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Effects of climate change on European ducks: what do we know and what do we need to know?

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The consequences of climate change for bird populations have received much attention in recent decades, especially amongst cavity-nesting songbirds, yet little has been written on ducks (Anatidae) despite these being major elements of wetland diversity and important quarry species. This paper reviews the major known consequences of climate change for birds in general, and relates these to the limited information available specifically for ducks. Climate change can influence migration distance and phenology, potentially affecting patterns of mortality, as well as distribution and reproductive success in ducks. Studies addressing effects of climate change are, however, restricted to very few duck species, including mallard *Anas platyrhynchos* and common eider *Somateria mollissima*. Shifts in winter duck distributions have been observed, whereas the mismatch hypothesis (mistiming between the periods of peak energy requirements for young and the peak of seasonal food availability) has received limited support with regard to ducks. We propose a range of monitoring initiatives, including population surveys, breeding success monitoring schemes and individual duck marking, which should later be integrated through population modelling and adaptive management to fill these gaps.

Key words: climate change, demography, ducks, fitness, geographic distribution, phenology, survival

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Studies worldwide increasingly demonstrate humaninduced global environmental changes influencing wildlife, particularly through habitat loss linked to agricultural changes, urbanisation and industrial development (e.g. Julliard et al. 2003; for ducks see e.g. Bethke & Nudds 1995, Duncan et al. 1999). However, in the last two decades, the potential consequences of global climate change for animal populations have emerged as ranking amongst the greatest perceived threats to biodiversity (e.g. Hughes 2000, McCarty 2001, Walther et al. 2002).

Birds have traditionally received considerable research attention, so it is no surprise that the consequences of climate change on their populations have been widely explored (e.g. Møller et al. 2011). However, for practical and other reasons, studies are skewed towards specific bird groups, especially cavity-nesting songbirds (e.g. Both et al. 2006, Thorup et al. 2007). Such species may be especially affected by a changing climate due to their small size and relatively high energy requirements. In addition, the availability of long-term data series on changes in abundance and breeding success makes it easier to assess the potential consequences of climate change for these birds (review in Sæther & Engen 2011).

Ducks (Anatidae) are well-studied and common worldwide, and many are important game species (Kear 1990). Apart from some sea ducks, most duck species exclusively use wetlands, which are generally considered as one of the most threatened habitats given a changing climate (IPCC 1997). However, research on the potential impacts of global climate change on ducks has been limited: the search string "duck + climate change" on the Web of Science (10 April 2013) yielded only 61 relevant hits, compared to > 2,800 scientific papers on climate change and birds in general (Møller et al. 2011). Much more effort has therefore been directed to studying the consequences of climate change for small and elusive passerine species, which are notably difficult to study throughout their complete annual cycle (Knudsen et al. 2011). The comparatively few studies on ducks are surprising given that wintering duck populations have been monitored in the Palearctic for decades (e.g. Wetlands International 2006), as have the breeding populations in North America (USFWS 2011). Furthermore, ducks are easy to observe and can also be fitted with telemetry devices owing to their large body size (e.g. Miller et al. 2005). Though caution is always necessary when fitting external devices to wild animals (e.g. Saraux et al. 2011), this creates great potential for assessing the impact of climate change at the individual level in these species.

By comparing what we know about the consequences of climate change for birds in general and for ducks in particular, this paper highlights the crucial gaps that we need to fill for the latter group. We propose a road map for developing European duck research and monitoring in this domain over the coming years. The focus is on European ducks, following the gaps in research and monitoring highlighted by Elmberg et al. (2006) for this continent. Both environmental and political constraints may be very different in the Old and the New World. Here, we first provide an overview of expected climate change and its potential consequences on ecosystems. Secondly, we review the known effects of climate change on birds, and provide an overview of the current knowledge in ducks. Finally, we provide a priority list of research to better understand the effects of climate change on European ducks.

Climate change: what can we expect?

A number of publications review the expected consequences of climate change, based on the work of the Intergovernmental Panel on Climate Change (IPCC). Here, we outline some points reviewed by Hurrell & Trenberth (2011) that may be the most relevant for ducks. Future changes in climate may not affect all parts of the globe to the same extent. Unfortunately, the changes in Europe are expected to be particularly intense in the strongholds of breeding duck populations, i.e. arctic areas and boreal forests (e.g. IPCC 1997). Predictions foresee not simply a gradual increase in mean temperature, but also cascade effects of temperature rise, including an increase in general climate stochasticity (IPCC 2012). General temperature increase is likely to reduce winter harshness and lead to earlier springs. More specifically, over the next 25 years, the midwinter (December-February) temperatures are expected to increase by 1.7-4.6°C in southern Europe and around the Mediterranean, and by 2.6-8.2°C in northern Europe, depending on model projections (Solomon et al. 2007). Such a change in temperature could lead to major northwards shifts of optimal bird wintering areas.

Precipitation regimes are also expected to change, with more precipitation at high latitudes, but a greater risk of drought in areas such as the Mediterranean basin. Documented changes in wind speed

have also been reported from different parts of the world, including Europe (Pryor et al. 2012). Changes in wind regimes could affect the timing and energetics of avian migration. Moreover, the extent of cloud cover and hence micro-climate have already changed dramatically in parts of the continent (Tang et al. 2012).

Sea level is expected to rise between 0.9 to 1.3 m during this century (Grinsted et al. 2010), which is likely to profoundly modify coastal habitats, as well as bird numbers and distribution, since these are directly affected by water levels (Holm & Clausen 2006). In a pristine ecosystem, sea-level rise will flood low-lying land, with shorelines simply moving inland and creating new shallow coastal habitats. However, much of the land around the North and Baltic Seas are lowlands protected by dikes or seawalls, which would otherwise flood. Some of these areas will continue to be protected (e.g. urban zones), but protection of other areas, such as agricultural land, will become increasingly economically unattractive (e.g. Beintema 2007). Some lowlands may therefore eventually be abandoned, which would create new waterbird habitats (e.g. managed retreat in southeastern England).

Ducks and climate change: what do we know?

Changes in phenology and breeding success

The most frequently documented effect of climate change on birds is an advancement of spring migration (reviews in Hughes 2000, Walther et al. 2002, Crick 2004, Gordo 2007, Ambrosini et al. 2011, Knudsen et al. 2011). Advanced migration phenology may result from milder winter conditions reducing thermoregulatory challenges and/or enhancing food resources, enabling earlier acquisition of optimal body reserves which allows early departure (e.g. Bridge et al. 2010, Fox & Walsh 2012, Fox et al. 2012). Fouquet et al. (2009) showed that the first greylag goose Anser anser migratory flights in western France were recorded three weeks earlier in the mid-2000s than in the 1980s, while Greenland white-fronted geese Anser albifrons flavirostris departed 15 days earlier in 2007 than in 1993 (Fox & Walsh 2012). In the latter study, the advancement in the departure date was highly correlated with changes in mean body condition amongst the population, but not directly correlated with temperature measures. Hence, earlier departure dates are not themselves proof of the direct effects of climate. In

accordance, earlier spring departures of whooper swans Cygnus cygnus have been linked to improvement in foraging conditions induced by climate change (Stirnemann et al. 2012). In addition, increased intra-specific competition also contributed to earlier departures (Miller-Rushing et al. 2008). Nevertheless, since most of the 81 migratory bird species examined arrived earlier in Finland in spring during years with positive North Atlantic Oscillation index values (hereafter NAO; positive values characterising mild and rainy winters in northern Europe), climate change is at least partly responsible for shifts in bird migration dates (Vähätalo et al. 2004). However, the actual processes underlying events in spring migration are complex. Some species show earlier departure dates today than in the past, but spend more time at migration stopovers. Consequently, arrival dates at the breeding grounds have not changed despite the fact that northern areas are experiencing faster rates of relative warming compared to those further south (Bauer et al. 2008, Fox et al. 2012).

Based on current knowledge, it seems that some ducks have indeed advanced their spring migration dates in response to climate warming. Northern pintail Anas acuta and northern shoveler A. clypeata responded to decreasing winter harshness (increasing NAO indices) and earlier springs by arriving earlier at their European breeding grounds (Vähätalo et al. 2004; see also Rainio et al. 2006). Similarly, all 17 duck species examined by Murphy-Klassen et al. (2005) advanced spring arrival dates by up to five days per decade at breeding sites in Manitoba, Canada, during the 20th century (see also Møller et al. 2008). In southwest Finland, arrival dates of common eiders Somateria mollissima to the breeding areas were more tightly connected with the local ice conditions than large-scale climate pattern (NAOindex), but breeding dates were not associated with climatic variables (Lehikoinen et al. 2006). Oja & Pöysä (2007) found no effect of the NAO index on the timing of hatching in mallard Anas platyrhynchos and common goldeneye Bucephala clangula in two Finnish study areas. These authors concluded that annual variation in the timing of breeding was so large in these species that it would be difficult to detect any long-term change anyway. This is consistent with Drever et al. (2012) who consider mallard and American wigeon Anas americana as flexible breeders that can easily adapt to fluctuating environments. Conversely, some species have a narrower time window for breeding, e.g. lesser scaup Aythya

affinis which adjust their breeding based on the photoperiod rather than temperature or habitat availability, and should hence be more likely affected by climate change in the long-term (DeVink et al. 2008, Gurney et al. 2011).

A major consequence of global warming on breeding bird phenology is the increasing risk of disconnection between the peak of food availability and the timing of hatching, i.e. the period when parent birds need to gather most of the energy (mismatch hypothesis), which may dramatically affect breeding success (e.g. Visser et al. 1998, Thomas et al. 2001, Gaston et al. 2009). For example, Møller et al. (2008) showed that European bird species that advanced spring migration had positive population trends, while species that did not change their timing of migration were either stable or declining. In ducks, availability of invertebrate prey has long been known to crucially affect duckling survival (e.g. Sudgen 1973). The fact that insect prey sometimes show very clear peaks of mass emergence has lead to the belief that ducks time their breeding to such superabundance in food (e.g. chironomids in Danell & Sjöberg 1977). This could cause a mismatch if ducks were not able to track potential shifts in emergence dates following climate change. Drever & Clark (2007), however, found weak evidence for the mismatch hypothesis linking breeding date and nest success in ducks breeding in the Canadian prairies. It may be that too much emphasis has been placed on insect emergence peaks, based on a few studies conducted in flooded wetlands and near-Arctic areas, where such peaks are very clear (Danks & Oliver 1972, Danell & Sjöberg 1977). Recent studies in a broader range of habitat types questioned the generality of such patterns in insect emergence (Dessborn et al. 2009, Sjöberg et al. 2011), and the lack of clear peaks in food availability in most habitats may explain why there is no clear evidence of the mismatch theory in ducks.

This is not to say that duck phenology is not sensitive to climate change. First, climate change during winter and early spring may lead to increases in the body condition of ducks ahead of spring migration. This could translate into enhanced breeding output, either directly because birds have stored more reserves for reproduction (capital breeders; e.g. common eiders in Lehikoinen et al. 2006), or indirectly because birds are less constrained during migration and possibly reach their breeding grounds earlier and in better condition (Guillemain et al. 2008; see Fox et al. (1992) for the importance of

winter harshness for common teal *Anas crecca* body condition). The earliest breeding mallards, common teal and common eiders do indeed produce more offspring than later breeders (Dzus & Clark 1998, Elmberg et al. 2005, Öst et al 2008; see Sjöberg et al. 2011 for a review of duck studies).

Secondly, global climate change may drive changes in local weather conditions encountered by ducks at the breeding grounds. Local temperature, for instance, is known to affect duck nest-initiation date (Langford & Driver 1979). Earlier springs result in earlier ice-break-up, which dictates habitat availability and the start of breeding, as found for two early arriving species, mallard and common goldeneye (e.g. Fredga & Dow 1983, Oja & Pöysä 2007). Positive relationships between warmer and drier springs and duck nest success have also been recorded by Drever et al. (2004) and Drever & Clark (2007) in the American prairies. The beneficial short-term effects of climate change may then be due to the release of thermal stress on ducklings rather than a change in food availability. Indeed, newly hatched precocial young of dabbling ducks Anas spp., in particular, have poor thermoregulation capacity (Koskimies & Lahti 1964), leading to decreased survival under harsh weather (Bengtson 1972, Krapu et al. 2000, Pietz et al. 2003).

Climate change may also affect duck breeding success through changes in habitat quantity and/or quality. Dzus & Clark (1998) suggested that declining wetland density during the breeding season, i.e. decreasing area of foraging habitat, may be responsible for the observed pattern of decreasing breeding success of mallards over time. That type of habitat deterioration is frequent in the North American prairies where seasonal wetlands dominate. In contrast, experimental manipulation showed no effect of varying hatching date on the survival of mallard ducklings on boreal lakes with stable water levels (Sjöberg et al. 2011). Over time, climate change may nonetheless have a negative impact on total reproductive output of ducks through e.g. a decrease in wetland availability through drought in southern Europe (as in the prairie region), or through clutch and duckling losses due to more rainy springs and summers in boreal areas at the Holarctic scale.

In summary, little has been done so far to assess whether or not ducks show a clear long-term change in annual phenology in response to climate warming, although the short-term effects of weather fluctuation have been studied more frequently. Mismatches between changes in phenology of ducks and habitat

quality do not seem to be as important as for smaller terrestrial species. However, we need more studies, especially on the relationship between the phenology of duck food and survival of breeding females and young ducklings, before generalisations can be made about effects of climate change on duck breeding success. Lastly, earlier springs may also affect duck population dynamics in a more indirect way. In many countries the opening date of the hunting season is relatively fixed in late summer. If earlier springs lead to advanced breeding phenology, this will result in birds having a greater flying ability at the end of the summer, and hence a potentially greater ability to avoid hunters and reduce hunting mortality (Oja & Pöysä 2005). Finally, a cautionary note concerns the very nature of many of the above studies, which are, by default, mostly correlational, so one should be careful when drawing conclusions about the actual impact of climate change until confirmed by experiments.

Changes in geographic ranges

The second most well-documented effect of climate change on birds is a change in distribution, typically a general northward shift of geographic ranges (e.g. Thomas & Lennon 1999, Hughes 2000, McCarty 2001, Hatzofe & Yom-Tov 2002, Huntley et al. 2007). In winter, milder climate may allow migratory birds to remain closer to their breeding grounds (e.g. Fox et al. 2005, Knudsen et al. 2011). Migration is hazardous and energetically costly, and therefore individual birds should attempt to winter as close to ultimate breeding areas as is compatible with maintaining their own condition for overwinter survival (Ketterson & Nolan 1976, Cristol et al. 1999; see Owen & Dix 1986 and Carbone & Owen 1995 specifically for ducks). Any increase in mean winter temperatures should, therefore, translate into a northward shift of wintering ranges of migratory birds, i.e. shorter migration journeys (e.g. Visser et al. 2009).

Changes in winter range could potentially have profound fitness consequences. Species that were formerly important quarry species in one country may become scarce because of such range changes, whilst becoming common in other countries which lack a winter hunting tradition and/or with lower winter hunting pressure because the species did not formerly occur there. Also, in a conservation context, safeguard networks designed to protect and support populations based on historical patterns of distribution and abundance may become less effective in

enhancing long-distance migrant populations, if geographic ranges change. Hence, distributional shifts driven by climate change may have unprecedented indirect population impacts affecting fitness parameters. Lastly, the extent to which climate change may affect the post-breeding migration of males towards specific moulting sites (e.g. Salomonsen 1968) is unknown.

Climate change may cause a northward shift of the breeding environment as optimal breeding zones retreat northwards. Birds may attempt to track this by migrating to higher latitudes, just as they try to track climate change in time by advancing their spring migration dates (Thomas & Lennon 1999, Hughes 2000, Crick 2004, Huntley et al. 2007, Knudsen et al. 2011). However, most female ducks are strongly philopatric (e.g. Anderson et al. 1992), which may dampen shifts in breeding ranges compared to the rate of change in northern environmental conditions.

In contrast, climate change is likely to have a stronger and probably more rapid effect on the winter distribution of ducks. The winter distribution of most dabbling and diving duck species (i.e. species other than sea ducks) is largely driven by temperature, since access to water is critical for these aquatic species that rely on ice-free open freshwater for food supply and/or safety from predation (Lebreton 1973, Schummer et al. 2010). Sea ducks, such as the common eider, may be well adapted to cold winter conditions since their annual apparent survival rates are unrelated to winter harshness (Hario et al. 2009a, Ekroos et al. 2012b), suggesting that changes in winter temperature may have only limited, direct effects. Recent studies suggest that the direct costs of thermoregulation may play less of a role in determining the geographical distribution of wintering ducks in Europe than their body size would predict, implicating food availability and other factors as being more important than simply ambient temperature (Dalby et al. 2013a). Nevertheless, winter severity is a major factor influencing where ducks decide to winter (Ridgill & Fox 1990) and also likely plays a major role in annual survival for some species. The main reasons are elevated thermoregulatory costs, longer migration routes to unfamiliar areas, restricted food supply and differential exposure to hunting, competition and predation. Short-term fluctuations in weather also affect duck distribution during winter, since many common duck species show 1) more southerly ring recoveries during colder spells within winters (Ridgill & Fox 1990), 2) more

northern distribution during higher NAO index values (in sea ducks; Zipkin et al. 2010), or 3) a greater tendency to increase migration distances towards the south or southwest during cold weather (in mallard; Sauter et al. 2010).

Beyond short-term responses to adverse weather conditions, long-term geographic shifts in wintering duck population distributions have also been documented. These are likely to be responses to climate change, since wintering duck populations have consistently moved northwards, eastwards or otherwise towards areas that were previously considered too cold for these birds during winter (Švažas et al. 2001, Lehikoinen et al. 2008, 2013, Musil et al. 2011, Ekroos et al. 2012a, Gunnarsson et al. 2012). In some cases the shift in wintering range has been mostly due to a gradual shortening of the migration distances from the breeding grounds (e.g. mallard; Sauter et al. 2010, Gunnarsson et al. 2012). However, some duck populations may end up wintering in areas which they previously avoided, presumably due to past climatic constraints, e.g. various species in southern Sweden (Nilsson 2008) or Steller's eiders *Polysticta* stelleri now wintering in the Russian White Sea (Zydelis et al. 2006, Aarvak et al. 2012). In some cases, such distribution changes have been associated with increased annual survival rates, possibly due to shorter migration journeys and/or because some birds now winter in northern European countries, where hunting pressure may be lower than where they wintered in the past (Gunnarsson et al. 2012).

However, such patterns of changes in distribution have mostly been demonstrated for mallard, which is one of the more widespread duck species. Mallard often exploit man-made habitats, and their populations are reinforced by the release of millions of birds annually in Europe for hunting purposes (e.g. Champagnon et al. 2009). Clearly, additional studies of a wider range of duck species are needed to assess the changes in winter distribution and their possible consequences for duck survival rates. Furthermore, changes in winter distribution may not always have positive consequences like those described above for mallard survival. Major changes in duck wintering ranges may mean that the current network of protected wetlands designed to protect these birds may gradually lose their usefulness, necessitating interactive administrative adjustments to accommodate range-shifting birds as these increasingly rely on formerly unprotected areas.

Climate change may seem like a benign phenomenon that simply causes ducks to slightly adjust their

ranges northwards. However, climate change involves more than just temperature increase. For example, changes in precipitation regimes may cause dramatic changes to wetlands (e.g. through drought) that could profoundly affect duck distribution both in winter (e.g. Doñana marshes; Almaraz et al. 2012) and during the breeding season. For example, North American prairie potholes and parkland wetlands may face both quantitative and qualitative deterioration of habitat owing to more drought years in coming decades (e.g. Larson 1995). This could force some ducks to switch to alternative breeding grounds further north in the boreal forest, which is expected to result in a general decrease in the size of North American duck populations (Sorenson et al. 1998, Forcey et al. 2011, Withey & van Kooten 2011). Furthermore, some duck populations already breed at the northern edge of the continent, in which case future climate change is expected to result in range contractions (e.g. greater scaup Aythya marila in Huntley et al. 2007).

Climate change may also interact with other human-induced environmental changes. For instance, emissions from agriculture have eutrophicated water ecosystems in northern Europe (Ekholm & Mitikka 2006), and nutrient flow from the catchment area will likely increase further, due to predicted rainfall increase, especially during winter time (Meier et al. 2012). Some waterbird species preferring nutrient-rich environments often situated near farmlands are declining in Finland, as compared to colonisers of oligotrophic lakes, which suggests that the former are actually hampered by ongoing hypereutrophication (Pöysä et al. 2013).

To summarise, future climate change is expected to affect the geographic range of ducks, and this will likely be due to more than just a simple latitudinal shift, with probable significant impacts on future population dynamics.

Ducks and climate change: what do we not know?

The section above highlights that existing data are strongly biased towards a relatively limited number of species (much European knowledge actually being based on mallard or common eider studies; *cf.* Ekroos et al. 2012a, Dalby et al. 2013b), while other ducks with a different diet (herbivores) or a smaller body size (hence being more energy-limited) may be affected differently by climate change. The second

main gap in knowledge highlighted by this review is our currently limited ability to relate the short-term effects of climate change (e.g. change in egg-laying date or in winter distribution) to their longer-term impact on duck populations, via changes in individual survival or fecundity.

One key issue to address is the potential generality of changes in duck phenology and distribution over recent decades, and if such changes are likely to continue in the future. The behavioural plasticity of ducks may actually make such assessments difficult (Oja & Pöysä 2007). Based on 31 years of monitoring of autumn migrating waterfowl on the southern coast of Finland, Eurasian wigeon Anas penelope, common teal, tufted duck Aythya fuligula, velvet scoter Melanitta fusca and common goldeneye have delayed their migration, which might have repercussions for adult survival due to varying hunting and predation pressures along the migration routes (Lehikoinen & Jaatinen 2012). In Finland, mallard and common goldeneye have advanced the timing of breeding in early spring, leading to smaller proportions of unfledged birds at the onset of the hunting season and hence possibly lower hunting mortality of young birds and brood-rearing females (Oja & Pöysä 2005). The extent to which modified spring migration phenology or changes in stop-over site preference are occurring, and whether this may actually affect vital rates of populations, remains poorly understood. Useful information on migration and breeding phenology could be gathered fairly easily by monitoring duck numbers and arrival dates at stop-over areas where they do not winter (e.g. garganey Anas querquedula in western Europe), or directly on the breeding grounds in northern Europe that are unsuitable as duck habitats during the non-breeding periods (see e.g. Murphy-Klassen et al. 2005). This may be more challenging for species with a wide geographic range (since the arrival of southerly migrants might be masked by the occurrence of wintering birds), and would thus need regular replicated counts in several countries along wintering and stop-over sites. However, stable isotope analyses (e.g. Hobson 1999, Yerkes et al. 2007) or the analysis of ring-recovery information could be used for this purpose (Guillemain et al. 2006, Calenge et al. 2010). Still, we critically lack knowledge on the long-term consistency of changes in spring phenology and their link with subsequent individual breeding success. This may be especially difficult to determine in birds with such a flexible behaviour as some duck species (see Drever et al. 2012). For example, tufted ducks

arrive relatively early at breeding lakes, but their clutch initiation date is one of the latest among ducks breeding in northern Europe. We do not know how the timing of clutch initiation and breeding success of such species could respond to changes in the timing of spring thaw.

Several studies have documented changes in duck distributions, especially in winter. Many of these are mostly based on increases in numbers in areas where the species were formerly absent or far less abundant (e.g. Nilsson 2005, 2008, Musil et al. 2011, Ekroos et al. 2012a). However, most wintering duck populations in western Europe are increasing (Wetlands International 2006), and changes in numbers at some specific sites may thus not reflect geographic shifts towards a particular area, but instead reflect increasing numbers everywhere (see also Dalby et al. 2013b). Once possible changes in distribution are detected, the consequences of such shifts for demographic parameters will again have to be analysed, as done for mallard by Gunnarsson et al. (2012).

One major weakness in the knowledge highlighted in our study is the lack of general (i.e. multi-specific and geographically broad) research results about the likely consequences of global climate change for demographic parameters in ducks, i.e. that goes beyond the simple effect of annual weather on local vital rates. Such broad-scale knowledge is crucially necessary, as large-scale climate may be associated more closely with animal population dynamics than local weather fluctuations (Hallett et al. 2004). The link between climate change and duck breeding success may also be indirect and hence very difficult to detect. In Arctic ecosystems, the annual breeding success of some ground-nesting birds is thought to be linked to annual lemming cycles (e.g. Lemmus sibirica and Dicrostonyx torquatus), because lemming predators shift to bird eggs and young during poor rodent years (e.g. Bêty et al. 2001). Climate change (especially during the Arctic winter) may alter lemming cycles, hence reducing food availability for their predators in spring and summer (Ims & Fuglei 2005). The shift of these predators to duck eggs and young as alternative prey has, in turn, been hypothesised to result in decreased breeding success of long-tailed duck Clangula hyemalis on the Taimyr Peninsula (Hario et al. 2009b). Furthermore, the amplitude of rodent abundance peaks has also decreased across Europe, and is most likely driven by climate (Cornulier et al. 2013), which could affect breeding duck populations on a larger scale. Nevertheless, it remains unknown if climate change also affects duck

survival in other predator-prey systems across the year cycle. For instance, the annual apparent survival of common eider was not observed to be affected by fluctuations in winter NAO index (Hario et al. 2009a, Ekroos et al. 2012b). Finally, climate change may affect current relationships between ducks and their parasites, but, as in other bird species, it is unknown at present whether such changes will be mostly detrimental (e.g. newly colonising species bringing new parasites) or positive (e.g. changes of the environment altering the parasites' own life conditions; Merino & Møller 2011).

More generally, although body condition of ducks may have improved over time (Anteau & Afton 2004, Guillemain et al. 2010b, Gunnarsson et al. 2011), possibly because climate warming leads to milder conditions especially in winter, no systematic concomitant trend in survival rate has been observed (Gunnarsson et al. (2012) recorded improved survival, while J. Champagnon, O. Devineau, P. Lair, J-D. Lebreton, G. Massez, M. Gauthier-Clerc & M. Guillemain (unpubl. data) did not).

A road map for effective duck monitoring in Europe

The impact of climate change consists of several interacting abiotic factors, which, in turn, are expected to interact with other facets of global change such as deterioration and loss of key habitats (see e.g. Anteau 2012). The consequences of global climate change have likely already affected duck populations, and will continue to do so profoundly in the future. Improved knowledge about changes in duck phenology and distribution throughout the annual cycle, and any associated fitness consequences, are essential if we are to be able to recommend appropriate policy and actions for conservation and other management purposes. This is particularly important for those species that are exploited by hunters. The existing European monitoring schemes already provide useful data, and previous sections of our paper have highlighted some of the important and feasible analyses that should be carried out in the near future. However, some of these monitoring schemes need to be modified, and others should be initiated, in the coming years if we are serious about tackling the possible effects of climate change on duck demography. Because ducks are migratory birds, successful management may critically depend on flyway-scale monitoring efforts (e.g. Elmberg et al. 2006, Ekroos et al. 2012a).

In North America, there is heavy emphasis on the prairie pothole region when it comes to management

of duck populations in relation to climate change because this is one of the major duck production areas of the continent (see e.g. Bethke & Nudds 1995, Withey & van Kooten 2011, Anteau 2012, Loesch et al. 2012). The prairie pothole region is, however, a system quite different from the main breeding areas of European ducks, which more generally nest in the boreal biome, and thus American management actions may not always be directly transferable to European duck populations. Furthermore, this literature review shows that climate change likely not only affects duck population dynamics during the breeding season, but may also affect the distribution of these birds in their moulting, staging and wintering areas. We hence propose a range of initiatives that should be promoted throughout the various parts of the annual cycle, and eventually suggest how the results of these could be integrated, by modelling, to predict the likely consequences of climate change for duck population dynamics at the flyway scale.

Expand duck counts over space and time, and distinguish counted birds by sex and age classes

Most duck management in Europe is currently based on censuses carried out in mid-January (Elmberg et al. 2006). Where standardised and consistent counts are carried out, they contribute to monitoring changes in overall duck numbers and possible changes in winter distribution. It is, therefore, essential that these bird counts continue. However, it is also necessary to develop such counts in areas/ countries where ducks are not currently numerous or present, but where climate change is likely to increase duck numbers in the future. Changes in winter distribution may otherwise fail to be monitored and the detection of trends in the overall size of wintering duck populations would be incomplete (see e.g. common eider in Ekroos et al. 2012a and mallard in Dalby et al. 2013b). Regular counts at other times of the non-breeding cycle should also be implemented to track changes in phenology and identify potential key areas for protection. Simple duck counts fail to provide direct information on the distribution and abundance of age and sex classes, which could provide substantial insight into population dynamics, including biassed sex ratios in time and space, and variation in annual breeding success (Lehikoinen et al. 2008, Mitchell et al. 2008, Ekroos et al. 2012a). Since it is only mature females that produce eggs, there is a considerable need to establish sampling protocols to track female survival and age ratios over time. Most duck species are highly sexually dimorphic, and organising bird counts that separate sexes is realistic. This would provide valuable insights into the population structure of ducks. Furthermore, because we currently have few methods for assessing annual reproductive success in these populations, and its variation in time and space, we suggest that the distribution of individuals across age classes should be determined, as the proportion of young individuals in the population can be used as a proxy for annual breeding success (e.g. Ebbinge & Spaans 1995). Age determination in the field is indeed possible from a distance in some cases (e.g. male Eurasian wigeon; Campredon 1983). For the other species, alternative methods based on ringed and/or hunted birds should be considered and are listed below.

Promote the monitoring of annual breeding numbers and reproductive success

In order to understand mechanisms underlying climate change effects on duck populations, we need more information on possible effects on critical demographic components. In particular, we need information on how dates of clutch initiation vary with the timing of spring thaw for different species, but also how laying date translates into recruitment. Accurate data on these aspects could be derived from studies focussing on the breeding biology of ducks. Information on the timing of breeding can also be derived from brood surveys, as demonstrated by the waterfowl monitoring programme in Finland (Pöysä et al. 1993, Oja & Pöysä 2007; see also Rönkä et al. 2011). Data mining to combine the results of this long-term programme with existing ice-thaw date records is necessary to assess the possible role of spring conditions on timing of breeding and, ultimately, breeding success. The latter information could be obtained by combining the results from pair counts (i.e. breeding numbers) and brood counts done in the same areas (e.g. Elmberg et al. 2003). Furthermore, a standardised and regionally representative monitoring scheme would enable identification of regional differences in climate change impacts on critical demographic components. Therefore, even though monitoring of breeding numbers and production is labourious and time consuming, due to low breeding densities of most boreal ducks, we recommend that such monitoring schemes should be established at selected sampling sites in all European countries holding notable breeding populations of ducks.

Collect more hunting bag data

Millions of ducks are shot annually by hunters in Europe (Mooij 2005), which could provide an invaluable source of demographic information. First, assessing the annual bag per species over their respective flyways would be a major step forward in understanding the dynamics of such exploited populations (cf. Pöysä et al. 2013). National hunting bag collection schemes exist in a few countries (notably Nordic countries such as Denmark, Finland and Iceland; see Dalby et al. 2013b), but are completely lacking in most countries of the same flyways, which means that the number of harvested ducks per population and year remains unknown. In addition to collecting global hunting bag data, setting up a wing and tail feather collection scheme at the European scale is necessary for providing information on the age and sex ratios of individuals shot throughout the season (using reference manuals such as Boyd et al. 1975 or Rousselot & Trolliet 1991). It is probable that the birds shot by hunters will be a biased sample of the population (e.g. Heitmeyer et al. 1993, Guillemain et al. 2007). They would, however, still provide a reliable index of annual breeding success and sex ratios if collected with a standardised protocol over years (Mitchell et al. 2008). Such information has already allowed estimation of juvenile common teal and Eurasian wigeon survival rates in autumn (Guillemain et al. 2010a, 2013), and would help tackling the demographic consequences of climate change.

Catch, ring, mark and tag ducks

Promoting duck ringing throughout Europe is necessary to better understand shifts in duck phenology and geographic distribution induced by climate change, as well as stop-over duration at both migration staging sites and winter quarters (e.g. Choquet et al. 2013). Capture-Mark-Recapture analyses are crucially needed to clear the highlighted gap between short-term effects of climate change on duck phenology and distribution, and the longer-term impact of such changes on duck demographic rates

Simple recoveries of ringed birds provide information on geographic ranges and individual movements between sites during a given period of time (e.g. Guillemain et al. 2005 for common teal). However, such studies require huge numbers of ringed birds to accumulate enough recoveries, and the ring reporting rate is furthermore known to be declining over time (Guillemain et al. 2011). Beyond

simple metal ringing, we suggest that duck marking schemes at large scales should be encouraged, e.g. using nasal saddles that can be read from a distance (Rodrigues et al. 2001). Such markings relieve the need to recapture or recover ringed birds, which is notably more difficult than observing saddled birds from a distance. Obviously, compared to recoveries of dead birds, individual marking also allows for multiple observations of the same individual, which has proven to be useful in determining individual turnover rates at migration sites (e.g. Caizergues et al. 2011, Gourlay-Larour et al. 2013). Developing a network of capture and marking sites is therefore a promising method for monitoring possible changes in duck demographic parameters over time, in response to climate change. In addition to visual marks, data loggers are now available and have been used successfully with ducks (e.g. Miller et al. 2005, Gaidet et al. 2010). Satellite telemetry is clearly a promising approach for the coming years to better understand individual movement patterns.

Lastly, existing duck capture operations are mostly opportunistic, i.e. the main ringing sites have been set up where ducks were most abundant, primarily during the autumn and winter. Such catching operations are sometimes extremely successful (e.g. Devineau et al. 2010). However, catching ducks in autumn/winter is usually very time consuming, and not always successful due to various factors, e.g. adverse weather. Furthermore, winter ringing does not provide any direct information about the geographic origin of the captured birds, although that could be obtained using stable isotope techniques on feathers grown at the breeding grounds and collected at ringing (e.g. Fox et al. 2007). As well as developing marking in addition to ringing, we hence suggest to adopt a strategic approach in the future, whereby coordinated operations are set up to mark large numbers of ducks where they are most easily caught, such as at postbreeding moulting sites (e.g. Viksne et al. 2010).

Modelling duck population changes

Modelling may reveal the responses of duck populations to environmental changes (including those of climate change) and underline the most influential demographic and life history variables. A step towards demographic modelling could be applying long-term duck monitoring estimates in state-space modelling of population and observation processes in parallel, thus trying to quantify observation errors and actual population regulating parameters (Den-

nis et al. 2006). Recently, multivariate state-space modelling has been applied to quantify the impacts of climate variability during breeding, moulting, migration and wintering on winter population sizes in duck communities. For example, Almaraz et al. (2012) showed, using this approach, that life history characteristics and migrating behaviour of waterfowl are affected by climate variability. Collecting demographic time-series data and integrating such information with population size and environmental data into multivariate state-space models will constitute a unified approach, combining the outputs of the three main methodological developments proposed above (see Schaub & Abadi (2011) for a review of integrated population models and their application in avian studies). Other modelling approaches should also be considered, such as e.g. maximum entropy algorithm modelling (Fuller et al. 2008) or behaviour-based models (e.g. Pettifor et al. 2000). Whatever the modelling approach selected, the main idea would be to combine the data, obtained in the field from the monitoring schemes proposed above, into a predictive model that will help anticipate the consequences of future climate change. As such, this constitutes a major challenge for the research field of duck demography for the coming years.

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