

Habitat management favouring hunted waterbird species prevents distribution changes in response to climate warming

Elie Gaget, T. Galewski, J E Brommer, I. Le Viol, F. Jiguet, N. Baccetti, T. Langendoen, B. Molina, F. Moniz, C. Moussy, et al.

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- 1 Habitat management favouring hunted waterbird species prevents distribution
- 2 changes in response to climate warming
- 3 Elie Gaget¹, Thomas Galewski², Jon. E. Brommer¹, Isabelle Le Viol³, Frederic Jiguet⁴, Nicola Baccetti⁵,
- 4 Tom Langendoen⁶, Blas Molina⁷, Filipe Moniz⁸, Caroline Moussy⁹, Marco Zenatello⁵ & Matthieu
- 5 Guillemain¹⁰
- 6 1 Department of Biology, University of Turku, Turku, Finland
- 7 2 Institut de recherche pour la conservation des zones humides méditerranéennes, Tour du Valat, le
- 8 Sambuc, Arles, 13200 France
- 9 3 Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire
- 10 naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France. Station
- de Biologie Marine, 29900, Concarneau, France
- 12 4 Centre d'Écologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire
- 13 naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP 135, 57 Rue Cuvier,
- 14 75005, Paris, France
- 15 5 Institute Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Ozzano dell'Emilia, Italy
- 16 6 Wetlands International, Ede, The Netherlands
- 17 7 Sociedad Española de Ornitología (SEO/BirdLife), Madrid, Spain
- 18 8 Instituto da Conservação da Natureza e das Florestas, Centro de Estudos de Migrações e Proteção
- 19 de Aves, Av. Combatentes da Grande Guerra, 2890-015 Alcochete, Portugal
- 20 9 LPO-BirdLife France, Fonderies Royales, Rochefort Cedex, France
- 21 10 Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées,
- 22 La Tour du Valat, Le Sambuc, France
- 24 Corresponding author: elie.gaget@gmail.com, Department of Biology, University of Turku, Turku,
- 25 Finland

- 26 ORCID:
- 27 Isabelle Le Viol 0000-0003-3475-5615
- 28 Matthieu Guillemain 0000-0002-0354-771X
- 29 Marco Zenatello 0000-0002-9225-6737
- 30 Elie Gaget 0000-0003-3462-9686

Abstract

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Climate warming is driving species to shift their geographic distribution poleward to track suitable climatic conditions. Two strategies have been suggested to help species respond to climate warming: facilitating distribution change or improving persistence. We questioned whether habitat management in favour of duck hunting activities interacted with duck responses to climate warming. We studied non-breeding waterbird community changes (110 species) over 28 years at 851 sites in South-West Europe, where habitat management is a common practice to attract and hunt ducks. We hypothesized that duck species targeted by habitat management do not need to track temperature changes as much as non-hunted species, because of the availability of suitable habitats provided by hunting land managers. We used the Community Temperature Index (CTI) to assess the temporal responses of communities and species to climate warming. We compared the effect of hunting status to other functional traits on species responses, controlling for phylogenetic relatedness. The CTI trend has increased over the study period, indicating a community adjustment to climate warming. However, hunted ducks contributed to almost 40% of the negative contributions to this community adjustment, suggesting that hunted ducks do not shift their distribution as much as the other waterbirds do. Winter fidelity associated with the provision of attractive feeding grounds might explain why ducks did not seem to shift their distribution in response to climate warming. This study suggests the broad impact of human activities on wildlife, including on large-scale distribution processes, and questions the longterm consequences on duck populations.

Keywords: climate change, duck, Community Temperature Index, Mediterranean, persistence, wintering

54 Introduction

- Global warming is a major threat to biodiversity, leading to massive species distribution changes (Parmesan & Yohe 2003). Global temperatures have increased by 1.1°C since the pre-industrial period (IPCC 2021), and are expected to reach +2°C to +5°C by 2100 (Raftery et al. 2017). A possible step backwards to pre-industrial temperatures in the next centuries is uncertain (IPCC 2021). Therefore, temperature changes are not only rapid, but also likely to last over time.
 - Species responses to climate warming are diverse but their intensity is largely insufficient (Radchuk et al. 2019, Lenoir et al. 2020). Species may respond to climate warming through changes in migration distance, geographic shift, phenology, plasticity, or microevolution (Jiguet et al. 2007, Moller et al. 2010, Dawson et al. 2011, Elmberg et al. 2014). The most commonly observed and documented response is geographical distribution change, leading to changes in community composition in response to temperature changes at the local scale (Devictor et al. 2012). For instance, temperature increases might cause local population increases at the cold edge of species distributions, and decreases in population sizes at the warm distribution edge (Parmesan & Yohe 2003, Thomas et al. 2006, Pavón-Jordan et al. 2015). Species can also persist locally, either by finding micro-refuges (e.g. at higher altitude, Massimino et al. 2020) or by tolerating changes through phenotypic or genetic adaptation (plasticity, micro-evolution) (Charmantier et al. 2008, Karell et al. 2011). Functional traits play an important role to shape species responses to climate warming (Brommer 2008). Species sharing the same characteristics, like climatic niche, body mass, migration strategies, might be more likely to respond in a similar way (Jiguet et al. 2007) while facing the same vulnerabilities to temperature increase (Aubin et al. 2016). Species responses to climate warming may also be modulated by local environmental factors, like habitat quality (Dawson et al. 2011, Lenoir et al. 2020) and conservation efforts (Gaget et al. 2022).
 - Helping species respond to climate warming is mainly considered under two complementary climate adaptation strategies: facilitation and persistence (Bonebrake et al. 2018, Prober et al. 2019, Pearce-Higgins et al. 2022). Facilitation focuses on helping species shifting their geographical distribution and settle in new areas in response to global warming (e.g. Maclean & Rehfisch 2008, Guillemain & Hearn 2017). It aims at adjusting the rate of species distribution change to the thermal isocline shift. For example, increasing connectivity between protected habitats facilitates colonization processes in response to climate warming (McGuire et al. 2016). Conversely, persistence aims at maintaining species in an environment despite temperature changes. It may indirectly be based on the intrinsic abilities of species to tolerate the changes (e.g. plasticity) or involve management measures to provide additional resources or create microrefugia benefiting a targeted species. For example, food supply may decrease the local extinction risk of species vulnerable to climate warming (Correira et al. 2015). Both facilitation and persistence strategies are likely to influence the response of species to climate warming (Bonebrake et al. 2018, Prober et al. 2019).
 - Empirical evidence of long-term species response to climate change has rarely been demonstrated under the persistence strategy (Correira et al. 2015, Pearce-Higgins et al. 2019). Indeed, as anthropogenic climate change is a relatively recent biodiversity pressure, conservation measures have not primarily aimed at improving long-term species persistence in response to temperature increase specifically. In contrast, efforts have historically aimed at improving species conservation, with consequences on their distribution regarding temperature change. For example, the creation of

protected areas to preserve migratory waterbirds during cold spells in Western Europe (Ogilvie 1983, Guillemain et al. 2002) are also buffering the negative impact of temperature increase on some cold-dwelling waterbirds (Gaget et al. 2021). Similarly, the provision of supplementary foods in British gardens changed the migration behaviour of the Eurasian blackcap (*Sylvia atricapilla*), of which many individuals are no longer migrating South (Plummer et al. 2015). Such anthropogenic influences can be examined a posteriori in the light of climate warming (Pearce-Higgins et al. 2022).

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Here, we question the effect of habitat management for hunting purposes on waterfowl responses to climate warming at international scale in South-West Europe. Duck hunting is a popular practice in this region yielding 2.4 million harvested ducks annually (EEA 2020). Indeed, habitat management for hunting purposes is a local, but widespread practice (FACE 2019), aiming at attracting targeted waterfowl species to hunting grounds during the non-breeding period. Pro-active habitat management actions for hunting purposes include the creation of man-made ponds, spreading of seeds as bait, artificial flooding, vegetation clearing including the creation of openings in reedbeds, and other actions (e.g. Mathevet & Guillemain 2016, Vallecillo et al. 2019). Economic incentive for such intensive management actions is that sites with high abundance of ducks can yield high income by renting out hunting rights (e.g. Niang et al. 2016). Specific habitat management targeted to boost abundance of hunted species is often carried out in large private properties, e.g. in the Camargue, Southern France (Tamisier & Grillas 1994) and provide prestigious social status and reputation of the land-owner, e.g. in Italy. However, if such management measures attract hunted duck species in large numbers, they may not be so attractive to other waterbird species, unless for species sharing common habitat or diet characteristics with hunted ducks, such as granivorous and herbivorous species (Tamisier and Dehorter 1999, Mouronval et al. 2014). In particular, such habitat management are not expected to provide benefits to invertebrate or fish eating species (e.g. shorebirds, herons) (Toureng et al. 2000). Gaget et al. (2018) showed that in the south-western European Union Member States, waterbird responses to climate warming were correlated with their protection status. Hunted species had a lower response to climate warming through distribution change than the other species. Here, we further explore the reason for this interaction between hunting status and climate warming, by investigating the possible role of habitat management practices on hunted ducks.

We studied community reshufflings from 110 non-breeding waterbird species in south-western Europe over 28 years on 851 sites. Many of these waterbirds breed at northern latitudes and overwinter in wetlands in this region. Our main interest was to explore whether the distributional changes of duck species, which are actively targeted by hunting in this region, differ from those of other hunted and non-hunted waterbird species, while controlling for functional traits that differ between these species. To infer distribution changes we used the Community Temperature Index (CTI) framework, a community weighted mean index used to measure the average temperature affinity of all the species of a community, based on individual species temperature index (STI) (Devictor et al. 2012). We assessed temporal changes of CTI over years for the non-breeding waterbird community using abundance time series collected at site level through the International Waterbird Census (Delany 2010) and STI calculated as the mean winter temperature values across the non-breeding distribution of the species (Gaget et al. 2021). Under a climate warming scenario, we expected the avian community at a given site to change over time towards species with a higher thermal affinity. Thus, the CTI was expected to increase over time. Such community reshuffling has already been documented for nonbreeding waterbirds in the western Palearctic (Gaget et al. 2021) and in numerous other studies (Devictor et al. 2012, Auffret and Thomas 2019, Fourcade et al. 2019). We then assessed the species' contributions to this temporal increase in CTI. Our main interest was whether this contribution depends on the species' hunting status (hunted ducks, other hunted species and non-hunted species), while accounting for functional traits (species thermal affinity, body mass, generation length, diet and migration strategy) and phylogeny (Jiguet et al. 2007, Brommer 2008) to control for potential confounding effects. Because of the intensive management practices in the study region (Tamisier & Grillas 1994, Pernollet et al. 2015a, Zenatello et al. 2021), we expected that hunted ducks would be slower to adjust their distribution to climate warming compared to non-hunted waterbirds, because management of hunting areas may provoke a greater site fidelity. We thus expected that hunting status shapes a species' response to climate warming.

Methods

We studied non-breeding waterbird abundance time series collected from 1993 to 2020 at 851 sites in Portugal, Spain, France and Italy. The data were collected for the International Waterbird Census coordinated by Wetlands International (Delany 2010), resulting in one survey per year performed by skilled ornithologists in mid-January on hundreds of wetlands. We filtered the original dataset (n = 3,288 sites) to ensure the quality of the data. To do so, we restricted the list of waterbird species to the list of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (www.unepaewa.org), we removed count events with less than two species to allow estimation of species contributions to CTI trend (see below) and we removed species with less than 100 individuals observed among all sites included in the study. Because of the particular focus on ducks, we removed sites without any hunted duck observation. We retained sites with at least five surveys and one survey per decade (1990s, 2000s and 2010s), resulting in a subset of 851 sites with 20.5±6.2 surveys on average (±SD) (see map Appendix 1). Considering taxonomic changes that occurred during the study period, Larus michahellis, L. cachinnans and L. argentatus were lumped into one 'species' L. michahellis. This lumping has a negligible impact on most of the study area where L. michahellis is largely dominant over the two other species, with the exception of the French Atlantic coast. The dataset used for the analyses resulted in 17,462 surveys of 851 sites over 28 years, with a cumulative record of 119 million birds from 110 species (Appendix 2).

We considered three hunting status categories between species: eleven duck species mainly targeted by habitat management, 25 other hunted waterbirds and 75 non-hunted species (Appendix 2). Hunted ducks are Northern Pintail (*Anas acuta*), Common Teal (*A. crecca*), Mallard (*A. platyrhynchos*), Eurasian Wigeon (*Mareca penelope*), Gadwall (*M. strepera*), Northern Shoveler (*Spatula clypeata*), Garganey (*S. querquedula*), Common Pochard (*Aythya ferina*), Tufted Duck (*A. fuligula*), Greater Scaup (*A. marila*) and Red-crested Pochard (*Netta rufina*). These species are all listed in Annex II of the Birds Directive, meaning that they can be hunted according to the regulation of the European Union or Member States (Red-crested Pochard is hunted in France and Spain only, and Greater Scaup is hunted in France only). The other hunted species are listed in Annex II of the Birds Directive and hunted at least in one Member State of the study area, and include species such as Greylag Goose (*Anser anser*), Coot (*Fulica atra*), Lapwing (*Vanellus vanellus*) and Eurasian Curlew (*Numenius arquata*). The non-hunted species are not listed in Annex II, or listed in Annex II but not hunted in the study area, including species such as Mute Swan (*Cygnus olor*), Ferruginous Duck (*Aythya nyroca*), Grey Heron (*Ardea cinerea*), Eurasian Spoonbill

(Platalea leucorodia), Little Grebe (Tachybaptus ruficollis), Great Cormorant (Phalacrocorax carbo) and
Mediterranean Gull (Larus melanocephalus).

We document species functional traits and phylogenetic proximities to control for potential confounding effects (Appendix 2). Functional traits were species thermal affinity, body mass, generation length, diet and migration strategy. These functional traits are expected to influence bird response to climate warming (Jiguet et al. 2007, Brommer 2008). Species thermal affinity was defined as the Species Temperature Index (STI), calculated as the average temperature in January (1950-2000, www.worldclim.org, spatial resolution of 0.25°) on the non-breeding species distribution (BirdLife International & HBW 2018) from Gaget et al. (2018). Body mass (continuous, log transformation) and diet (Plant, Omnivore, Invertebrate, Vertebrate) were extracted from Wilman et al. (2014) (where omnivore corresponds to a combination of less than 50% of all other categories), generation length (continuous) from IUCN (2021) and migration strategy (resident, short, long) from Storchová et al. (2018). Migration strategies were represented in similar proportions between hunting status categories, with most of hunted ducks being short to long-distance migrants (Storchová et al. 2018; Appendix 2). To control for species phylogeny, we used phylogeny trees from BirdTree (https://birdtree.org).

We used temperature anomalies to assess changes in winter temperatures on the survey sites over the study period. We collected average monthly temperatures gridded at 0.5° resolution, from the Climatic Research Unit v4.05 (Harris et al. 2020). Winter temperatures anomalies were computed each winter at site level as the average of the mean monthly temperatures for the 3-month period of November, December and January, i.e. the duration expected to impact waterbird distribution at winter time (Gaget et al. 2020), minus the average monthly temperatures from November to January for the 1993-2020 period.

Statistical analyses

- To assess and explain patterns of species responses to climate warming, we first calculated the longterm trend of CTI over years, then we assessed species contribution to the CTI trend, and finally we investigated the effect of hunting status and functional traits on species contribution, taking species phylogeny into account.
- The CTI is a community weighted mean index used to measure the average temperature affinity of all the species included in the community based on individual STI (Devictor et al. 2012). The CTI is the average STI weighted by the log_e(abundance + 1) of the species observed during a survey (Gaget et al. 2018). We calculated one CTI value per count event, based on all the species observed at this time among the 110 waterbird species included in the study. Over time, a CTI can increase in response to climate warming by a relative increase of species with high STI, or a relative decrease of species with low STI.
- We assessed CTI temporal trends with a linear mixed effect model (LMM) with the CTI as the response variable and year as a fixed effect. Sites, nested in countries, were used as a random effect to account for heterogeneity among sites and national monitoring schemes (Gaget et al. 2018). Spatial autocorrelation was taken into account with an exponential structure on the geographic coordinates

(Gaget et al. 2018). We used the same model with temperature anomalies as response variable, to assess temporal changes in temperature anomalies. To visualize inter-annual changes in CTI and temperature anomalies, we also used the same models but with year as a categorical variable.

To assess the contribution of each species to CTI trends, we ran a jackknife analysis by removing each species in turn from the CTI before running LMMs on partial CTIs. Hence, species contribution to the CTI temporal trends was assessed as the difference between the original temporal trend (all species included) and the temporal trend of the model based on the partial CTI (all but one species). Species contributions were then reported as a percentage of influence, positive or negative, on the CTI trends (Gaget et al. 2018). Note that species contributions are relative values, comparing species to the whole community. A negative contribution to a positive CTI trend means that a species is contributing relatively less than the other species to the community adjustment to climate warming.

Finally, we used phylogenetic generalized least squares (PGLS) models to assess differences between species contribution to CTI changes. We compared species contributions between hunting statuses and functional traits (species thermal affinity, body mass, generation length, diet and migration strategy), considering species phylogeny. We used a forward model selection approach to select the most parsimonious model with predictors explaining the most species contributions, i.e. selecting models with the lowest AIC among a delta AIC <2 (Burnham and Anderson 2002). Phylogeny is a potential factor structuring adaptive bird response to climate change (Hällfors et al. 2020). Hunted ducks are from the same Anatidae family and often share the same genus. Their intrinsic sensitivity to climate warming and adaptive capacities are likely closer among each other than with species from other taxonomic clades. Consequently, contrasting species groups exposes the analytical framework to a potential confounding effect. To avoid this bias, we accounted for phylogenetic relatedness by adding the phylogeny tree as a Brownian correlation structure in the models. In addition, we assessed the multicollinearity between functional traits with the Variance Inflation Factor (VIF).

- We performed two sensitivity analyses (Appendix 3) to ensure that the results were independent of 1) the site protection status, because protected areas can also interact with wintering waterbird responses to climate warming (Gaget et al. 2021), and of 2) the number of surveys per site, by selecting only sites with more than 25 surveys over the 28 years period.
- Statistical analyses were performed in R 4.1.2 (R Development Core Team 2021). LMM and PGLS were run with package 'nlme' (Pinheiro et al. 2017), Nagelkerke pseudo R-squared were assessed with package 'rcompanion' (Mangiafico 2016) and VIF with package 'performance' (Lüdecke et al. 2019).

Results

- The Community Temperature Index (CTI) showed a very clear linear increase over years (β = 0.045 ± 0.001 SE, p < 0.001), indicating that the avian community was, on average, changing according to species thermal affinity (Fig. 1). Winter temperatures increased by 0.6°C on average over the study period on the studied sites (β = 0.023 ± 0.001 SE, p < 0.001).
- However, not all species contributed equally to this change in CTI. Species diet and hunting status were the main factors explaining species contribution ($\beta_{Plant} = -2.61 \pm 1.19 \ (\pm SE) \ [-4.74;-0.48] \ (95\%CI)$, $\beta_{Invertebrate} = -0.15 \pm 1.19 \ [-0.39;0.09]$, $\beta_{Vertebrate} = -1.27 \pm 1.20 \ [-1.45;-1.09]$, $\beta_{Omnivore} = 1.06 \pm 1.19$

[0.86;1.26]; $\beta_{\text{Hunted ducks}} = -3.62 \pm 1.24$ [-5.09;-2.15], $\beta_{\text{Other hunted}} = 0.57 \pm 1.19$ [-2.20;1.57], $\beta_{\text{Non-hunted}} = 0.82 \pm 1.19$ [0.15;0.89]), whereas other predictors had little effect (Table 1, Appendix 4). Multicollinearity between species diet and hunting status was low (VIF = 1.05). Most of the variance explained by the model was related to species diet (82%), with plant eating species contributing predominantly negatively to the CTI change (Fig. 2). Indeed, 83% of the plant-eating species had negative contributions, compared to 48%, 44% and 64% for species eating invertebrates, vertebrates and being omnivores, respectively (omnivores potentially comprising some plant-eating diet). Hunting status also strongly affected species contributions to CTI change (Table 1, Fig. 2). Most (73%) of hunted duck species contributions were negative (summing to -39.8%). Only Mallard, Greater Scaup and Garganey, among 11 hunted duck species, made positive contributions to CTI change (summing to +15.5%), although the Mallard accounted for almost all positive contribution (+14.9%; Fig. 2). Among the other hunted and non-hunted species, 63% and 52% of the species contributed negatively, respectively.

The sensitivity analyses conducted 1) without sites included inside protected areas and 2) only on site with more than 25 surveys, returned fairly similar results, indicating the importance of the species hunting status to explain species contributions to CTI change (Appendix 3).



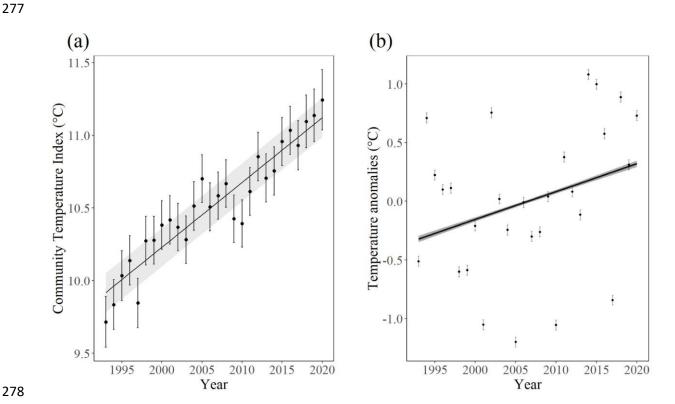


Figure 1: Temporal trends of (a) Community Temperature Index (CTI) ±95% CI and (b) temperature anomalies ±95% CI. Note that although temperature and CTI share the same unit, the scales are not proportional, i.e. a temperature increase of +1°C does not lead to the same CTI increase (Gaget et al. 2021).

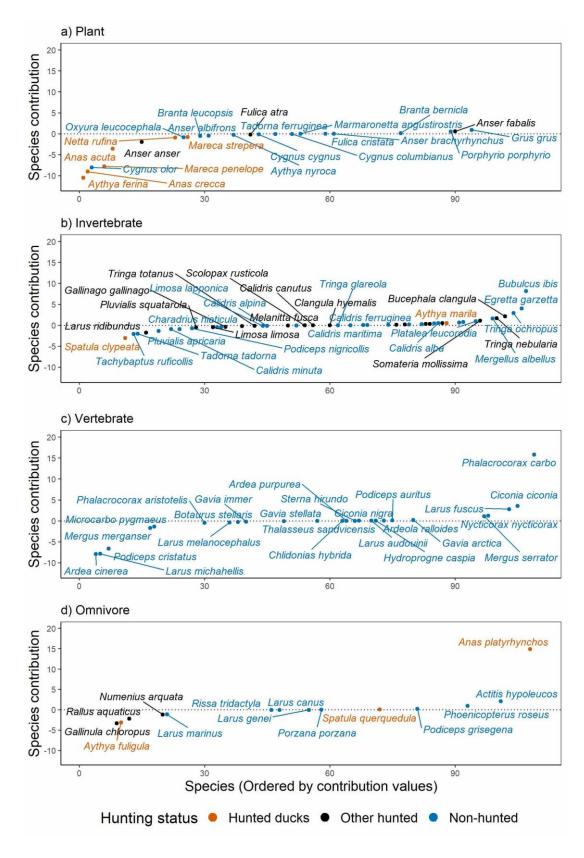


Table 1: Selection of the best models based on AIC and parsimony (Delta AIC <2 and lowest DF), identifying predictors the most related to species contributions. The F-value corresponds to the sum of the effects and DF is degrees of freedom. The best model to explain species contribution considers both species hunting status and diet (in bold). Models are fitted with phylogenetic generalized least squares (PGLS). Diet, hunting status and migration are factors and STI (Species Temperature Index), body mass and generation length are quantitative variables (See Appendix 4 for full model selection).

Formula	AIC	Delta AIC	Pseudo R-square	F-value	DF
Diet + Hunting status	697.2	1.4	0.058	2.329	6
Hunting status + Diet + Generation length	695.8	0.0	0.097	6.835	7
Hunting status + Diet + Body mass	696.3	0.5	0.077	4.410	7
Hunting status + Diet + Migration	696.5	0.7	0.060	2.410	8

Discussion

Over the study period (1993-2020), the observed CTI increase demonstrates that non-breeding waterbird communities have changed, with warm-dwelling species becoming relatively more abundant than cold-dwelling species in the region. This community change was expected because of the temperature increase in the study area, suggesting that non-breeding waterbird communities are reshuffling in response to climate warming. This finding is fully consistent with other studies on non-breeding waterbirds (Godet et al. 2011, Pavón-Jordán et al. 2017, Gaget et al. 2018, Gaget et al. 2021), breeding birds (Devictor et al. 2012) and other taxa (Devictor et al. 2012, Auffret and Thomas 2019, Fourcade et al. 2019) in Europe. This reshuffling is a long-term process caused by species distribution changes in response to climate warming, with warm-dwelling species colonizing new sites at the leading distribution edge and cold-dwelling getting extirpated at the trailing distribution edge (Thomas et al. 2006, Gaget et al. 2021).

While the community on average has responded to climate change, individual species responses varied. Some species distribution strongly tracked climate warming, and such species had, in the CTI framework used in this study, positive contributions to the CTI trend. Examples include Common Sandpiper (*Actitis hypoleucos*), Goldeneye (*Bucephala clangula*) and White stork (*Ciconia ciconia*). However, other species barely adjusted their distribution to climate warming and these species had negative contributions to the CTI trend. We here showed that most ducks targeted by habitat management for hunting purposes (except Mallard, and to a lesser extent Garganey and Greater Scaup) had negative contributions to the CTI trend. This finding therefore suggested that habitat management may influence species response to climate warming. We believe there are two non-mutually exclusive explanations for this finding.

Firstly, managing sites to benefit hunted species may have lowered the propensity of these species to adjust their distribution to climate warming. Indeed, intensification of habitat management for hunting purposes has been suggested as one of the reasons for contemporary changes in duck diet, body condition and migration phenology (Mathevet & Tamisier 2002; Guillemain et al. 2015). Various habitat management actions are commonly used to attract wintering ducks (e.g. Mathevet & Guillemain 2016, Vallecillo et al. 2019). One potentially important management action is food supplementation, where seeds (wheat, corn or rice) are provided as bait, a common practice in South-West European countries (Brochet et al. 2012). For example, such bait may account for half of the Teal food intake in some areas (Legagneux 2007), and feeding activity for this duck species has shifted these past decades from natural habitats to artificially managed freshwater marshes (Brochet et al. 2012). Over the same period, Teal body mass has increased by more than 10% at their major Camargue wintering site in southern France (Guillemain et al. 2010), and arrival date at this wintering ground has advanced (Guillemain et al. 2015). Intensive water level management is another management practice likely influencing duck distribution change or local persistence in response to climate warning. Wetlands are flooded in summer, including temporary ponds that otherwise would be dry. The aim of this summer flooding is to maximize plant biomass growth in these ponds to coincide with the arrival of ducks from their breeding grounds in autumn (Tamisier & Grillas 1994, Davis et al. 2014). Supplementation of freshwater in brackish habitats (e.g., coastal lagoons), aims also to increase habitat diversity hence attracting freshwater duck species. All such management actions improve habitat quality and attractiveness to ducks, resulting in large alterations of duck distribution in the last decades, which now concentrate in areas of intensive habitat management for hunting purposes (Zenatello et al. 2014, 2021). Habitat management for hunting purposes may hence have counterbalanced the effect of climate warming and "retain" hunting ducks to these wintering grounds, which they would otherwise abandon for more northern areas.

Secondly, hunted ducks may have been slower to adjust their distribution to climate change because agricultural practices were particularly beneficial for these species. In particular, rice fields are flooded and used as foraging grounds by ducks during the non-breeding season, with ducks feeding on non-harvested rice and weed seeds (Pernollet et al. 2015a). Other waterbird species use rice fields for feeding to a lesser extent, except for species than can specialize on rice, such as the Greater Flamingo (*Phoenicopterus roseus*) during the seeding period in spring (Pernollet et al. 2015a). In Portugal, Spain, France and Italy, some wetlands hosting a large number of ducks are close to large rice producing areas, e.g. Ebro delta, Albufera, Camargue, Pavia. In such regions, the number of wintering ducks was positively related to the area of flooded harvested ricefields (Pernollet et al. 2015b). Furthermore, rice farming practices and management of sites to promote hunting are not mutually exclusive, since harvested ricefields can also be flooded for hunting purposes (Niang et al. 2016, Pernollet 2016). Indeed, in addition to agronomic benefits, this practice provides suitable wintering grounds for ducks and may therefore promote site fidelity.

Despite these explanations, our current analysis cannot definitely infer the reasons for the slower distribution adjustment of hunted ducks to climate warming compared to other waterbirds. In particular, we conducted a comparison between species and not between sites. To establish that hunting-oriented site management promotes persistence of hunted ducks, site-level information on management practices and intensity in South-West Europe is needed. Spatialized data on habitat management for hunting purposes are currently lacking at regional or national scale. Importantly, ducks are often mobile over large areas within their winter range (Caizergues et al. 2011, Gourlay-

Larour et al. 2012) and may hence be affected by large scale management driven by regional factors in addition to site-specific management, such as land-use policy or socio-cultural practices. The fact that ducks commute daily between a day-roost (generally protected sites where they can rest and where they are surveyed) and surrounding nocturnal feeding areas (functional units *sensu* Tamisier & Tamisier 1981) further inflates uncertainty in how these species are affected by habitat management in a given area (Vallecillo 2021). An experimental design contrasting the effect of site management on duck carrying capacity would be challenging because of the mismatch between diurnal bird monitoring and nocturnal feeding behaviour (Brochet et al. 2009).

Responses to climate warming differ between species for many reasons, including, among others, species movement ability or adaptive capacities, (Dawson et al. 2011). Our best model only explained 5.8% of the differences between species contributions, suggesting that an important part of the variation was not captured by the tested functional traits. This might have been expected because waterbirds share more ecological characteristics than we could get by analyzing a more phylogenetically diverse bird community (e.g. Jiguet et al. 2007, Brommer 2008). Consequently, accurate traits might be neglected, e.g. at population-level across species flyways, but needed to reflect local adaptations to environmental parameters, including climate warming (DeMarche et al. 2019).

Waterbird diet was an important predictor of species contribution to CTI trend, but other functional traits were not. Plant eating species mainly contributed negatively to the community changes. One likely reason might be that species sharing similar feeding ecology to hunted ducks, mostly plant eaters, were also affected by habitat management, like coots and swans (Brochet et al. 2009). Thus, habitat management for hunting purposes may also benefit plant eaters in general, to some extent. Generation length actually explained a fair amount of variation, but was not selected according to parsimony. It may therefore be an additional factor explaining why some species have a delayed distribution change (Maclean et al. 2008). Indeed, juvenile settlement can influence over-winter location when mature, meaning that long-lived species might need more time to shift their distribution than short-lived species (Godet et al. 2011).

Mallards did not follow the same pattern as the other hunted ducks. We found that their distribution was tracking climate warming. Indeed, this species has started to shorten its migration distance decades ago along its European flyway, likely in response to temperature increases (Sauter et al. 2010; Gunnarsson et al. 2012, Guillemain et al. 2015). Previous work highlighted that the Mallard clearly responds to winter temperatures, both in North America (Schummer et al. 2010) and in Europe (Dalby et al. 2013). Its metabolism and opportunistic feeding strategy may explain these findings (Schummer et al. 2010): its larger size and weight allow Mallard to endure negative temperatures more easily than smaller species, disadvantaged by their greater surface area to volume ratio. It is also a relative habitat generalist species exploiting numerous wetland habitats, small, even degraded or urban and can switch from water to terrestrial feeding while the other duck species are more wetland dependent. Accordingly, Mallard are likely to winter closer to their temperature limits than other duck species, resulting in a different trade-off between saving energy from migration and thermal regulation, and likely a quicker response to climate warming by a distribution change. It cannot be excluded, however, that the fact that millions of mallards are released annually in Europe (Champagnon et al. 2013) also blurs the relationship between environmental conditions and the geographic distribution of this species (Söderquist et al. 2013). Garganey and Greater Scaup were the two other duck species with a positive contribution to the CTI trend. This result should however be considered with great caution, given both species are rare winter visitors in the study area, the former usually wintering in Africa and the latter at more northern latitudes. Indeed, Garganey and Greater Scaup numbers had a cumulative abundance of 983 and 37,634 counted individuals in our dataset, respectively, compared to 15.3 million Mallards.

Perspectives

The economic incentive provided by hunting is expected to drive landowners to manage habitat to locally boost hunted species abundance. This kind of habitat improvements could locally release hunted species from some of the adverse effects of climate change, but also impede current or future distributional changes. Consistent with this prediction, and based on community changes in 110 waterbird species over a large region (south-west Europe), we demonstrated here that hunted ducks are indeed slower in their response to climate warming compared to other waterbirds. Although our analysis did not directly infer that site management for hunting purposes drives this outcome, we suggest the pattern we found may be general. Because hunting is a global phenomenon, more studies exploring the interactions between site management and climate change as drivers of altered distributional changes are needed to understand whether hunted ducks are more persistent against climate change because of habitat management, or trapped there despite the ongoing climate warming. While hunted ducks may in the short-term benefit from such artificial land management, this may already have negative consequences for other elements of biodiversity (Tamisier & Grillas 1994), and may be detrimental for the ducks themselves in the longer run.

In addition to the potential effect of habitat management on waterbird responses to climate warming, harvesting can also have a direct impact on population dynamics through removal of individuals (Cooch et al. 2014). Among studied populations of non-breeding hunted ducks, several were stable or increasing over both short and long terms, such as Northern Pintail, Common Teal, Gadwall and Redcrested Pochard, while for others the trends were declining at least in one studied country, such as in Mallard, Eurasian Wigeon, Common Pochard and Tufted Duck (EEA 2020). Sustainable management of duck populations is required to maintain these species at a favorable conservation status. Management planning needs international collaborations at species distribution level, using hunting data and demographic parameters (Holopainen et al. 2018). Whether the distribution of harvested populations is changing or not in response to climate warming should be carefully considered, to anticipate ecologic, cultural and economic challenges (Guillemain et al. 2013).

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Author Contributions Statement

- 454 EG, TG and MG conceived the ideas and designed methodology; NB, TL, BL, FM, CM and MZ collected
- 455 the data; EG analysed the data; EG and MG led the writing of the manuscript. All authors contributed
- 456 critically to the drafts and gave final approval for publication.

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References

- 459 Aubin, I., Munson, A. D., Cardou, F., Burton, P. J., Isabel, N., Pedlar, J. H., ... & McKenney, D.
- 460 (2016). Traits to stay, traits to move: a review of functional traits to assess sensitivity and
- adaptive capacity of temperate and boreal trees to climate change. Environmental
- 462 Reviews, 24(2), 164-186.
- Auffret, A. G., & Thomas, C. D. (2019). Synergistic and antagonistic effects of land use and non-
- native species on community responses to climate change. Global change biology, 25(12),
- 465 4303-4314.
- 466 BirdLife International and Handbook of the Birds of the World (2018) Bird species distribution
- maps of the world. http://datazone.birdlife.org/species/requestdis
- Bonebrake, T. C., Brown, C. J., Bell, J. D., Blanchard, J. L., Chauvenet, A., Champion, C., ... &
- 469 Pecl, G. T. (2018). Managing consequences of climate-driven species redistribution requires
- integration of ecology, conservation and social science. Biological Reviews, 93(1), 284-305.
- 471 Brochet, A. L., Gauthier-Clerc, M., Mathevet, R., Béchet, A., Mondain-Monval, J. Y., & Tamisier,
- 472 A. (2009). Marsh management, reserve creation, hunting periods and carrying capacity for
- wintering ducks and coots. Biodiversity and Conservation, 18(7), 1879-1894.
- 474 Brochet, A. L., Mouronval, J. B., Aubry, P., Gauthier-Clerc, M., Green, A. J., Fritz, H., &
- Guillemain, M. (2012). Diet and feeding habitats of Camargue dabbling ducks: what has
- 476 changed since the 1960s?. Waterbirds, 35(4), 555-576.
- Brommer, J. E. (2008). Extent of recent polewards range margin shifts in Finnish birds depends
- on their body mass and feeding ecology. Ornis Fennica, 85(4), 109-17.

- Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: a Practical
- 480 Information-theoretic Approach, 2nd edn. New York: Springer.
- Caizergues, A., Guillemain, M., Arzel, C., Devineau, O., Leray, G., Pilvin, D., Lepley, M., Massez,
- 482 G. & Schricke, V. (2011) Emigration rates and population turnover of Teal (*Anas crecca*) in
- two major wetlands of Western Europe. Wildlife Biology 17: 373-382.
- 484 Champagnon, J., Crochet, P.A., Kreisinger, J., Čížková, D., Gauthier-Clerc, M., Massez, G.,
- Söderquist, P., Albrecht, T. & Guillemain, M. (2013) Assessing the genetic impact of massive
- restocking on wild mallard. Animal Conservation, 16(3), pp.295-305.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E., & Sheldon, B. C. (2008).
- Adaptive phenotypic plasticity in response to climate change in a wild bird population.
- 489 science, 320(5877), 800-803.
- 490 Cooch, E. G., Guillemain, M., Boomer, G. S., Lebreton, J. D., & Nichols, J. D. (2014). The effects
- of harvest on waterfowl populations. Wildfowl, 220-276.
- 492 Correia, D. L., Chauvenet, A. L., Rowcliffe, J. M., & Ewen, J. G. (2015). Targeted management
- buffers negative impacts of climate change on the hihi, a threatened New Zealand
- 494 passerine. Biological Conservation, 192, 145-153.
- Dalby, L., Fox, A. D., Petersen, I. K., Delany, S., & Svenning, J. C. (2013). Temperature does not
- dictate the wintering distributions of E uropean dabbling duck species. Ibis, 155(1), 80-88.
- Davis, J. B., Guillemain, M., Kaminski, R. M., Arzel, C., Eadie, J. M., & Rees, E. C. (2014). Habitat
- and resource use by waterfowl in the northern hemisphere in autumn and winter.
- 499 Wildfowl, 17-69.
- 500 Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond
- predictions: biodiversity conservation in a changing climate. science, 332(6025), 53-58.
- 502 Delany S. (2010) Guidance on Waterbird Monitoring Methodology: Field Protocol for
- 503 Waterbird Counting (Wetlands International).
- DeMarche, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into
- forecasts of species' distribution and abundance under climate change. Global Change
- 506 Biology, 25(3), 775-793.
- 507 Devictor, V., Van Swaay, C., ... & Jiguet, F. (2012). Differences in the climatic debts of birds and
- butterflies at a continental scale. Nature climate change, 2(2), 121-124.
- 509 EEA, European Environment Agency (2020) State of nature in the EU Results from reporting
- 510 under the nature directives 2013-2018. https://nature-
- art12.eionet.europa.eu/article12/summary

- 512 Elmberg, J., Hessel, R., Fox, A.D. & Dalby, L. (2014) Interpreting seasonal range shifts in
- migratory birds: a critical assessment of 'short-stopping' and a suggested terminology. J.
- 514 Ornithol. 155: 571-579.
- 515 FACE (2019) Hunting and Conservation 5th report of the FACE Biodiversity Manifesto.
- 516 https://www.face.eu/wp-content/uploads/2020/06/BDM-Report-2019.pdf
- 517 Fourcade, Y., Åström, S., & Öckinger, E. (2019). Climate and land-cover change alter
- 518 bumblebee species richness and community composition in subalpine areas. Biodiversity
- and conservation, 28(3), 639-653.
- 520 Gaget, E., Galewski, T., Jiguet, F., Guelmami, A., Perennou, C., Beltrame, C., & Le Viol, I. (2020).
- 521 Antagonistic effect of natural habitat conversion on community adjustment to climate
- warming in nonbreeding waterbirds. Conservation Biology, 34(4), 966-976.
- 523 Gaget, E., Galewski, T., Jiguet, F., & Le Viol, I. (2018). Waterbird communities adjust to climate
- warming according to conservation policy and species protection status. Biological
- 525 conservation, 227, 205-212.
- 526 Gaget, E., Pavón-Jordán, D., Johnston, A., Lehikoinen, A., Hochachka, W. M., Sandercock, B. K.,
- 527 ... & Brommer, J. E. (2021). Benefits of protected areas for nonbreeding waterbirds
- adjusting their distributions under climate warming. Conservation Biology, 35(3), 834-845.
- 529 Gaget, E., Johnston, A., Pavón-Jordán, D., Lehikoinen, A. S., Sandercock, B. K., Soultan, A., ... &
- Brommer, J. E. (2022). Protected area characteristics that help waterbirds respond to
- climate warming. Conservation Biology. DOI: <u>10.1111/cobi.13877</u>
- Godet, L., Jaffré, M., & Devictor, V. (2011). Waders in winter: long-term changes of migratory
- bird assemblages facing climate change. Biology letters, 7(5), 714-717.
- Gourlay-Larour, M.L., Schricke, V., Sorin, C., L'Hostis, M. & Caizergues, A. (2012) Movements
- of wintering diving ducks: new insights from nasal saddled individuals. Bird Study 59: 266-
- 536 278.
- Guillemain, M., Fritz, H. & Duncan, P. (2002) The importance of protected areas as nocturnal
- feeding grounds for dabbling ducks wintering in Western France. Biol. Cons. 103: 183-198.
- Guillemain, M., Fuster, J., Lepley, M., Mouronval, J. B., & Massez, G. (2009). Winter site fidelity
- is higher than expected for Eurasian Teal Anas crecca in the Camargue, France. Bird Study,
- 541 56(2), 272-275.
- 542 Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J. &
- 543 Simon, G. (2010) Wintering French Mallard and Teal are heavier and in better body
- condition than 30 years ago: effects of a changing environment? Ambio 39: 170-180.

- Guillemain, M., Pöysä, H., Fox, A. D., Arzel, C., Dessborn, L., Ekroos, J., ... & Moller, A. P. (2013).
- Effects of climate change on European ducks: what do we know and what do we need to
- 547 know?. Wildlife Biology, 19(4), 404-419.
- Guillemain, M., Pernollet, C.A., Massez, G., Cavallo, F., Simon, G. & Champagnon, J. (2015)
- Disentangling the drivers of changes in Common Teal migration phenology over 50 years:
- land use vs. climate change effects. Journal of Ornithology 156: 647-655.
- Guillemain, M. & Hearn, R. (2017). Ready for climate change? Geographic trends in the
- protection status of critical sites for Western Palearctic ducks. Biodiv. Cons. 26: 2347-2360.
- 553 Gunnarsson, G., Waldenström, J., & Fransson, T. (2012). Direct and indirect effects of winter
- harshness on the survival of Mallards Anas platyrhynchos in northwest Europe. Ibis, 154(2),
- 555 307-317.
- Hällfors, M. H., Antão, L. H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., & Saastamoinen,
- M. (2020). Shifts in timing and duration of breeding for 73 boreal bird species over four
- decades. Proceedings of the National Academy of Sciences, 117(31), 18557-18565.
- Harris, I., Osborn, T.J., Jones, P. et al. (2020). Version 4 of the CRU TS monthly high-resolution
- gridded multivariate climate dataset. Sci Data 7, 109.
- Holopainen, S., Arzel, C., Elmberg, J., Fox, A. D., Guillemain, M., Gunnarsson, G., ... & Pöysä, H.
- 562 (2018). Sustainable management of migratory European ducks: finding model species.
- 563 Wildlife Biology, 2018(1), 1-11.
- 564 IPCC (2021). Climate Change 2021: The Physical Science Basis. Contribution of Working Group
- I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.
- 566 Cambridge University Press. In Press.
- 567 IUCN. (2021) The IUCN Red List of Threatened Species. Version 2021-3.
- https://www.iucnredlist.org. Accessed on [14/04/2022].
- Jiguet, F., Gadot, A. S., Julliard, R., Newson, S. E., & Couvet, D. (2007). Climate envelope, life
- 570 history traits and the resilience of birds facing global change. Global Change Biology, 13(8),
- 571 1672-1684.
- Karell, P., Ahola, K., Karstinen, T., Valkama, J., & Brommer, J. E. (2011). Climate change drives
- 573 microevolution in a wild bird. Nature communications, 2(1), 1-7.
- Legagneux, P., Duhart, M., & Schricke, V. (2007). Seeds consumed by waterfowl in winter: a
- review of methods and a new web-based photographic atlas for seed identification. Journal
- 576 of Ornithology, 148(4), 537-541.

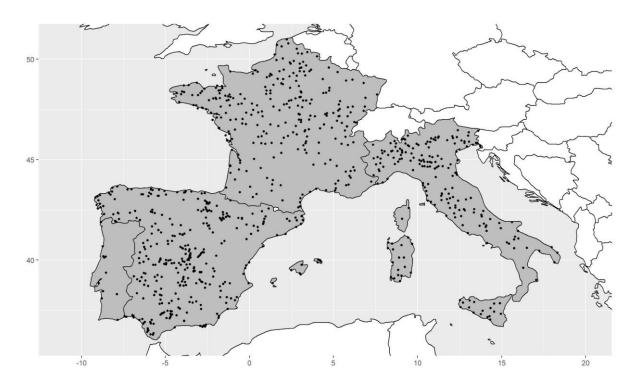
- 577 Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G.
- 578 (2020). Species better track climate warming in the oceans than on land. Nature Ecology &
- 579 Evolution, 4(8), 1044-1059.
- Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2019). Package 'performance'. CRAN
- Maclean, I. & Rehfisch, M. (2008) Guidelines on the measures needed to help waterbirds adapt
- to climate change. AEWA Conservation Guidelines No. 12, AEWA Technical Series No. 27,
- 583 Bonn.
- Mangiafico, S.S. (2016) Summary and Analysis of Extension Program Evaluation in R, version
- 585 1.19.10. rcompanion.org/handbook/.
- 586 Mathevet, R. & Guillemain, M. (2016). Que ferons-nous des canards sauvages ? Chasse, nature
- et gestion adaptative. Editions Quae, Versailles, France: 96p.
- 588 Massimino, D., Beale, C. M., Suggitt, A. J., Crick, H. Q., Macgregor, N. A., Carroll, M. J., ... &
- Pearce-Higgins, J. W. (2020). Can microclimate offer refuge to an upland bird species under
- climate change?. Landscape Ecology, 35(9), 1907-1922.
- 591 McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving
- climate connectivity in a fragmented landscape. Proceedings of the National Academy of
- 593 Sciences, 113(26), 7195-7200.
- Møller, A. P., Fiedler, W., & Berthold, P. (Eds.). (2010). Effects of climate change on birds. OUP
- 595 Oxford.
- Mouronval, J. B., Brochet, A. L., Aubry, P., & Guillemain, M. (2014). Les anatidés hivernant en
- 597 Camargue se nourrissent-ils dans les marais aménagés pour la chasse?. Faune sauvage,
- 598 303, 14-21.
- Niang, A., Pernollet, C. A., Gauthier-Clerc, M., & Guillemain, M. (2016). A cost-benefit analysis
- of rice field winter flooding for conservation purposes in Camargue, Southern France.
- Agriculture, Ecosystems & Environment, 231, 193-205.
- 602 Ogilvie, M.A. (1983) A migration study of the Teal (Anas crecca) in Europe using ring
- recoveries. PhD Thesis, University of Bristol, UK.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
- across natural systems. Nature 42:37–42
- Pavón-Jordán, D., Fox, A.D., Clausen, ... & Lehikoinen, A. (2015). Climate-driven changes in
- 607 winter abundance of a migratory waterbird in relation to EU protected areas. Div. Distr.
- 608 21:571-582

- Pavón-Jordán, D., Santangeli, A., & Lehikoinen, A. (2017). Effects of flyway-wide weather
- 610 conditions and breeding habitat on the breeding abundance of migratory boreal
- waterbirds. Journal of avian biology, 48(7), 988-996.
- Pernollet, C.A., Guelmani, A., Green, A.J., Curco, A., Dies, B., Bogliani, G., Tesio, F., Brogi, A.,
- Gauthier-Clerc, M. & Guillemain, M. (2015a) A comparison of wintering duck numbers
- among European rice production areas with contrasting flooding regimes. Biological
- 615 Conservation, 186: 214-224.
- Pernollet, C.A., Simpson, D., Gauthier-Clerc, M. & Guillemain, M. (2015b). Rice and duck, a
- good combination? Identifying the incentives and triggers for rice farming and duck
- conservation. Agriculture, Ecosystems & Environment 214: 118-132.
- Pernollet, C.A. (2016) L'utilisation des rizières par les canards hivernants : vers une gestion des
- rizières en interculture favorable aux canards et aux agriculteurs. PhD thesis, University of
- 621 Montpellier, France.
- Pearce-Higgins, J. W., Antão, L. H., Bates,... & Morecroft, M. D. (2022). A framework for climate
- change adaptation indicators for the natural environment. Ecological indicators, 136,
- 624 108690.
- Pearce-Higgins, J. W., Lindley, P. J., Johnstone, I. G., Thorpe, R. I., Douglas, D. J., & Grant, M. C.
- 626 (2019). Site-based adaptation reduces the negative effects of weather upon a southern
- range margin Welsh black grouse Tetrao tetrix population that is vulnerable to climate
- 628 change. Climatic Change, 153(1), 253-265.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer,
- R. (2017). Package 'nlme'. Linear and nonlinear mixed effects models, version, 3(1).
- Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K., & Toms, M. P. (2015). Is
- supplementary feeding in gardens a driver of evolutionary change in a migratory bird
- 633 species?. Global Change Biology, 21(12), 4353-4363.
- 634 Prober, S. M., Doerr, V. A., Broadhurst, L. M., Williams, K. J., & Dickson, F. (2019). Shifting the
- conservation paradigm: a synthesis of options for renovating nature under climate change.
- 636 Ecological Monographs, 89(1), e01333.
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation
- for Statistical Computing, Vienna. https://www.r-project.org/index.html
- Radchuk, V., Reed, T., Teplitsky, ... & Kramer-Schadt, S. (2019). Adaptive responses of animals
- to climate change are most likely insufficient. Nature communications, 10(1), 1-14.
- Raftery, A. E., Zimmer, A., Frierson, D. M., Startz, R., & Liu, P. (2017). Less than 2 C warming by
- 642 2100 unlikely. Nature climate change, 7(9), 637-641.

- 643 Sauter, A., Korner-Nivergelt, F. & Jenni, L. (2010). Evidence of climate change effects on within-
- winter movements of European Mallards Anas platyrhynchos. Ibis, 152(3), 600-609.
- 645 Schummer, M. L., Kaminski, R. M., Raedeke, A. H., & Graber, D. A. (2010). Weather-related
- indices of autumn–winter dabbling duck abundance in middle North America. The Journal
- of Wildlife Management, 74(1), 94-101.
- 648 Scott, D. A. & Rose, P. M. (1996) Atlas of Anatidae populations in Africa and Western Eurasia.
- Wetlands International Publication 41, Wageningen, The Netherlands.
- 650 Söderquist, P., Gunnarsson, G., & Elmberg, J. (2013). Longevity and migration distance differ
- between wild and hand-reared mallards Anas platyrhynchos in Northern Europe. European
- 652 Journal of Wildlife Research, 59(2), 159-166.
- 653 Storchová, L., & Hořák, D. (2018). Life-history characteristics of European birds. Global Ecology
- and Biogeography, 27(4), 400-406.
- Tamisier, A., & Dehorter, O. (1999). Camargue, canards et foulques: fonctionnement et
- devenir d'un prestigieux quartier d'hiver. Centre ornithologique du Gard.
- Tamisier, A., & Grillas, P. (1994). A review of habitat changes in the Camargue: an assessment
- of the effects of the loss of biological diversity on the wintering waterfowl community.
- Biological conservation, 70(1), 39-47.
- Tamisier, A. & Tamisier, M.C. (1981) L'existence d'unités fonctionnelles démontrée chez les
- sarcelles d'hiver en Camargue par la biotélémétrie. Revue d'Ecologie (Terre & Vie) 35 : 563-
- 662 579.
- Toureng, C., Bennetts, R. E., Sadoul, N., Mesleard, F., Kayser, Y., & Hafner, H. (2000). Long-
- term population and colony patterns of four species of tree-nesting herons in the
- 665 Camargue, South France. Waterbirds, 236-245.
- Thomas, C. D., Franco, A. M., & Hill, J. K. (2006). Range retractions and extinction in the face
- of climate warming. Trends in Ecology & Evolution, 21(8), 415-416.
- Vallecillo, D., Defos du Rau, P., Olivier, A., Champagnon, J., Guillemain, M., Croce, N., Massez,
- G., Petit, J., Beck, N. & Mondain-Monval, J.Y. (2019) Expériences cynégétiques innovantes
- en Camargue : des pistes pour la chasse au gibier d'eau de demain ? Faune Sauvage 323 :
- 671 33-39.
- Vallecillo, D. (2021) Modélisation de la répartition spatio-temporelle des oiseaux d'eau en
- 673 Camargue un outil pour la gestion. PhD thesis, University of Montpellier, France: 248p
- 674 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014).
- 675 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals:
- 676 Ecological Archives E095-178. Ecology, 95(7), 2027-2027.

677 678 679	Zenatello, M., Baccetti, N. & Borghesi, F. (2014) Risultati dei censimenti degli uccelli acquatici svernanti in Italia. Distribuzione, stima e trend delle popolazioni nel 2001-2010. ISPRA, Serie Rapporti, 206/2014
680 681	Zenatello, M., Baccetti, N. & Luchetta, A. (2021) International Waterbird Census Report – Italy 2009-2018. Report of the Mediterranean Waterbirds Network, Tour du Valat, 12p.
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683	
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Appendix 2. Species functional traits and hunting status. We considered three hunting status categories between species: eleven duck species listed in Annex II of the Birds Directive, the other species listed in Annex II of the Birds Directive hunted in at least one Member State, and the non-hunted species not listed in Annex II, or listed in Annex II but not hunted in the study area. The STI was calculated as the average temperature in January (1950-2000, www.worldclim.org, spatial resolution of 0.25°) on the non-breeding species distribution (BirdLife International & HBW 2018) from Gaget et al. (2018). Body mass (continuous, log transformation) and diet (Plant, Omnivore, Invertebrate, Vertebrate) were extracted from Wilman et al. (2014), generation length (continuous, in years) from IUCN (2021) and migration strategy (resident, short, long) from Storchová et al. (2018).

Species	Diet	Hunting status	Generation length	STI	Migration strategy	Body mass (log)
Oxyura leucocephala	Plant	Non-hunted	6	1.26971416	Short	6.50
Clangula hyemalis	Invertebrate	Other hunted	9	-2.499599758	Short	6.77
Somateria mollissima	Invertebrate	Other hunted	9	-7.528618341	Short	7.63
Mergellus albellus	Invertebrate	Non-hunted	5.7	-1.579129112	Short	6.41
Mergus merganser	Vertebrate	Non-hunted	7.3	-0.39697332	Short	7.28
Mergus serrator	Vertebrate	Non-hunted	7.3	-1.082901954	Short	6.92
Bucephala clangula	Invertebrate	Other hunted	8	-1.10518807	Short	6.82
Melanitta nigra	Invertebrate	Other hunted	7.5	2.279566759	Short	6.96
Melanitta fusca	Invertebrate	Other hunted	7.5	0.669883387	Short	7.50
Tadorna tadorna	Invertebrate	Non-hunted	10.9	4.30007485	Short	7.05
Tadorna ferruginea	Plant	Non-hunted	10.9	8.879664277	Res	7.12
Netta rufina	Plant	Hunted duck	7	5.352488457	Short	7.02
Aythya fuligula	Omnivore	Hunted duck	7.3	10.45232776	Short	6.55
Aythya marila	Invertebrate	Hunted duck	8.2	0.428197756	Short	6.91
Aythya ferina	Plant	Hunted duck	7.6	11.33614757	Short	6.71
Aythya nyroca	Plant	Non-hunted	7.6	9.773350072	Short	6.35
Marmaronetta angustirostris	Plant	Non-hunted	7	5.953747563	Short	6.17
Mareca penelope	Plant	Hunted duck	6.4	16.53006205	Short	6.65

Mareca strepera	Plant	Hunted duck	7.1	11.73496464	Res	6.82
Anas acuta	Plant	Hunted duck	6.8	16.89718621	Short	6.85
Anas crecca	Plant	Hunted duck	6.3	12.72483539	Short	5.84
Anas platyrhynchos	Omnivore	Hunted duck	6.6	-0.020462632	Short	6.74
Spatula querquedula	Omnivore	Hunted duck	6.5	23.06512822	Long	5.79
Spatula clypeata	Invertebrate	Hunted duck	6.5	14.91201976	Short	6.42
Branta bernicla	Plant	Non-hunted	10.9	2.863382582	Short	7.15
Branta leucopsis	Plant	Non-hunted	10.5	1.685984156	Short	7.43
Anser albifrons	Plant	Non-hunted	11.3	2.533119452	Short	7.83
Anser fabalis	Plant	Other hunted	11.4	-2.514040367	Short	7.92
Anser brachyrhynchus	Plant	Non-hunted	11.4	2.021202386	Short	7.88
Anser anser	Plant	Other hunted	11.6	4.465428485	Short	8.10
Cygnus columbianus	Plant	Non-hunted	12.7	2.436899298	Short	8.76
Cygnus cygnus	Plant	Non-hunted	12.3	-1.490706698	Short	9.14
Cygnus olor	Plant	Non-hunted	12.2	1.269147723	Res	9.28
Platalea leucorodia	Invertebrate	Non-hunted	7.2	17.95014398	Short	7.53
Plegadis falcinellus	Invertebrate	Non-hunted	6.7	23.13696657	Long	6.44
Ciconia nigra	Vertebrate	Non-hunted	15.9	22.98346583	Long	7.98
Ciconia ciconia	Vertebrate	Non-hunted	16.5	22.94906346	Long	8.15
Gavia stellata	Vertebrate	Non-hunted	9.8	3.054206132	Short	7.30
Gavia arctica	Vertebrate	Non-hunted	9.8	0.763783716	Short	7.72
Gavia immer	Vertebrate	Non-hunted	9.8	-0.043080125	Short	8.51
Nycticorax nycticorax	Vertebrate	Non-hunted	8.8	23.47202582	Long	6.70
Ardeola ralloides	Vertebrate	Non-hunted	6.7	23.78935548	Long	5.66
Ardea cinerea	Vertebrate	Non-hunted	10.3	18.73373742	Short	7.28
Ardea purpurea	Vertebrate	Non-hunted	10.5	23.86808726	Long	6.97

Bubulcus ibis	Invertebrate	Non-hunted	8.1	22.96031792	Res	5.91
Casmerodius albus	Vertebrate	Non-hunted	9.1	21.85591657	Short	6.77
Egretta garzetta	Invertebrate	Non-hunted	6.6	21.26252234	Long	5.75
Ixobrychus minutus	Invertebrate	Non-hunted	4.1	24.01168239	Long	4.61
Botaurus stellaris	Vertebrate	Non-hunted	5.5	18.39468171	Res	7.19
Phalacrocorax aristotelis	Vertebrate	Non-hunted	8.8	2.298892	Res	7.48
Phalacrocorax pygmeus	Vertebrate	Non-hunted	8.1	2.744268717	Short	6.52
Phalacrocorax carbo	Vertebrate	Non-hunted	11.3	18.40826409	Short	7.84
Lymnocryptes minimus	Invertebrate	Other hunted	5.4	20.02804147	Short	3.93
Limosa limosa	Invertebrate	Other hunted	8.6	21.01453888	Long	5.67
Limosa lapponica	Invertebrate	Non-hunted	8.9	19.22660394	Short	5.68
Arenaria interpres	Invertebrate	Non-hunted	7.3	17.86138751	Short	4.92
Calidris alpina	Invertebrate	Non-hunted	8.1	11.83058422	Short	3.97
Calidris maritima	Invertebrate	Non-hunted	7.6	-2.482943324	Short	4.19
Calidris minuta	Invertebrate	Non-hunted	6.8	22.77386732	Long	3.10
Calidris alba	Invertebrate	Non-hunted	8.1	18.86150911	Long	3.96
Calidris temminckii	Invertebrate	Non-hunted	7.1	23.31781746	Long	3.18
Calidris ferruginea	Invertebrate	Non-hunted	7.6	23.43021111	Long	4.08
Calidris canutus	Invertebrate	Other hunted	6.8	19.07810312	Long	4.96
Tringa ochropus	Invertebrate	Non-hunted	5.6	21.09896305	Short	4.28
Tringa erythropus	Invertebrate	Other hunted	5.6	21.03462626	Long	5.07
Tringa nebularia	Invertebrate	Other hunted	6.3	23.15678175	Long	5.24
Tringa glareola	Invertebrate	Non-hunted	5.2	23.5308322	Long	4.14
Tringa totanus	Invertebrate	Other hunted	6.2	15.48429434	Short	4.87
Tringa stagnatilis	Invertebrate	Non-hunted	5.6	23.22543672	Long	4.36
Actitis hypoleucos	Omnivore	Non-hunted	6.8	23.15678175	Long	3.89
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Scolopax rusticola	Invertebrate	Other hunted	6.3	4.242742	Short	5.73
Gallinago gallinago	Invertebrate	Other hunted	4.8	18.58383523	Short	4.74
Numenius arquata	Omnivore	Other hunted	5	18.88781824	Short	6.69
Numenius phaeopus	Invertebrate	Other hunted	9.1	22.05833801	Long	5.90
Larus minutus	Invertebrate	Non-hunted	10.5	3.7	Short	4.78
Larus genei	Omnivore	Non-hunted	10.5	11.89835354	Short	5.64
Larus ridibundus	Invertebrate	Other hunted	9.6	6.581840595	Short	5.65
Larus canus	Omnivore	Non-hunted	9.8	1.617542777	Short	6.02
Larus marinus	Omnivore	Non-hunted	12	-2.491862384	Short	7.41
Larus michahellis	Vertebrate	Non-hunted	13	4.57847	Short	7.00
Larus fuscus	Vertebrate	Non-hunted	13.9	18.5800917	Short	6.64
Larus audouinii	Vertebrate	Non-hunted	13	11.45294748	Short	6.28
Larus melanocephalus	Vertebrate	Non-hunted	10.1	9.305989705	Short	5.55
Rissa tridactyla	Omnivore	Non-hunted	12.9	4.798985422	Res	6.03
Sterna caspia	Vertebrate	Non-hunted	12.2	21.40258537	Long	6.49
Sterna hirundo	Vertebrate	Non-hunted	11.5	25.24947703	Long	4.87
Sterna sandvicensis	Vertebrate	Non-hunted	10.8	12.38123263	Short	5.30
Chlidonias hybrida	Vertebrate	Non-hunted	9.9	21.65184602	Long	4.44
Charadrius alexandrinus	Invertebrate	Non-hunted	5	19.1981442	Short	3.77
Vanellus vanellus	Invertebrate	Other hunted	9	4.516681624	Short	5.39
Charadrius dubius	Invertebrate	Non-hunted	5	23.79976584	Long	3.68
Charadrius hiaticula	Invertebrate	Non-hunted	5.1	22.10771097	Short	4.18
Recurvirostra avosetta	Invertebrate	Non-hunted	8.7	22.04492438	Short	5.72
Himantopus himantopus	Invertebrate	Non-hunted	7.3	22.12582625	Long	5.18
Haematopus ostralegus	Invertebrate	Other hunted	13.7	15.34138378	Short	6.27
Pluvialis squatarola	Invertebrate	Other hunted	6	18.83630341	Short	5.53

Pluvialis apricaria	Invertebrate	Non-hunted	5.2	5.356544857	Short	5.37
Fulica cristata	Plant	Non-hunted	7	22.58950745	Res	6.72
Porzana porzana	Omnivore	Non-hunted	2.7	23.546673	Long	4.48
Gallinula chloropus	Omnivore	Other hunted	5.9	16.30709877	Res	5.83
Fulica atra	Plant	Other hunted	7	5.864663198	Res	6.58
Porphyrio porphyrio	Plant	Non-hunted	5.9	22.11989646	Res	6.65
Rallus aquaticus	Omnivore	Other hunted	4.6	4.523513575	Res	4.72
Grus grus	Plant	Non-hunted	13.4	14.71592338	Short	8.61
Phoenicopterus roseus	Omnivore	Non-hunted	16.3	20.58416977	Short	8.02
Tachybaptus ruficollis	Invertebrate	Non-hunted	5.4	18.5962031	Short	5.14
Podiceps auritus	Vertebrate	Non-hunted	7.1	3.393542644	Short	6.12
Podiceps grisegena	Omnivore	Non-hunted	7.1	2.273349328	Short	6.93
Podiceps cristatus	Vertebrate	Non-hunted	7.1	10.08300404	Short	6.60
Podiceps nigricollis	Invertebrate	Non-hunted	7.1	17.99795243	Short	6.02

Appendix 3. Sensitivity analysis.

1) Protected areas

We performed a sensitivity analysis to ensure that the results from the main text were not affected by site protection status. Indeed, protected areas can affect wintering waterbird response to climate warming, by increasing species persistence (Gaget al. 2021). The risk is then to observe the effect of site protection on wintering waterbird community change rather than the potential effect of hunting management. It is important however to note that hunting activities can occur inside protected areas. This means that we cannot dissociate the effect of the protected area and the potential effect of hunting management inside protected areas. To ensure that our results were not affected by protected areas, we removed all protected sites from this sensitivity analysis. Protected sites were identified following the methodology described in Gaget et al. (2021). We performed the same analyses, without protected sites, as in the main text. We investigated temporal change in Community Temperature Index (CTI), species contributions and assessed the differences of contribution between species, depending on hunting status and functional traits.

We identified 411 monitored sites outside a protected area, totalling 8,229 surveys. The CTI temporal trend was positive and significant (β = 0.042 ± 0.002 SE, p < 0.001). Species contributions to the CTI trends were fairly similar to the full analysis (Fig. A3.1). Species diet, hunting status and generation length were the main factors explaining species contribution, whereas other predictors had little effect (Table A3.1). Multicollinearity was low between species diet and hunting status (VIF = 1.09) and between species diet and generation length (VIF = 1.14). Consequently, this sensitivity analysis confirmed that species diet and hunting status are important factors explaining species contribution to CTI trend independently from site protection. In addition, generation length significantly contributed to explain species contributions in this subset of sites. Generation length can indeed be an important factor together with site fidelity, because juvenile settlement can influence over-winter location at adult stage, meaning that long-lived species might need more time to shift their distribution than short-lived species (see general discussion).

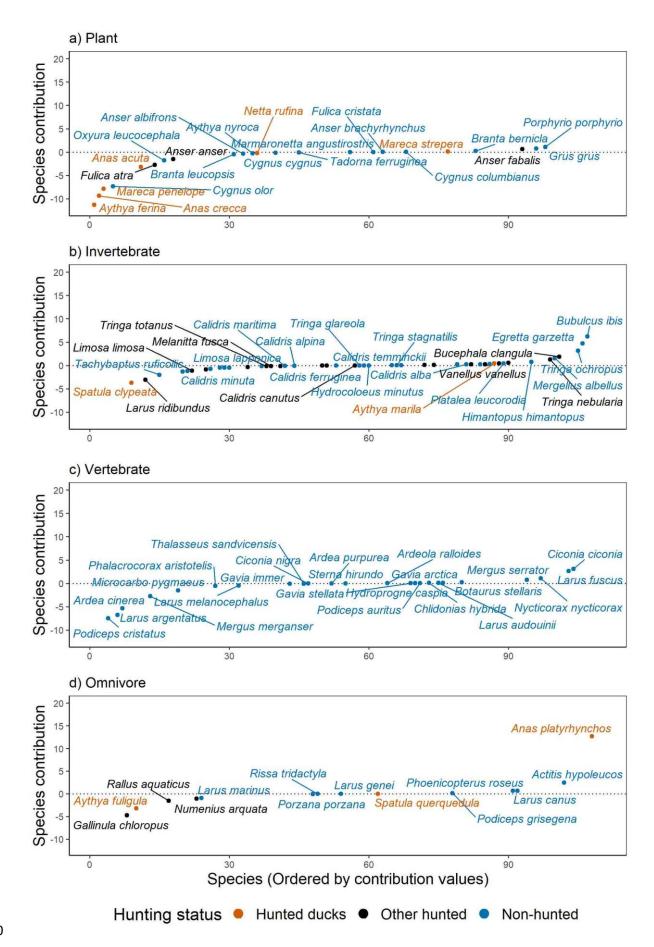


Figure Appendix 3.1: Species contributions (%) to the Community Temperature Index (CTI) temporal trend, depending on species diet (plant, invertebrate, vertebrate, omnivore) and hunting status (hunted ducks, other hunted and non-hunted), with species ordered by their contribution value (n = 110 species). The horizontal dotted line represents a null contribution. Not all species names are shown for esthetic reason.

Table Appendix 3.1. Model selection identifying predictors the most related to species contributions based on AIC (delta AIC<2) and parsimony. The F-value corresponds to the sum of the effects and DF is degrees of freedom. The best model to explain species contribution considers both species hunting status, generation length and diet (in bold). Models are fitted with phylogenetic generalized least squares (PGLS). Diet, hunting status and migration are factors and STI (Species Temperature Index), body mass and generation length are quantitative variables.

			Pseudo R-		
Formula	AIC	Delta AIC	squared	F-value	DF
Hunting status + Diet + Generation					
length	699.7	0.0	0.105	7.574	7
Hunting status + Diet + Body mass	700.5	0.8	0.083	4.901	7
Hunting status + Diet + Migration	701.1	1.4	0.062	2.512	8
Diet + Hunting status	701.8	2.1	0.062	2.514	6
Diet + Generation length	704.9	5.2	0.085	6.095	5
Diet + Migration	705.5	5.8	0.050	1.830	6
Diet + Body mass	705.7	6.0	0.063	3.389	5
Diet	706.2	6.5	0.048	1.794	4
Hunting status + Diet + STI	707.3	7.6	0.062	2.516	7
Hunting status	709.5	9.8	0.010	0.521	3
Diet + STI	711.7	12.0	0.049	1.836	5
Migration	712.4	12.7	0.005	0.294	3
Null model	713.5	13.8	0.000	0.000	1
Body mass	714.2	14.5	0.005	0.574	2
Generation length	714.4	14.7	0.019	2.041	2
STI	719.1	19.4	0.001	0.020	2

2) Sites with more than 25 surveys over 28 years

We performed a sensitivity analysis to ensure that the results from the main text were not affected by the number of surveys per site. We removed all sites with less than 25 surveys from this sensitivity analysis and performed the same analyses as in the main text. We investigated temporal change in Community Temperature Index (CTI), species contributions and assessed the differences of contribution between species, depending on hunting status and functional traits.

We identified 288 monitored sites outside a protected area, totalling 7,703 surveys. The CTI temporal trend was positive and significant (β = 0.053 ± 0.002 SE, p < 0.001). Species contributions to the CTI trends were fairly similar to the full analysis (Fig. A3.2). Species diet, hunting status and generation length were the main factors explaining species contribution, whereas other predictors had little effect (Table A3.2). Multicollinearity was low between species diet and hunting status (VIF = 1.05). Consequently, this sensitivity analysis confirmed that species diet and hunting status are important factors explaining species contribution to CTI trend independently from site survey effort.

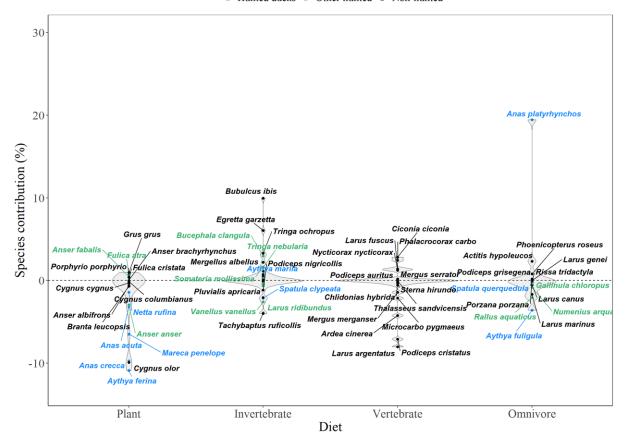


Figure Appendix 3.2: Violin plot of species contributions (%) to the Community Temperature Index (CTI) temporal trend, depending on species diet. Color scale indicates hunting status; hunted ducks (blue), other hunted species (green), non-hunted species (black). Not all species names are shown for esthetic reason.

 Table Appendix 3.2. Model selection identifying predictors the most related to species contributions based on AIC (delta AIC<2) and parsimony. The F-value corresponds to the sum of the effects and DF is degrees of freedom. The best model to explain species contribution considers both species hunting status, generation length and diet (in bold). Models are fitted with phylogenetic generalized least squares (PGLS). Diet, hunting status and migration are factors and STI (Species Temperature Index), body mass and generation length are quantitative variables.

			Pseudo R-		
Formula	AIC	Delta AIC	squared	F-value	DF
Hunting status + Diet + Migration	690.7	0.0	0.112	4.669	8
Hunting status + Diet + Body mass	691.0	0.3	0.122	6.173	7
Diet + Hunting status	691.5	0.8	0.108	4.528	6
Hunting status + Diet + Generation					
length	692.1	1.4	0.129	7.001	7
Diet + Migration	695.5	4.8	0.094	3.654	6
Diet	696.2	5.5	0.092	3.567	4

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Hunting status + Diet + STI	696.2	5.5	0.116	5.483	7
Diet + Body mass	696.4	5.7	0.100	4.541	5
Diet + Generation length	697.2	6.5	0.108	5.558	5
Diet + STI	701.1	10.4	0.098	4.326	5
Hunting status	704.4	13.7	0.010	0.543	3
Migration	707.9	17.2	0.001	0.022	3
Null model	708.3	17.6	0.000	0.000	1
Body mass	709.5	18.8	0.001	0.073	2
Generation length	711.0	20.3	0.003	0.365	2
STI	712.9	22.2	0.001	1.061	2

Appendix 4. Model selection identifying predictors the most related to species contributions based on AIC (delta AIC<2) and parsimony. The F-value corresponds to the sum of the effects and DF is degree of freedom. The best model to explain species contribution considers both species hunting status and diet (in bold). Models are fitted with phylogenetic generalized least squares (PGLS). Diet, hunting status and migration are factors and STI (Species Temperature Index), body mass and generation length are quantitative variables.

Formula	AIC	Delta AIC	Pseudo R-squared	F-value	DF
Hunting status + Diet + Generation length	695.8	0.0	0.097	6.835	7
Hunting status + Diet + Body mass	696.3	0.5	0.077	4.410	7
Hunting status + Diet + Migration	696.5	0.7	0.060	2.410	8
Diet + Hunting status	697.2	1.4	0.058	2.329	6
Diet + Generation length	700.3	4.5	0.083	5.879	5
Diet + Migration	700.6	4.8	0.049	1.849	6
Diet + Body mass	700.9	5.1	0.061	3.328	5
Diet	701.3	5.5	0.047	1.757	4
Hunting status + Diet + STI	702.9	7.1	0.058	2.323	7
Hunting status	704.8	9.0	0.007	0.36	3
Diet + STI	707.0	11.2	0.048	1.751	5
Migration	707.5	11.7	0.005	0.273	3
Null model	708.4	12.6	0.000	0.001	1
Body mass	709.2	13.4	0.004	0.455	2
Generation length	709.6	13.8	0.016	1.804	2
STI	714.0	18.2	0.001	0.052	2