

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

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▶ To cite this version:

Elie Gaget, T. Galewski, J E Brommer, I. Le Viol, F. Jiguet, et al.. Habitat management favouring hunted waterbird species prevents distribution changes in response to climate warming. Animal Conservation, In press, $10.1111/{\rm acv.12872}$. hal-04255558

HAL Id: hal-04255558 https://hal.science/hal-04255558v1

Submitted on 24 Oct 2023 $\,$

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- 1 Habitat management favouring hunted waterbird species prevents distribution
- 2 changes in response to climate warming
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33 Abstract

34 Climate warming is driving species to shift their geographic distribution poleward to track suitable 35 climatic conditions. Two strategies have been suggested to help species respond to climate warming: 36 facilitating distribution change or improving persistence. We questioned whether habitat 37 management in favour of duck hunting activities interacted with duck responses to climate warming. 38 We studied non-breeding waterbird community changes (110 species) over 28 years at 851 sites in 39 South-West Europe, where habitat management is a common practice to attract and hunt ducks. We 40 hypothesized that duck species targeted by habitat management do not need to track temperature 41 changes as much as non-hunted species, because of the availability of suitable habitats provided by 42 hunting land managers. We used the Community Temperature Index (CTI) to assess the temporal 43 responses of communities and species to climate warming. We compared the effect of hunting status 44 to other functional traits on species responses, controlling for phylogenetic relatedness. The CTI trend 45 has increased over the study period, indicating a community adjustment to climate warming. However, 46 hunted ducks contributed to almost 40% of the negative contributions to this community adjustment, 47 suggesting that hunted ducks do not shift their distribution as much as the other waterbirds do. Winter 48 fidelity associated with the provision of attractive feeding grounds might explain why ducks did not 49 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 long-50 51 term consequences on duck populations.

52 Keywords: climate change, duck, Community Temperature Index, Mediterranean, persistence,53 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,

59 temperature changes are not only rapid, but also likely to last over time.

60 Species responses to climate warming are diverse but their intensity is largely insufficient (Radchuk et 61 al. 2019, Lenoir et al. 2020). Species may respond to climate warming through changes in migration 62 distance, geographic shift, phenology, plasticity, or microevolution (Jiguet et al. 2007, Moller et al. 63 2010, Dawson et al. 2011, Elmberg et al. 2014). The most commonly observed and documented 64 response is geographical distribution change, leading to changes in community composition in 65 response to temperature changes at the local scale (Devictor et al. 2012). For instance, temperature 66 increases might cause local population increases at the cold edge of species distributions, and 67 decreases in population sizes at the warm distribution edge (Parmesan & Yohe 2003, Thomas et al. 68 2006, Pavón-Jordan et al. 2015). Species can also persist locally, either by finding micro-refuges (e.g. 69 at higher altitude, Massimino et al. 2020) or by tolerating changes through phenotypic or genetic 70 adaptation (plasticity, micro-evolution) (Charmantier et al. 2008, Karell et al. 2011). Functional traits 71 play an important role to shape species responses to climate warming (Brommer 2008). Species 72 sharing the same characteristics, like climatic niche, body mass, migration strategies, might be more 73 likely to respond in a similar way (Jiguet et al. 2007) while facing the same vulnerabilities to 74 temperature increase (Aubin et al. 2016). Species responses to climate warming may also be 75 modulated by local environmental factors, like habitat quality (Dawson et al. 2011, Lenoir et al. 2020) 76 and conservation efforts (Gaget et al. 2022).

77 Helping species respond to climate warming is mainly considered under two complementary climate 78 adaptation strategies: facilitation and persistence (Bonebrake et al. 2018, Prober et al. 2019, Pearce-79 Higgins et al. 2022). Facilitation focuses on helping species shifting their geographical distribution and 80 settle in new areas in response to global warming (e.g. Maclean & Rehfisch 2008, Guillemain & Hearn 81 2017). It aims at adjusting the rate of species distribution change to the thermal isocline shift. For 82 example, increasing connectivity between protected habitats facilitates colonization processes in 83 response to climate warming (McGuire et al. 2016). Conversely, persistence aims at maintaining 84 species in an environment despite temperature changes. It may indirectly be based on the intrinsic 85 abilities of species to tolerate the changes (e.g. plasticity) or involve management measures to provide 86 additional resources or create microrefugia benefiting a targeted species. For example, food supply 87 may decrease the local extinction risk of species vulnerable to climate warming (Correira et al. 2015). 88 Both facilitation and persistence strategies are likely to influence the response of species to climate 89 warming (Bonebrake et al. 2018, Prober et al. 2019).

90 Empirical evidence of long-term species response to climate change has rarely been demonstrated 91 under the persistence strategy (Correira et al. 2015, Pearce-Higgins et al. 2019). Indeed, as 92 anthropogenic climate change is a relatively recent biodiversity pressure, conservation measures have 93 not primarily aimed at improving long-term species persistence in response to temperature increase 94 specifically. In contrast, efforts have historically aimed at improving species conservation, with 95 consequences on their distribution regarding temperature change. For example, the creation of 96 protected areas to preserve migratory waterbirds during cold spells in Western Europe (Ogilvie 1983, 97 Guillemain et al. 2002) are also buffering the negative impact of temperature increase on some cold-98 dwelling waterbirds (Gaget et al. 2021). Similarly, the provision of supplementary foods in British 99 gardens changed the migration behaviour of the Eurasian blackcap (*Sylvia atricapilla*), of which many 100 individuals are no longer migrating South (Plummer et al. 2015). Such anthropogenic influences can be

101 examined a posteriori in the light of climate warming (Pearce-Higgins et al. 2022).

102 Here, we question the effect of habitat management for hunting purposes on waterfowl responses to 103 climate warming at international scale in South-West Europe. Duck hunting is a popular practice in this 104 region yielding 2.4 million harvested ducks annually (EEA 2020). Indeed, habitat management for 105 hunting purposes is a local, but widespread practice (FACE 2019), aiming at attracting targeted 106 waterfowl species to hunting grounds during the non-breeding period. Pro-active habitat management 107 actions for hunting purposes include the creation of man-made ponds, spreading of seeds as bait, 108 artificial flooding, vegetation clearing including the creation of openings in reedbeds, and other actions 109 (e.g. Mathevet & Guillemain 2016, Vallecillo et al. 2019). Economic incentive for such intensive 110 management actions is that sites with high abundance of ducks can yield high income by renting out 111 hunting rights (e.g. Niang et al. 2016). Specific habitat management targeted to boost abundance of 112 hunted species is often carried out in large private properties, e.g. in the Camargue, Southern France 113 (Tamisier & Grillas 1994) and provide prestigious social status and reputation of the land-owner, e.g. 114 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 115 116 characteristics with hunted ducks, such as granivorous and herbivorous species (Tamisier and Dehorter 117 1999, Mouronval et al. 2014). In particular, such habitat management are not expected to provide 118 benefits to invertebrate or fish eating species (e.g. shorebirds, herons) (Toureng et al. 2000). Gaget et 119 al. (2018) showed that in the south-western European Union Member States, waterbird responses to 120 climate warming were correlated with their protection status. Hunted species had a lower response to 121 climate warming through distribution change than the other species. Here, we further explore the 122 reason for this interaction between hunting status and climate warming, by investigating the possible 123 role of habitat management practices on hunted ducks.

124 We studied community reshufflings from 110 non-breeding waterbird species in south-western Europe 125 over 28 years on 851 sites. Many of these waterbirds breed at northern latitudes and overwinter in 126 wetlands in this region. Our main interest was to explore whether the distributional changes of duck 127 species, which are actively targeted by hunting in this region, differ from those of other hunted and 128 non-hunted waterbird species, while controlling for functional traits that differ between these species. 129 To infer distribution changes we used the Community Temperature Index (CTI) framework, a 130 community weighted mean index used to measure the average temperature affinity of all the species 131 of a community, based on individual species temperature index (STI) (Devictor et al. 2012). We 132 assessed temporal changes of CTI over years for the non-breeding waterbird community using 133 abundance time series collected at site level through the International Waterbird Census (Delany 2010) 134 and STI calculated as the mean winter temperature values across the non-breeding distribution of the 135 species (Gaget et al. 2021). Under a climate warming scenario, we expected the avian community at 136 a given site to change over time towards species with a higher thermal affinity. Thus, the CTI was 137 expected to increase over time. Such community reshuffling has already been documented for non-138 breeding waterbirds in the western Palearctic (Gaget et al. 2021) and in numerous other studies 139 (Devictor et al. 2012, Auffret and Thomas 2019, Fourcade et al. 2019). We then assessed the species' 140 contributions to this temporal increase in CTI. Our main interest was whether this contribution 141 depends on the species' hunting status (hunted ducks, other hunted species and non-hunted species), 142 while accounting for functional traits (species thermal affinity, body mass, generation length, diet and 143 migration strategy) and phylogeny (Jiguet et al. 2007, Brommer 2008) to control for potential 144 confounding effects. Because of the intensive management practices in the study region (Tamisier & 145 Grillas 1994, Pernollet et al. 2015a, Zenatello et al. 2021), we expected that hunted ducks would be 146 slower to adjust their distribution to climate warming compared to non-hunted waterbirds, because 147 management of hunting areas may provoke a greater site fidelity. We thus expected that hunting 148 status shapes a species' response to climate warming.

149

150 Methods

We studied non-breeding waterbird abundance time series collected from 1993 to 2020 at 851 sites in 151 152 Portugal, Spain, France and Italy. The data were collected for the International Waterbird Census 153 coordinated by Wetlands International (Delany 2010), resulting in one survey per year performed by 154 skilled ornithologists in mid-January on hundreds of wetlands. We filtered the original dataset (n = 155 3,288 sites) to ensure the quality of the data. To do so, we restricted the list of waterbird species to 156 the list of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (www.unep-157 aewa.org), we removed count events with less than two species to allow estimation of species 158 contributions to CTI trend (see below) and we removed species with less than 100 individuals observed 159 among all sites included in the study. Because of the particular focus on ducks, we removed sites 160 without any hunted duck observation. We retained sites with at least five surveys and one survey per 161 decade (1990s, 2000s and 2010s), resulting in a subset of 851 sites with 20.5±6.2 surveys on average 162 (±SD) (see map Appendix 1). Considering taxonomic changes that occurred during the study period, 163 Larus michahellis, L. cachinnans and L. argentatus were lumped into one 'species' L. michahellis. This 164 lumping has a negligible impact on most of the study area where L. michahellis is largely dominant over 165 the two other species, with the exception of the French Atlantic coast. The dataset used for the 166 analyses resulted in 17,462 surveys of 851 sites over 28 years, with a cumulative record of 119 million 167 birds from 110 species (Appendix 2).

168 We considered three hunting status categories between species: eleven duck species mainly targeted 169 by habitat management, 25 other hunted waterbirds and 75 non-hunted species (Appendix 2). Hunted 170 ducks are Northern Pintail (Anas acuta), Common Teal (A. crecca), Mallard (A. platyrhynchos), Eurasian 171 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) 172 173 and Red-crested Pochard (Netta rufina). These species are all listed in Annex II of the Birds Directive, 174 meaning that they can be hunted according to the regulation of the European Union or Member States 175 (Red-crested Pochard is hunted in France and Spain only, and Greater Scaup is hunted in France only). 176 The other hunted species are listed in Annex II of the Birds Directive and hunted at least in one Member 177 State of the study area, and include species such as Greylag Goose (Anser anser), Coot (Fulica atra), Lapwing (Vanellus vanellus) and Eurasian Curlew (Numenius arguata). The non-hunted species are not 178 179 listed in Annex II, or listed in Annex II but not hunted in the study area, including species such as Mute 180 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*).

183 We document species functional traits and phylogenetic proximities to control for potential 184 confounding effects (Appendix 2). Functional traits were species thermal affinity, body mass, 185 generation length, diet and migration strategy. These functional traits are expected to influence bird 186 response to climate warming (Jiguet et al. 2007, Brommer 2008). Species thermal affinity was defined 187 as the Species Temperature Index (STI), calculated as the average temperature in January (1950-2000, 188 www.worldclim.org, spatial resolution of 0.25°) on the non-breeding species distribution (BirdLife 189 International & HBW 2018) from Gaget et al. (2018). Body mass (continuous, log transformation) and 190 diet (Plant, Omnivore, Invertebrate, Vertebrate) were extracted from Wilman et al. (2014) (where 191 omnivore corresponds to a combination of less than 50% of all other categories), generation length 192 (continuous) from IUCN (2021) and migration strategy (resident, short, long) from Storchová et al. 193 (2018). Migration strategies were represented in similar proportions between hunting status 194 categories, with most of hunted ducks being short to long-distance migrants (Storchová et al. 2018; 195 Appendix 2). To control for species phylogeny, we used phylogeny trees from BirdTree 196 (https://birdtree.org).

197 We used temperature anomalies to assess changes in winter temperatures on the survey sites over 198 the study period. We collected average monthly temperatures gridded at 0.5° resolution, from the 199 Climatic Research Unit v4.05 (Harris et al. 2020). Winter temperatures anomalies were computed each 200 winter at site level as the average of the mean monthly temperatures for the 3-month period of 201 November, December and January, i.e. the duration expected to impact waterbird distribution at 202 winter time (Gaget et al. 2020), minus the average monthly temperatures from November to January 203 for the 1993-2020 period.

204

205 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.

224 To assess the contribution of each species to CTI trends, we ran a jackknife analysis by removing each 225 species in turn from the CTI before running LMMs on partial CTIs. Hence, species contribution to the 226 CTI temporal trends was assessed as the difference between the original temporal trend (all species 227 included) and the temporal trend of the model based on the partial CTI (all but one species). Species 228 contributions were then reported as a percentage of influence, positive or negative, on the CTI trends 229 (Gaget et al. 2018). Note that species contributions are relative values, comparing species to the whole 230 community. A negative contribution to a positive CTI trend means that a species is contributing 231 relatively less than the other species to the community adjustment to climate warming.

232 Finally, we used phylogenetic generalized least squares (PGLS) models to assess differences between 233 species contribution to CTI changes. We compared species contributions between hunting statuses 234 and functional traits (species thermal affinity, body mass, generation length, diet and migration 235 strategy), considering species phylogeny. We used a forward model selection approach to select the 236 most parsimonious model with predictors explaining the most species contributions, i.e. selecting 237 models with the lowest AIC among a delta AIC <2 (Burnham and Anderson 2002). Phylogeny is a 238 potential factor structuring adaptive bird response to climate change (Hällfors et al. 2020). Hunted 239 ducks are from the same Anatidae family and often share the same genus. Their intrinsic sensitivity to 240 climate warming and adaptive capacities are likely closer among each other than with species from 241 other taxonomic clades. Consequently, contrasting species groups exposes the analytical framework 242 to a potential confounding effect. To avoid this bias, we accounted for phylogenetic relatedness by 243 adding the phylogeny tree as a Brownian correlation structure in the models. In addition, we assessed 244 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).

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253 Results

The Community Temperature Index (CTI) showed a very clear linear increase over years ($\beta = 0.045 \pm 0.001$ 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 ($\beta = 0.023 \pm 0.001$ 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 ($\beta_{Plant} = -2.61 \pm 1.19$ (±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], $\beta_{Omnivore} = 1.06 \pm 1.19$

 $[0.86;1.26]; \beta_{Hunted ducks} = -3.62 \pm 1.24 [-5.09;-2.15], \beta_{Other hunted} = 0.57 \pm 1.19 [-2.20;1.57], \beta_{Non-hunted} = 0.82$ 261 ± 1.19 [0.15;0.89]), whereas other predictors had little effect (Table 1, Appendix 4). Multicollinearity 262 263 between species diet and hunting status was low (VIF = 1.05). Most of the variance explained by the 264 model was related to species diet (82%), with plant eating species contributing predominantly 265 negatively to the CTI change (Fig. 2). Indeed, 83% of the plant-eating species had negative 266 contributions, compared to 48%, 44% and 64% for species eating invertebrates, vertebrates and being 267 omnivores, respectively (omnivores potentially comprising some plant-eating diet). Hunting status also 268 strongly affected species contributions to CTI change (Table 1, Fig. 2). Most (73%) of hunted duck 269 species contributions were negative (summing to –39.8%). Only Mallard, Greater Scaup and Garganey, 270 among 11 hunted duck species, made positive contributions to CTI change (summing to +15.5%), 271 although the Mallard accounted for almost all positive contribution (+14.9%; Fig. 2). Among the other 272 hunted and non-hunted species, 63% and 52% of the species contributed negatively, respectively.

- 273 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
- 275 hunting status to explain species contributions to CTI change (Appendix 3).
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- 277





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).

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Figure 2: 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.

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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

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302

303 Discussion

304 Over the study period (1993-2020), the observed CTI increase demonstrates that non-breeding 305 waterbird communities have changed, with warm-dwelling species becoming relatively more 306 abundant than cold-dwelling species in the region. This community change was expected because of 307 the temperature increase in the study area, suggesting that non-breeding waterbird communities are 308 reshuffling in response to climate warming. This finding is fully consistent with other studies on non-309 breeding waterbirds (Godet et al. 2011, Pavón-Jordán et al. 2017, Gaget et al. 2018, Gaget et al. 2021), 310 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 311 312 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 313 314 et al. 2006, Gaget et al. 2021).

315 While the community on average has responded to climate change, individual species responses 316 varied. Some species distribution strongly tracked climate warming, and such species had, in the CTI 317 framework used in this study, positive contributions to the CTI trend. Examples include Common 318 Sandpiper (Actitis hypoleucos), Goldeneye (Bucephala clangula) and White stork (Ciconia ciconia). 319 However, other species barely adjusted their distribution to climate warming and these species had 320 negative contributions to the CTI trend. We here showed that most ducks targeted by habitat 321 management for hunting purposes (except Mallard, and to a lesser extent Garganey and Greater 322 Scaup) had negative contributions to the CTI trend. This finding therefore suggested that habitat 323 management may influence species response to climate warming. We believe there are two non-324 mutually exclusive explanations for this finding.

325 Firstly, managing sites to benefit hunted species may have lowered the propensity of these species to 326 adjust their distribution to climate warming. Indeed, intensification of habitat management for hunting 327 purposes has been suggested as one of the reasons for contemporary changes in duck diet, body 328 condition and migration phenology (Mathevet & Tamisier 2002; Guillemain et al. 2015). Various 329 habitat management actions are commonly used to attract wintering ducks (e.g. Mathevet & 330 Guillemain 2016, Vallecillo et al. 2019). One potentially important management action is food 331 supplementation, where seeds (wheat, corn or rice) are provided as bait, a common practice in South-332 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 333 334 past decades from natural habitats to artificially managed freshwater marshes (Brochet et al. 2012). 335 Over the same period, Teal body mass has increased by more than 10% at their major Camargue 336 wintering site in southern France (Guillemain et al. 2010), and arrival date at this wintering ground has 337 advanced (Guillemain et al. 2015). Intensive water level management is another management practice 338 likely influencing duck distribution change or local persistence in response to climate warning. 339 Wetlands are flooded in summer, including temporary ponds that otherwise would be dry. The aim of 340 this summer flooding is to maximize plant biomass growth in these ponds to coincide with the arrival 341 of ducks from their breeding grounds in autumn (Tamisier & Grillas 1994, Davis et al. 2014). 342 Supplementation of freshwater in brackish habitats (e.g., coastal lagoons), aims also to increase habitat 343 diversity hence attracting freshwater duck species. All such management actions improve habitat 344 quality and attractiveness to ducks, resulting in large alterations of duck distribution in the last 345 decades, which now concentrate in areas of intensive habitat management for hunting purposes 346 (Zenatello et al. 2014, 2021). Habitat management for hunting purposes may hence have counter-347 balanced the effect of climate warming and "retain" hunting ducks to these wintering grounds, which 348 they would otherwise abandon for more northern areas.

349 Secondly, hunted ducks may have been slower to adjust their distribution to climate change because 350 agricultural practices were particularly beneficial for these species. In particular, rice fields are flooded 351 and used as foraging grounds by ducks during the non-breeding season, with ducks feeding on non-352 harvested rice and weed seeds (Pernollet et al. 2015a). Other waterbird species use rice fields for 353 feeding to a lesser extent, except for species than can specialize on rice, such as the Greater Flamingo 354 (Phoenicopterus roseus) during the seeding period in spring (Pernollet et al. 2015a). In Portugal, Spain, 355 France and Italy, some wetlands hosting a large number of ducks are close to large rice producing 356 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 357 358 farming practices and management of sites to promote hunting are not mutually exclusive, since 359 harvested ricefields can also be flooded for hunting purposes (Niang et al. 2016, Pernollet 2016). 360 Indeed, in addition to agronomic benefits, this practice provides suitable wintering grounds for ducks 361 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, Gourlay369 Larour et al. 2012) and may hence be affected by large scale management driven by regional factors 370 in addition to site-specific management, such as land-use policy or socio-cultural practices. The fact 371 that ducks commute daily between a day-roost (generally protected sites where they can rest and 372 where they are surveyed) and surrounding nocturnal feeding areas (functional units sensu Tamisier & 373 Tamisier 1981) further inflates uncertainty in how these species are affected by habitat management 374 in a given area (Vallecillo 2021). An experimental design contrasting the effect of site management on 375 duck carrying capacity would be challenging because of the mismatch between diurnal bird monitoring 376 and nocturnal feeding behaviour (Brochet et al. 2009).

377 Responses to climate warming differ between species for many reasons, including, among others, 378 species movement ability or adaptive capacities, (Dawson et al. 2011). Our best model only explained 379 5.8% of the differences between species contributions, suggesting that an important part of the 380 variation was not captured by the tested functional traits. This might have been expected because 381 waterbirds share more ecological characteristics than we could get by analyzing a more 382 phylogenetically diverse bird community (e.g. Jiguet et al. 2007, Brommer 2008). Consequently, 383 accurate traits might be neglected, e.g. at population-level across species flyways, but needed to 384 reflect local adaptations to environmental parameters, including climate warming (DeMarche et al. 385 2019).

386 Waterbird diet was an important predictor of species contribution to CTI trend, but other functional 387 traits were not. Plant eating species mainly contributed negatively to the community changes. One 388 likely reason might be that species sharing similar feeding ecology to hunted ducks, mostly plant 389 eaters, were also affected by habitat management, like coots and swans (Brochet et al. 2009). Thus, 390 habitat management for hunting purposes may also benefit plant eaters in general, to some extent. 391 Generation length actually explained a fair amount of variation, but was not selected according to 392 parsimony. It may therefore be an additional factor explaining why some species have a delayed 393 distribution change (Maclean et al. 2008). Indeed, juvenile settlement can influence over-winter 394 location when mature, meaning that long-lived species might need more time to shift their distribution 395 than short-lived species (Godet et al. 2011).

396 Mallards did not follow the same pattern as the other hunted ducks. We found that their distribution 397 was tracking climate warming. Indeed, this species has started to shorten its migration distance 398 decades ago along its European flyway, likely in response to temperature increases (Sauter et al. 2010; 399 Gunnarsson et al. 2012, Guillemain et al. 2015). Previous work highlighted that the Mallard clearly 400 responds to winter temperatures, both in North America (Schummer et al. 2010) and in Europe (Dalby 401 et al. 2013). Its metabolism and opportunistic feeding strategy may explain these findings (Schummer 402 et al. 2010): its larger size and weight allow Mallard to endure negative temperatures more easily than 403 smaller species, disadvantaged by their greater surface area to volume ratio. It is also a relative habitat 404 generalist species exploiting numerous wetland habitats, small, even degraded or urban and can switch 405 from water to terrestrial feeding while the other duck species are more wetland dependent. 406 Accordingly, Mallard are likely to winter closer to their temperature limits than other duck species, 407 resulting in a different trade-off between saving energy from migration and thermal regulation, and 408 likely a quicker response to climate warming by a distribution change. It cannot be excluded, however, 409 that the fact that millions of mallards are released annually in Europe (Champagnon et al. 2013) also 410 blurs the relationship between environmental conditions and the geographic distribution of this 411 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.

417

418 Perspectives

419 The economic incentive provided by hunting is expected to drive landowners to manage habitat to 420 locally boost hunted species abundance. This kind of habitat improvements could locally release 421 hunted species from some of the adverse effects of climate change, but also impede current or future 422 distributional changes. Consistent with this prediction, and based on community changes in 110 423 waterbird species over a large region (south-west Europe), we demonstrated here that hunted ducks 424 are indeed slower in their response to climate warming compared to other waterbirds. Although our 425 analysis did not directly infer that site management for hunting purposes drives this outcome, we 426 suggest the pattern we found may be general. Because hunting is a global phenomenon, more studies 427 exploring the interactions between site management and climate change as drivers of altered 428 distributional changes are needed to understand whether hunted ducks are more persistent against 429 climate change because of habitat management, or trapped there despite the ongoing climate 430 warming. While hunted ducks may in the short-term benefit from such artificial land management, this 431 may already have negative consequences for other elements of biodiversity (Tamisier & Grillas 1994), 432 and may be detrimental for the ducks themselves in the longer run.

433

434 In addition to the potential effect of habitat management on waterbird responses to climate warming, 435 harvesting can also have a direct impact on population dynamics through removal of individuals (Cooch 436 et al. 2014). Among studied populations of non-breeding hunted ducks, several were stable or 437 increasing over both short and long terms, such as Northern Pintail, Common Teal, Gadwall and Red-438 crested Pochard, while for others the trends were declining at least in one studied country, such as in 439 Mallard, Eurasian Wigeon, Common Pochard and Tufted Duck (EEA 2020). Sustainable management of 440 duck populations is required to maintain these species at a favorable conservation status. 441 Management planning needs international collaborations at species distribution level, using hunting 442 data and demographic parameters (Holopainen et al. 2018). Whether the distribution of harvested 443 populations is changing or not in response to climate warming should be carefully considered, to 444 anticipate ecologic, cultural and economic challenges (Guillemain et al. 2013).

446 Acknowledgments

447 We are grateful to the thousands of volunteers and professionals involved in the International 448 Waterbird Census, making this research possible. We thank M. Sorrenti and J. I. Dies for sharing their

449 knowledge on hunting management in Italy and Spain. We thank the Turku Collegium for Science,

450 Medicine and Technology for funding and 2 anonymous reviewers for comments that improved earlier

- 451 drafts of the manuscript.
- 452

453 Author Contributions Statement

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

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683

685 Appendix 1. Map of the study area, with the 851 monitored sites.



688 Appendix 2. Species functional traits and hunting status. We considered three hunting status 689 categories between species: eleven duck species listed in Annex II of the Birds Directive, the 690 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 691 692 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 693 (BirdLife International & HBW 2018) from Gaget et al. (2018). Body mass (continuous, log 694 695 transformation) and diet (Plant, Omnivore, Invertebrate, Vertebrate) were extracted from 696 Wilman et al. (2014), generation length (continuous, in years) from IUCN (2021) and migration 697 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

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

- 700 Appendix 3. Sensitivity analysis.
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702 1) Protected areas

704 We performed a sensitivity analysis to ensure that the results from the main text were not affected by 705 site protection status. Indeed, protected areas can affect wintering waterbird response to climate 706 warming, by increasing species persistence (Gaget al. 2021). The risk is then to observe the effect of 707 site protection on wintering waterbird community change rather than the potential effect of hunting 708 management. It is important however to note that hunting activities can occur inside protected areas. 709 This means that we cannot dissociate the effect of the protected area and the potential effect of 710 hunting management inside protected areas. To ensure that our results were not affected by protected 711 areas, we removed all protected sites from this sensitivity analysis. Protected sites were identified 712 following the methodology described in Gaget et al. (2021). We performed the same analyses, without 713 protected sites, as in the main text. We investigated temporal change in Community Temperature 714 Index (CTI), species contributions and assessed the differences of contribution between species, 715 depending on hunting status and functional traits.

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717 We identified 411 monitored sites outside a protected area, totalling 8,229 surveys. The CTI temporal 718 trend was positive and significant ($\beta = 0.042 \pm 0.002$ SE, p < 0.001). Species contributions to the CTI 719 trends were fairly similar to the full analysis (Fig. A3.1). Species diet, hunting status and generation 720 length were the main factors explaining species contribution, whereas other predictors had little effect 721 (Table A3.1). Multicollinearity was low between species diet and hunting status (VIF = 1.09) and 722 between species diet and generation length (VIF = 1.14). Consequently, this sensitivity analysis 723 confirmed that species diet and hunting status are important factors explaining species contribution 724 to CTI trend independently from site protection. In addition, generation length significantly 725 contributed to explain species contributions in this subset of sites. Generation length can indeed be an 726 important factor together with site fidelity, because juvenile settlement can influence over-winter 727 location at adult stage, meaning that long-lived species might need more time to shift their distribution 728 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.

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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

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751 2) Sites with more than 25 surveys over 28 years

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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.

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We identified 288 monitored sites outside a protected area, totalling 7,703 surveys. The CTI temporal trend was positive and significant ($\beta = 0.053 \pm 0.002$ 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.





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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.

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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.

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	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

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

- 787 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
- 789 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