding numbers in Garganey, our finding emphasizes the need to take into account nonbreeding-season drivers of population dynamics in the conservation of seasonal migrants (Sanderson et al. 2006; Robinson et al. 2008; Calvert et al. 2009). In particular, our analysis revealed that, while climate change impacts mediated through warmer spring temperatures may affect positively the numbers of Garganey in northern breeding grounds, and hence alleviate range expansion northward, these positive effects may be counteracted by negative effects of dry years and periods of drought in the wintering areas. Such counteracting interplay between climatic conditions in the wintering areas and climatic conditions during spring migration at northern latitudes needs to be carefully considered when building models aiming to predict range shifts and other responses of bird populations to climate change (Huntley et al. 2007; Brommer and Møller 2010; Jenouvrier 2013).

We found local hunting pressure to be of minor importance in driving the breeding numbers of Garganey in our study population. Neither did overall hunting pressure in Finland (i.e., total annual Garganey and Common Teal bag) seem to have an impact on the annual breeding numbers of Garganey in our study population. These results were not unexpected, after all. Garganey is an early autumn migrant in Finland, which is reflected also in Garganey bag: over 95 % of bagged Garganeys are shot in August (Kauppinen and Väänänen 1999; Väänänen 2001). Early autumn migration of the species means that Garganey may largely avoid to get shot in Finland. Hunting in the main wintering areas in West Africa may also drive breeding numbers in Europe, as captures especially in dry years may be substantial (Zwarts et al. 2009). Zwarts et al. (2009) used information on the estimated numbers of captured Garganey in the southern Inner Niger Delta and found them to be correlated with water level at February 15 in the area. Using that relationship, they estimated annual numbers of Garganey captured in the Inner Niger Delta over a period of years; the estimated annual numbers varied between 0 in wet years and 60,000–70,000 in dry years (Zwarts et al. 2009, fig. 166). These estimates cover the period of 1989-2005 of our Garganey time series; annual breeding numbers of Garganey in our study population are not correlated with these annual Garganey capture estimates (detrended breeding numbers vs. estimated numbers of captured birds during the preceding winter, Pearson correlation, $r = 0.010$, $df = 15$, $p = 0.71$). This suggests that, assuming the capture estimates provided by Zwarts et al. (2009) are appropriate and accurate enough, hunting in the main wintering areas is not driving the breeding numbers of Garganey in our study population. The number of birds taken in relation to the estimated total wintering population in West Africa (about 2,000 000 birds, Wetlands International 2013) is rather small, and therefore may not have a visible effect on population fluctuations.

In conclusion, our results demonstrate that climatic conditions during both spring migration and in the wintering areas affect fluctuations in the breeding numbers of a long-distance migrant. This finding underlines the need to consider the whole annual cycle when assessing climate change impacts on migratory species and when developing conservation and management plans for them. In particular, our analysis revealed how positive effects of warmer spring temperatures on population numbers may be counteracted by negative effects of dry years in the wintering areas. Our results are from a population at the extreme of the species' range and therefore should help in elucidating processes underlying range dynamics of migratory species. Finally, while effects of climate change on birds have been studied intensively (Møller et al. 2010b; Knudsen et al. 2011; Pautasso 2012; Reif 2013), our understanding of climate change impacts on ducks is limited (Guillemain et al. 2013). In particular, because ducks and other waterfowl are important quarry species all over the world, we encourage more studies in which effects of different types of human-imposed threats such as climate change and hunting pressure are considered simultaneously.

Acknowledgments We are grateful to Issa Lélé and Peter Lamb for the Sahel rainfall index, to Henriikka Simola, Finnish Meteorological Institute, for compiling the temperature data, and to local hunters for providing the wing samples of shot ducks. Comments by Preben Clausen and an anonymous reviewer helped to improve the manuscript and are highly appreciated.

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