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Source: Ardea, 109(2) : 1-23

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v109i3.a4

Long-term changes in the wintering population of the Dalmatian Pelican along the Black Sea-Mediterranean Flyway

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Barboutis C., Kassara C., Alexandrou O. & Catsadorakis G. 2021. Long-term changes in the wintering population of the Dalmatian Pelican along the Black Sea-Mediterranean Flyway. Ardea 109: ###–###. doi:10.5253/arde.v109i3.a4

Understanding spatiotemporal dynamics in wildlife populations is of paramount importance for their effective conservation, however longitudinal studies are relatively scarce for most animal groups. Waterbirds are an exception however, since midwinter surveys have been implemented in most areas of the world for over four decades. The Dalmatian Pelican *Pelecanus crispus* is a globally threatened emblematic wetland species of the Palearctic, with a wide distribution in Europe and Asia. Its global population is divided into three distinct groups that coincide with the Black Sea-Mediterranean Flyway, the Central Asian Flyway and the East Asian Flyway. In this study we used International Waterfowl Census data to assess long-term changes in the wintering population of the Dalmatian Pelican pertaining to the Black Sea-Mediterranean Flyway. We report national and regional population trends in SE Europe and Turkey and explore spatiotemporal patterns in the wintering numbers and distribution of the species in relation to climate variability during the last two decades. Our key findings suggest that during the past 30 years the abundance of wintering Pelicans increased across the entire study area. Within the eastern subpopulation this increase was most accentuated in the northern edge of the species' wintering distribution, which was associated with a local warming trend, and was coupled with a north-eastern shift in the distribution pattern, yet not driven by climate conditions. Other contributing factors, such as winter site fidelity, local food availability, finer scale climatic and habitat conditions, but also carry-over effects should be considered in future studies. Given the advancement of first laying dates in Dalmatian Pelicans in almost all breeding sites and the strict timing of IWC counts, we also propose the implementation of species-specific winter surveys, independently from IWC, to obtain a more thorough understanding of the dynamics of the Dalmatian Pelican's wintering population.

Key words: Dalmatian Pelican, SE Europe, Turkey, wintering, climate, midwinter surveys, time-series data

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The most revealing indirect evidence for understanding how movements and seasonal distribution patterns of animals respond to climatic seasonality comes from distribution studies over large areas and long-time periods. However, a huge effort is required to systematically collect field data, often across large geographic areas, in order to obtain reliable estimates of population trends and distribution shifts at the species' level. Consequently, longitudinal studies are lacking for most animal groups. Waterbirds however are an exception; for example, the most recent assessment of the status and trends of world's waterbird populations contained population estimates and trends for over 870 species (Wetlands International 2020), based on data collected during midwinter surveys (hereafter, IWC data) coordinated by Wetlands International.

Waterbirds, being ecologically dependent on wetlands and aquatic ecosystems, are considered important bio-indicators of environmental quality (Amat & Green 2010, Papadimitriou *et al.* 2017, Amano *et al.* 2018, Rahman & Ismail 2018) and provide a variety of ecosystem services to their environment (Green & Elmberg 2014). However, at the same time they are heavily impacted by natural and human-induced habitat deterioration and degradation (e.g. Zhang *et al.* 2019), as well as persecution, exhibiting widespread population declines (BirdLife International 2017). Over the years IWC data-based studies have contributed to waterbird conservation both at the national (e.g. Musil *et al.* 2011) and international level (e.g. Fox *et al.* 2010). For instance, recent studies have investigated the effectiveness of protected areas (e.g. Fouque *et al.* 2009, Pavón-Jordán *et al.* 2015) and the effect of environmental variability (e.g. Musilová *et al.* 2009, Nilsson 2014, Ramo *et al.* 2015), as well as contributing to the identification of important wetlands for waterbirds (e.g. Musilová *et al.* 2015).

Among the candidate drivers of population and distribution changes in wintering waterbirds of the Palearctic, climate variability, namely temperature, is most often documented in literature (e.g. Lehikoinen *et al.* 2013, Musilová *et al.* 2015, Pavón-Jordán *et al.* 2019). Waterbirds respond rapidly to harsh weather conditions in winter as low temperatures may directly affect survival (Schwemmer *et al.* 2014) and/or lead to population and range shifts (Maclean *et al.* 2008, Musilová *et al.* 2015). Changes in climate and their subsequent impact on wintering populations are not necessarily uniform across a species' distribution (Ramo *et al.* 2015). This fact renders the exploration of spatiotemporal patterns in different scales a crucial component in the study of long-term changes in waterbird populations.

The Dalmatian Pelican *Pelecanus crispus* is an emblematic wetland species of the Palearctic, with a wide distribution extending from Montenegro and Albania in the west to China in the east, and from Russia in the north to India in the south (Crivelli & Vizi 1981, BirdLife International 2020). The most recent estimation of its global population refers to roughly 22,000–27,000 mature individuals, with the largest breeding populations occurring in Kazakhstan, Russia and Greece (Catsadorakis & Portolou 2018). The species' global population is divided into three distinct groups that coincide with the Black Sea-Mediterranean Flyway, the Central Asian Flyway, and the East Asian Flyway (Catsadorakis & Portolou 2018). Long-distance migrants breeding in Russia, Kazakhstan and Mongolia overwinter in south Asia and East China, respectively. The Black Sea-Mediterranean Flyway population group consists of short-distance migrants overwintering in SE Europe and Turkey (Crivelli *et al.* 1991a, Catsadorakis & Portolou 2018). The conservation status of the Dalmatian Pelican has been improved in recent years, being downlisted in 2017 from 'Vulnerable' to 'Near Threatened' (BirdLife International 2018); however, ongoing threats such as drainage and degradation of wetlands, persecution, lack of law enforcement and high water level fluctuations (Catsadorakis & Portolou 2018) may still lead to substantial population decline and even local extinctions in the near future (BirdLife International 2020), while climatic effects have not been investigated to date.

In this study we used the IWC data to assess for the first-time long-term changes in the wintering population of the Dalmatian Pelican pertaining to the Black Sea-Mediterranean Flyway. We report national and regional population trends in SE Europe and Turkey

A group of immature (foreground) and adult (further back) Dalmatian Pelicans standing on the rarely forming ice cover of Lake Kerkini, Greece, in January 2017 (photo David Howse).

Figure 1. The location of the wetlands surveyed during midwinter counts from 1964 until 2017 in six countries along the Black Sea-Mediterranean Flyway. A dashed line indicates the approximate location of the Pindus mountain range that divides wintering birds into eastern (dots) and western (triangles) populations. The location of the two largest breeding colonies in the study area, namely Lake Mikri Prespa and Amvrakikos Gulf, is also indicated.

over the past 30 years and explore spatiotemporal patterns in the wintering numbers and distribution of the species in relation to climate variability during the last two decades. Despite the difficulty in distinguishing between wintering and passing birds, the inter-annual variability in the breeding phenology of those dispersive populations (Crivelli *et al.* 1997) and the methodological limitations of midwinter surveys, the IWC constitutes the only source of systematically collected data on the numbers of Dalmatian Pelicans occurring in SE Europe and Turkey in winter.

METHODS

Data preparation

We compiled all available IWC data of Dalmatian Pelicans along the Black Sea-Mediterranean Flyway. We first queried the Waterbird Population Estimates database (Wetlands International 2018) and then we carried out a data quality check based on published counts in literature (Crivelli *et al.* 1991a, Crivelli *et al.*1991b, Akarsu & Balkız 2010, Onmuş *et al.* 2011, Erciyas Yavuz & Kartal 2012, Erciyas Yavuz & İsfendiyaroğlu 2013) and personal communications (Portolou pers. comm.) to include only those countries with an adequate time-series of IWC data. Following this exercise, IWC data pertaining to six countries, namely Romania, Bulgaria, Albania, Montenegro, Greece and Turkey (Figure 1), comprised the initial datapool for subsequent analyses (Table 1). Ukraine was excluded as it included only 1 year of midwinter surveys.

Furthermore, even though the Dalmatian Pelican is a soaring-gliding bird that can easily undertake long flights (Efrat *et al.* 2019b) and pelicans are known to be able to cross large ecological barriers (Efrat *et al.* 2019a) and reach high altitudes (Shannon *et al.* 2002), the existing evidence (Crivelli pers. comm., Catsadorakis *et al.* 2015, Catsadorakis 2016 and references within) implies that the Pindus mountain range in western Greece constitutes a barrier separating two distinct subpopulations (Figure 1). The breeding colonies in the coastal wetlands along the Adriatic and Ionian coasts overwinter west and southwest of the Pindus mountain range. The eastern subpopulation, which consists of the remaining colonies in Greece, as well as of Bulgaria, Romania and Turkey, overwinter east of the same mountain range. A similar population divide is known for the American White Pelican *Pelecanus erythrorhynchos* (Anderson & Anderson 2005, Anderson & King 2005). We thus considered the existence of two subpopulations in the methods and results presented and discussed in this study, while emphasis was given to analysis of the eastern subpopulation that hosts the vast majority of both breeding and wintering individuals in our study system (Catsadorakis & Portolou 2018).

Data filtering

A total of 102,934 Dalmatian Pelicans were recorded in 201 wetlands from 1964 to 2017 in the six countries considered in this study, of which more than half were recorded in Greece (Table 1). In our study area, the species was first recorded in 1964 in Greece (in both western and eastern wetlands) and in Turkey in 1967, the same years the midwinter surveys began in each country; thus, we are uncertain about the year of first appearance of the species in wetlands of Greece and Turkey during the wintering period. The same applies for Albania and Montenegro where the surveys began relatively recently (1991 and 1993, respectively). However, in Bulgaria and Romania the surveys were already being implemented since 1966 and 1969, but the species was first recorded in 1977 and 1999, respectively.

We restricted our analyses to time periods of systematic data collection and/or of systematic presence of Dalmatian Pelicans in each country. In particular, due to the fact that in early years, i.e. from the mid '60s until the mid '80s, midwinter surveys were either scarce in Bulgaria and Romania or not regular in Turkey and Greece, we hereafter analysed midwinter count data from the mid '80s onwards for these four countries. In addition, in the case of Albania midwinter count data were available from 1993 onwards (Table 1, Figure 2). Furthermore, years where the available data were incomplete (i.e. Greece: 2002, 2003; Bulgaria: 2004, 2017) were treated as non-surveyed years. Subsequently, for each country we excluded sites where the occurrence of Dalmatian Pelicans was considered sporadic rather than representative of the species' wintering distribution, namely sites where less than 10 individuals were recorded in total over the considered time period (Table 1).

Regional and national Trends in population size

We evaluated (1) between-year changes (hereafter, indices) in the abundance of wintering Dalmatian Pelicans in each country and each subpopulation considering the first year as base year and (2) the associated trends, via log-linear Poisson regression models that were developed in R v. 3.5.3 (R Core Team 2019) using the 'rtrim' package (Bogaart *et al.* 2018). The TRIM model has been designed for the estimation of species populations trends based on time series of monitoring data with missing counts and thus was considered the most appropriate model for the present study. Both serial correlation among annual counts and

Table 1. Summary of midwinter count data of Dalmatian Pelicans considered in this study.

Country/Subpopulation	Initial data pool			Filtered data pool		
	Number of sites	Time period (year of first record)	Total count	Number of sites	Time period (considered in trend analysis)	Total count
Bulgaria	41	1966–2016 (1977)	13,444	23	1985–2016	13,369
Greece	52	1964–2017 (1964)	58,001	43	1986–2017	49,802
eastern	38	1964–2017 (1964)	46,791	34	1986–2017	40,057
western	14	1964–2017 (1964)	11,210	9	1987–2017	9745
Romania	72	1969–2015 (1999)	2785	36	2003–2015	2643
Turkey	29	1967–2015 (1967)	25,106	18	1986–2015	22,461
Albania	5	1993–2017 (1993)	3097	3	1993–2017	3085
Montenegro	2	1991–2017 (1991)	501	2	1991–2017	501
eastern subpopulation	180	1964–2017 (1964)	88,126	111	2005–2015	78,530
western subpopulation	21	1964–2017 (1964)	14,808	14	1993–2017	13,331

overdispersion were considered in the modelling process. The significance of overall trend rates were assessed via Wald tests (Pannekoek *et al.* 2018). Due to the scarcity of count data for several years (Table 1), time-series models could not be estimated. Instead, linear trend models were implemented, considering all years as potential change-points, i.e. where the trend changed significantly (Pannekoek *et al.* 2018). Change-points were automatically detected using Wald tests by enabling the stepwise selection option with default values, except for Turkey where the algorithm could not converge. Imputed indices were chosen for trend estimation, since they represent a more realistic change over time, especially when linear trend models are considered.

Due to the fact that the numbers of wintering Dalmatian Pelicans were very low from 1988 until 2002 in Romania (range: 0–16, median: 0; Figure 2) resulting in large standard errors in the estimated overall slope assessing the population trend, the aforementioned analyses were run for the period 2003–2015.

Temperature effects on population and distribution of the eastern subpopulation

We first explored spatiotemporal trends in temperature during the period when midwinter surveys were carried out within the eastern subpopulation. i.e. 1985–2017. For each year, we calculated the mean temperature recorded across November, December and January (GHCN CAMS temperature dataset; www.esrl.noaa.gov/psd/data/gridded/data.ghcncams.htm) considering the geographical region delimited by the surveyed wetlands of each country, except for Greece where we considered the geographical region defined by the surveyed wetlands east to the Pindus mountain range. Tracking data have shown that these three months represent the core winter period of the species in the Balkans (Efrat *et al.* 2019). Winter period for Dalmatian Pelicans was originally defined by Crivelli (1987) to be the period 1 December – 15 February, but there has been a proven shift and shrinkage of winter conditions since that time to December and January (Doxa *et al.* 2012). Furthermore, Crivelli *et al.* (1991a) indicated that autumn (i.e. November in this case) weather conditions might play a crucial role in the choice of wintering area, that is why the inclusion of November temperatures was important in the analysis.

We evaluated temporal trends at the country and subpopulation level using linear regression models for the mean temperature as a function of year. We also investigated whether the observed trend was uniform in the area by calculating the Spearman r_s coefficient among the temperatures of the countries pertaining to the eastern subpopulation.

Taking into consideration the population trend analysis results and the resulting pattern in spatiotemporal changes in temperature, we explored the effect of the latter on the annual counts of wintering Dalmatian Pelicans. To this end, we developed autoregressive models at the country and subpopulation level considering the annual count (log-transformed values) as the response variable, i.e. the sum of counts at surveyed sites in each year, the mean temperature (scaled values) as the explanatory term and the annual count of the previous year (log-transformed values) as the autoregressive term. We also included the number of surveyed sites as weight in the models to account for differences in the sampling intensity among years. We replicated the aforementioned analysis to explore any population shifts along the north-south axis as a result of temperature conditions in the northern part of the wintering distribution. More specifically, we pooled the annual counts of Turkey and Greece and checked whether their variability could be explained by changes in mean temperature across Bulgaria and Romania.

We then investigated whether the observed trend in the annual count was associated with similar changes in the species' distribution. More specifically, we calculated the ratio of occupied wetlands to the number of surveyed wetlands (hereafter, annual distribution index) as a measure of the annual occupied area. We then computed the Spearman r_s coefficient between the annual count and the annual distribution index at the country and subpopulation level.

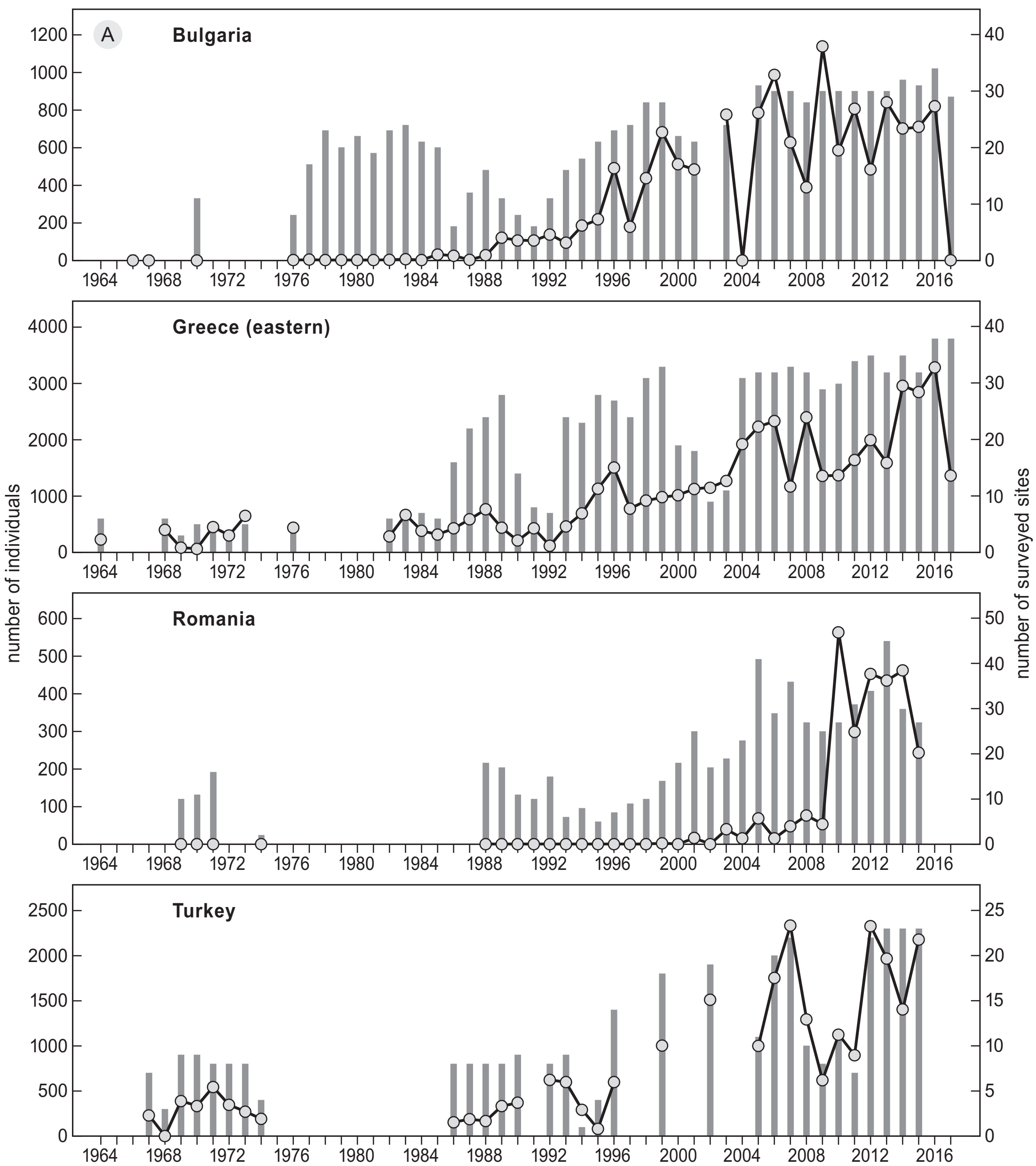
Finally, we explored the effect of temperature variability on the distribution pattern of the wintering Dalmatian Pelicans across the eastern subpopulation. To this end we estimated the minimum, maximum and weighted average of latitude and longitude based on the geographic coordinates of the wetlands where pelicans were present each year. The weighted average latitude and longitude was calculated considering the ratio between the annual count of pelicans at a given wetland and the maximum number of pelicans counted at all surveyed wetlands each year. We developed regression models for each of the aforementioned distribution estimates and considered year and mean temperature (scaled values in both cases) across the area as explanatory variables. As above, we included the number of surveyed sites as weight to account for differences in the sampling intensity among years.

In cases where data from multiple countries were pooled, only data from years where midwinter surveys were conducted in every country considered entered the corresponding analysis. All statistical analyses were performed in R v. 3.5.3 (R Core Team 2019), while the significance level was set at $\alpha = 0.05$.

RESULTS

The unfiltered data for the period 1964–1985 suggest that on average c. 539 ± 293 individuals (±SD, range: 189–1146) were overwintering annually in Greece and Turkey combined, whereas only 3 ± 8 individuals (range: 0–30) occurred in Bulgaria, despite the extensive coverage of surveys in the latter (Figure 2). Still, irregularity of surveys and limited number of surveyed wetlands did not allow any further analyses for that period.

For the purpose of this study, we analysed data from over 60% of the surveyed wetlands, where 91,861 Dalmatian Pelicans were counted from 1985 until 2017 (Table 1). For the period 2011–2015 where surveys were carried out across all the countries considered in this study, 5014 ± 894 (range: 3598–5954) wintering pelicans were counted annually on average in the eastern subpopulation, 829 ± 207 (range: 692–1186)



in the western subpopulation and 5843 ± 836 (range: 4431–6653) in total.

Regional and national population trends

Since the year 1985, when more systematic surveys began (apart from Romania where systematically collected data were lacking prior to 2003), annual counts at the national and subpopulation level seemed to increase despite interannual variability (Figure 2). The highest numbers in annual counts were recorded after 2007 in all countries considered, whereas the lowest numbers were recorded shortly after the systematic surveys started (Table S1). On the contrary, while the number of surveyed sites also increased over time, variability among years was substantial except for Bulgaria and eastern Greece after 2004 (Figure 2).

Based on the TRIM analysis results, the numbers of wintering Dalmatian Pelicans recorded annually in each country and subpopulation depended on the abundance of wintering pelicans of the previous year, as suggested by the high (in absolute numbers) serial autocorrelation (range: –0.442–0.637; Table 2). Strikingly, according to the TRIM model in the case of Romania and Montenegro more wintering pelicans are

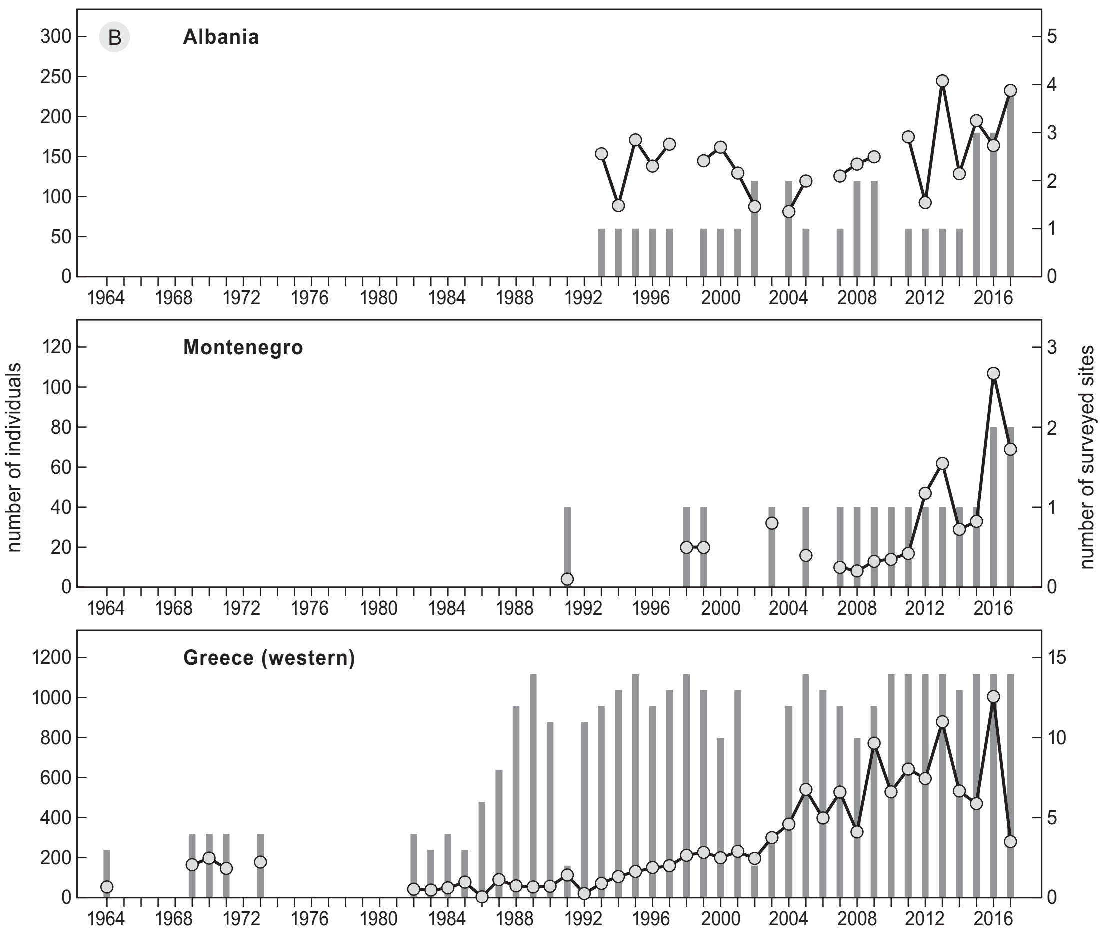


Figure 2. The total number of wintering Dalmatian Pelicans counted annually (grey circles connected with solid black line) and the corresponding number of surveyed sites (grey bars) in six countries along the Black Sea-Mediterranean flyway, presented separately for (A) the eastern and (B) western subpopulation.

Table 2. Results of regional and national trend analysis regarding the number of wintering Dalmatian Pelicans over the study period. Standard errors (SE) and *P*-values for the overall trend rate are also given.

Country/ Subpopulation	Period	Number of survey years	% missing counts	Overall trend (%)	SE	*P*	Trend classification	Serial correlation	Over-dispersion
Bulgaria	1985–2016	30	34.92	+10.9	0.011	<0.01	strong increase	–0.047	11.057
Greece	1986–2017	30	28.20	+5.7	0.007	<0.01	moderate increase	0.270	60.204
eastern	1986–2017	30	33.18	+4.7	0.008	<0.01	moderate increase	0.285	70.430
western	1987–2017	29	12.90	+9.7	0.005	<0.01	strong increase	0.157	3.706
Romania	2003–2015	13	52.14	+42.8	0.059	<0.01	strong increase	–0.442	10.326
Turkey	1986–2015	22	57.04	+8.0	0.027	<0.05	moderate increase	0.637	181.244
Albania	1993–2017	21	61.33	+0.6	0.004	0.107	stable	–0.315	3.691
Montenegro	1991–2017	16	66.67	+6.6	0.022	<0.01	moderate increase	–0.475	3.302
eastern subpopulation	2005–2015	11	25.57	+2.2	0.007	<0.05	moderate increase	0.065	25.136
western subpopulation	1993–2017	25	29.71	+5.8	0.005	<0.01	moderate increase	0.376	6.654

expected in years preceding years during which rather few pelicans are recorded. However, in both cases the estimated serial correlation was based on time-series that were either relatively short and/or pertained to a few wetland sites. Furthermore, in all cases the annual counts did not fit a Poisson distribution as suggested by the high overdispersion (range: 3.302–181.22; Table 2), which is expected in colonial species like the Dalmatian Pelican.

The estimated trend values suggested a strong increase in Romania (42.8%), Bulgaria (10.9%) and western Greece (9.7%) and a moderate increase in Turkey (8.0%), Montenegro (6.6%) and eastern Greece (4.7%; Table 2, Figure S1). For the Greek wetlands combined, a moderate increase of 5.7% was estimated (Table 2, Figure S1). In Albania the population size of overwintering Dalmatian Pelican remained stable over the years (0.6%; Table 2, Figure S1). At the subpopulation level, the trend rate suggested a greater increase in the case of the western subpopulation (5.8%) compared to the eastern subpopulation (2.2%), although the latter was calculated considering a substantially shorter time period (Table 2, Figure S1).

Temperature effects on population and distribution of the eastern subpopulation

During the considered time period (years 1985–2017) the mean temperature increased, particularly in Bulgaria and across the eastern subpopulation as a whole (Figure 3), and this increase was uniform across the study area (r_s = 0.67–0.94; Table S2).

However, as shown in Table 3, the rising temperatures seemed to affect the population size of wintering Dalmatian Pelicans only in Romania and Turkey, yet only marginally in the latter case (Figure S3). More specifically, the growth of the Romanian population was further exacerbated in milder winters, whereas an opposite pattern was observed for the Turkish population. The rising temperatures had no effect on the local wintering populations in Greece and Bulgaria nor did they incur population shifts from northern to southern countries. In addition, the abundance of wintering pelicans in one year was positively related to the abundance in the preceding year in all cases considered.

Furthermore, the population increase observed at the country level and across the eastern subpopulation was positively associated with an increase in the number of wetlands where wintering pelicans occurred (r_s = 0.59–0.83; Table S3, Figure S2). However, our analysis did not support any changes over the years nor any temperature effects on the centroid of the eastern subpopulation or on the minimum latitude and longitude (Table 4). But note that in these cases the models did not fit the data adequately (Table 4). Our results only supported a north-eastern expansion of the distribution of wintering Dalmatian Pelicans over the years as indicated by the positive effect of year on the maximum latitude and longitude (Table 4).

DISCUSSION

In this study we showed that wintering Dalmatian Pelicans pertaining to the Black Sea-Mediterranean Flyway, at least in the geographic area encompassing the eastern subpopulation, were already present in our

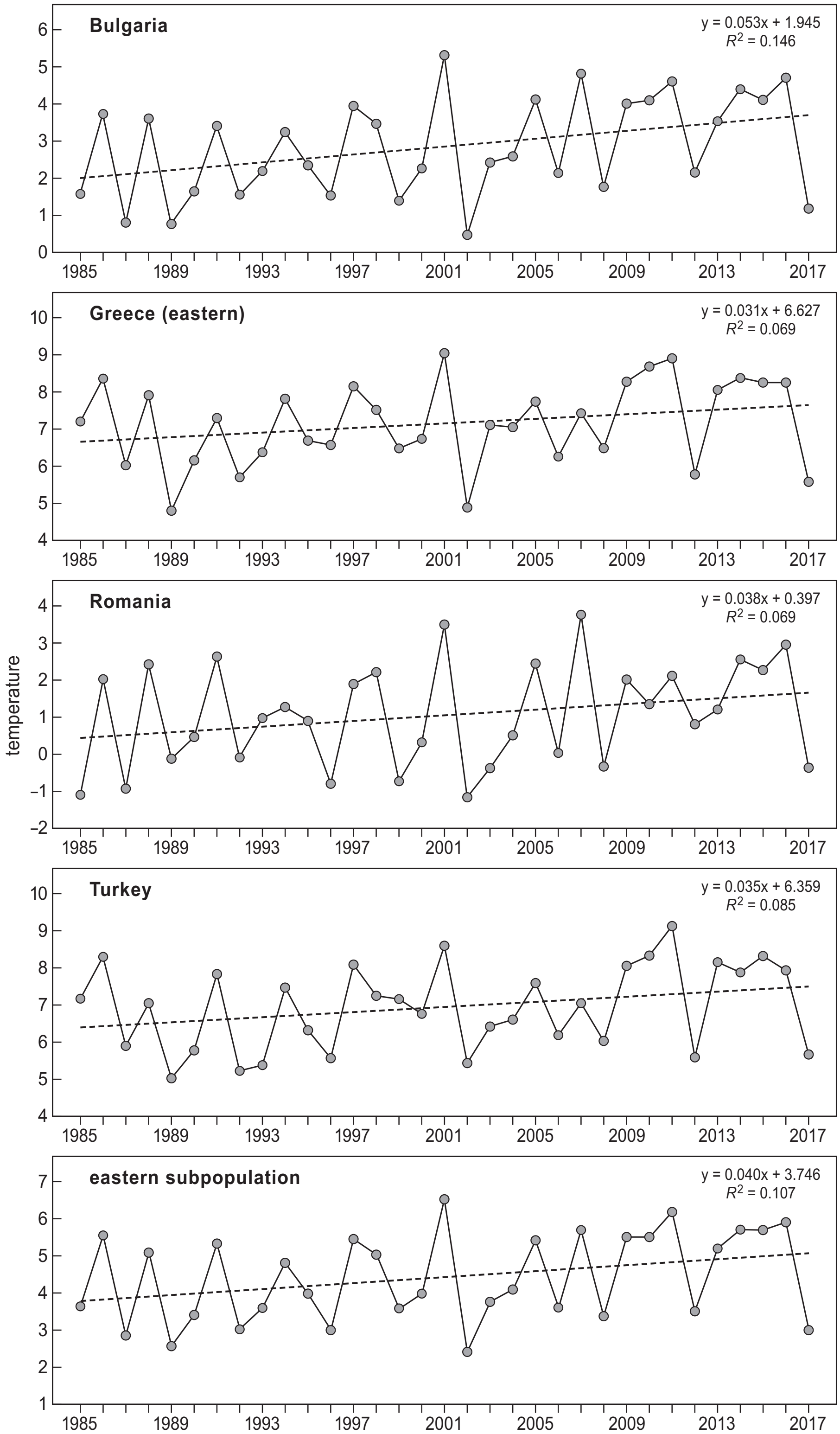


Figure 3. Variability in the mean temperature (°C) of November, December and January during the midwinter survey period 1985–2017 across the eastern subpopulation of the wintering Dalmatian Pelicans. The equation of the linear regression and the R^2 coefficient are given. The trend line (dotted line) is also indicated.

study system in 1964, specifically in wetlands of Greece and Turkey, and then progressively appeared in Bulgaria (1977) and in Romania (1999). Prior to the onset of systematic midwinter surveys, wintering numbers were relatively low, yet the surveys were conducted in a rather restricted number of wetlands. Still, thereafter annual counts suggest that the wetlands of the eastern subpopulation are the core of the wintering population of the species (in descending order: eastern Greece, Turkey, Bulgaria and Romania), while the wetlands of the western subpopulation host a substantially lower number of wintering Pelicans (in descending order: western Greece, Albania, Montenegro). Thus, overall Greece and Turkey represent the stronghold of the wintering population across the Black Sea-Mediterranean Flyway. The yearly estimate of the wintering population of the Dalmatian Pelican in our study system is nearly 5800 individuals on average based on data for the period 2011–2015.

The key findings in our study also support an increase in the numbers of wintering pelicans in all countries and in both subpopulations, except for Albania and Montenegro, during the past 30 years or so. Within the eastern subpopulation, in particular, the population increase was most accentuated in the northern edge of the wintering distribution and was coupled with a north-eastern expansion. The significant increase of the wintering population in the eastern

Table 3. Generalized Linear Model results regarding the effect of mean temperature (scaled values) of November, December and January on the number of wintering Dalmatian Pelicans (log-transformed value) within the eastern subpopulation. An autoregressive term (i.e. the number of wintering pelicans in the preceding year, log-transformed) was included in the models to account for potential temporal autocorrelation and density-dependence. Mean estimates with standard error (SE) of the coefficients of the explanatory variables are given. Statistically significant variables ($P < 0.05$) are shown in bold.

Country/Subpopulation	Survey period	Annual count of previous year		Mean temperature		Adjusted R^2	Model performance
		estimate	SE	estimate	SE		
Bulgaria	1985–2016	**1.000**	0.032	0.090	0.198	0.974	$F_{2,254} = 509.70$, $P < 0.001$
Greece (eastern)	1986–2017	**1.001**	0.014	0.063	0.103	0.995	$F_{2,26} = 2622$, $P < 0.001$
Turkey	1986–2015	**1.038**	0.023	–0.308**	0.150	0.992	$F_{2,14} = 1001$, $P < 0.001$
Romania	2003–2015	**0.993**	0.110	**1.302**	0.549	0.873	$F_{2,10} = 42.34$, $P < 0.001$
Greece (eastern) and Turkey*	1986–2015	**1.014**	0.010	–0.113	0.083	0.999	$F_{2,14} = 5481$, $P < 0.001$
eastern subpopulation	1988–2015	**1.011**	0.007	–0.104	0.058	0.999	$F_{2,12} = 9925$, $P < 0.001$

*Annual counts of the two countries were pooled and the mean temperature in Bulgaria and Romania was used in this case.
**Marginal effect: $P < 0.1$.

Table 4. Generalized Linear Model results regarding the effect of year (scaled values) and mean temperature (scaled values) of November, December and January on the distribution of wintering Dalmatian Pelicans within the eastern subpopulation. Mean estimates with standard errors (SE) of the coefficients of the explanatory variables are given. Statistically significant variables ($P < 0.05$) are shown in bold. Note that only models concerning the maximum latitude and maximum longitude had an adequate fit to the data (i.e. $P < 0.05$).

Model	Intercept		Year		Mean temperature		Adjusted R^2	Model performance
	estimate	SE	estimate	SE	estimate	SE		
Latitude								
weighted average	**40.569**	0.100	0.177	0.133	0.135	0.124	0.224	$F_{2,16} = 3.59$, $P = 0.051$
minimum	**37.483**	0.096	–0.243	0.129	0.255	0.120	0.147	$F_{2,16} = 2.56$, $P = 0.109$
maximum	**44.374**	0.129	**0.892**	0.172	–0.154	0.161	0.637	$F_{2,16} = 16.80$, $P < 0.001$
Longitude								
weighted average	**25.518**	0.134	0.038	0.180	–0.205	0.168	–0.006	$F_{2,16} = 0.95$, $P = 0.409$
minimum	**21.248**	0.156	–0.261	0.209	0.001	0.195	0.021	$F_{2,16} = 1.19$, $P = 0.329$
maximum	**29.089**	0.140	**0.626**	0.187	–0.264	0.174	0.348	$F_{2,16} = 5.793$, $P < 0.05$

subpopulation could only be partially explained by climate changes affecting the abundance of Dalmatian Pelicans only locally. However, this increase is consistent with the overall population increase of the breeding population in SE Europe and Turkey over the past 50 years (Barov & Derhé 2011, Catsadorakis & Portolou 2018) and hence deserves further investigation.

More specifically, the western subpopulation consists of 21 wetlands along the Adriatic and Ionian coast (including some islands) of which four host also breeding colonies. The overall trend was 5.8%, attributed to a strong increase of 9.7% in Greece given that in Albania and Montenegro local abundances are relatively stable. Before the year 2000 overall numbers never exceeded 400 individuals while in the last twenty years they may have reached or exceeded 700–1000 individuals, in accordance with the yearly estimate for the period 2011–2015 (i.e. 833 individuals in total). Most wintering pelicans occur in wetlands of western Greece (Amvrakikos and Messolonghi lagoons). The two small populations in Albania and Montenegro are slowly increasing but they are too small to significantly affect the overall population size in the western subpopulation.

The eastern subpopulation consists of the wetlands of north and northeast Greece and all wetlands of Bulgaria, Romania and Turkey, totalling in number 180 wetlands, of which 15–18 are also breeding wetlands. The majority of the wintering population (81%) is concentrated in 67 wetlands in the southernmost region, i.e. in Greece and Turkey, while the remaining is scattered in 113 wetlands in Bulgaria (n = 41) and Romania (n = 72). Within SE Europe and Turkey the key wintering sites for the birds of the major Greek breeding colonies at the eastern subpopulation are the wetlands of north and northeast Greece (e.g. Lake Kerkini, Porto Lago-Vistonis lagoons) and western Anatolia in Turkey (e.g. Lake Marmara, Lake Manyas, Büyük Menderes Delta; Crivelli *et al.* 1991b, Catsadorakis *et al.* 2015). The yearly estimate for the period 2011–2015 suggests a wintering population of c. 5000 individuals on average.

Within the eastern subpopulation the overall increase of the wintering numbers during the past 30 years or so in all four countries varied, ranging from 4.7–42.8%, the largest one involving Romania. However, the reported rates are not directly comparable, due to differences in the time scale/period examined in each case, as well as due to inter-annual differences in the number of surveyed sites in each country. Nonetheless, the observed increase in wintering birds can only be partially explained by a higher sampling effort, considering that the number of surveyed wetlands in the stronghold of the eastern subpopulation, i.e. eastern Greece, seems to have stabilized in recent years. In addition, there was a large interannual variability in the annual counts, yet the observed fluctuations were not synchronized in time across the study area.

The overall increase of the eastern subpopulation for 2005–2015 was estimated at 2.2%. Nevertheless, if we were able to consider midwinter counts for the entire period, i.e. 1985–2015, in the trend analysis, the overall increase would most probably exceed 20%. In that case, the overall increase would be numerically comparable to the strong increase of 15% from 1998 to 2017 observed in Iran, which lies in the Central Asian Flyway and hosts c. 37% of the species' wintering population globally (Ashoori *et al.* 2019). Still, it must be noted that while the increase in the eastern subpopulation was rather smooth, that of Iran was abrupt after 2009, which indicates that the two cases might have different underlying causes. In Iran in earlier years, pelicans had already passed through the country to their wintering destinations in Pakistan and India in mid-January, so during the IWC surveys only a few were met in Iran. However, the milder early winter conditions of recent years allowed pelicans to stay at higher latitudes in November and December delaying their southward migration. Thus, in mid-January they were counted during their journey through Iran in high numbers, which resulted in an abrupt increase in the observed trends (Ashoori *et al.* 2019).

In our case the observed population increase in the eastern subpopulation can only be partially explained by climate changes even though there was clearly a warming trend (though varying in magnitude locally) during the past 30 years across the entire area. The rise in winter temperature had a significant effect only at the edges of the wintering distribution, i.e. in Romania and Turkey (yet marginally in the latter case), and incurred population size changes only at the local level. More specifically, according to our results when milder conditions occur locally the Dalmatian Pelicans tend to occur in higher numbers in the wetlands of Romania but in lower numbers in the wetlands of Turkey. The population increase related to milder conditions in Romania could be explained by the incurred lower mortality rates (Maclean *et al.* 2007, Clark 2009) and/or increased food availability due to sustained periods of fish activity (Ultsch 1989). The latter could have also allowed wintering pelicans to delay their southward journey, as has been observed in Iran (Ashoori *et al.* 2019), which could also explain the negative effect of temperature on wintering pelicans in Turkey. However, this negative effect was not big enough to reverse the continuing increase of wintering pelicans over the years in the country. Indeed, substantial population shifts across the eastern subpopulation are unlikely as they were not supported by the models regarding both the population trend in the southern part (i.e. Greece and Turkey, pooled data) and the overall distribution pattern across the entire area. Regarding the latter, the centroid of the distribution has remained the same, but note the lack of statistical support of the model results.

Whichever the underlying factors, the observed north-eastern expansion of the overall wintering distribution is consistent with the observed increase in abundance of wintering Dalmatian Pelicans in Romania, but also in Bulgaria. Before 1999 in Romania and the 1990s in Bulgaria (Michev & Profirov 2003) there were almost no birds present in these two countries during the midwinter counts despite the fact that the local breeding populations at the time were not significantly different to present times (Crivelli *et al.* 1991b, Barov & Derhé 2012). Dalmatian Pelicans started appearing during the IWC in Romania after 2000, with their numbers increasing slowly up to 2010 where a strong increase took place. The most important wetlands for wintering pelicans in the country are Rusanesti Lake, Oltina Lake, Izbiceni and Frunzaru Lake. In Bulgaria, a similar increase was observed since the '90s, with main wintering sites being Ovcharitsa reservoir, Vaya complex, Atanasovsko Lake complex, Mandra-Poda complex and Rozov Kladenets reservoir. Similar patterns of wintering distribution shifts, i.e. towards north and northeast, have been recorded in several species of waterfowl in Europe as a response to changes in temperature (e.g. Žalakevičius & Švažas 2005, Maclean *et al.* 2008, Lehikoinen *et al.* 2013, Ramo *et al.* 2015). However, such climate effects on the distribution of wintering pelicans in the eastern subpopulation could not be verified in our study system.

The lack of a strong climate effect on both the population size and distribution of wintering Dalmatian Pelicans of the eastern subpopulation deserves further investigation. We should point out here that the spatial resolution of the dataset chosen as a proxy of the local climatic conditions in each country was rather coarse, namely 0.5×0.5 degrees, and thus might not be representative of the climatic conditions at each wetland site considered in this study. Therefore, given that the wintering population of Dalmatian Pelicans is unequally distributed among the wetlands of the study area, weather conditions prevailing in specific sites could have a large impact on the total national and regional annual counts in the study area.

Furthermore, other parameters, either natural or anthropogenic, related to the conditions prevailing in each wetland, such as fluctuations in water depth, ice cover, prey abundance and availability (e.g. Scholte 2006, Nager *et al.* 2010), but also water quality (e.g. Papadimitriou *et al.* 2017), could have also shaped the observed changes in the number and distribution of the Dalmatian Pelicans overwintering in our study area (Ashoori *et al.* 2019). Moreover, winter site fidelity could also influence the movement pattern of the species, thus ultimately affecting its wintering distribution (Robertson & Cooke 1999). Additionally, there is evidence, although limited, that the timing of breeding affects the propensity of pelicans to disperse and overwinter elsewhere (Crivelli *et al.* 1991b). Moreover, although the IWC data represent the most comprehensive data on wintering waterbird numbers, many pelican researchers (e.g. Crivelli *et al.* 1991a) consider that they are underestimations of the actual numbers, given that the midwinter surveys do not take place at roosting sites. Thus, considering the advancement of first laying dates for the Dalmatian Pelicans in almost all breeding sites in Greece (Doxa *et al.* 2012, O. Alexandrou & G. Catsadorakis unpubl. data) and the strict time-period of the IWC counts (i.e. mid-January), it is very likely that many birds might be counted already on their colonies or on their way to them (Musilová *et al.* 2014) which could lead to rapid increases in the near future during the IWC counts as seen in those recently published for Iran (Ashoori *et al.* 2019).

Another important aspect that was not assessed in our study is migratory connectivity and the related carry-over effects during the annual cycle. It was known since the 1980s from colour ringing results that Dalmatian Pelicans from Romanian and Bulgarian colonies overwinter in Greece and Turkey (Crivelli *et al.* 1991a). Visual observations of migrating and wintering birds in Bulgaria and re-sightings of colour-ringed birds (Catsadorakis 2016) imply that during the last 20 years a large percentage of birds breeding in the Danube delta and Bulgaria overwinter either at the Bulgarian coastal wetlands or other sites in Greece and Turkey (Catsadorakis *et al.* 2015). The reverse, i.e. Dalmatian Pelicans breeding in southern colonies that overwinter in northern countries, has also been supported by re-sightings of colour ringed individuals (Crivelli *et al.* 1991a, Gül 2014) and satellite telemetry data (O. Alexandrou unpubl. data) indicating that breeding pelicans from Lake Mikri Prespa overwinter in Turkey (c.

630 km away) and Romania (c. 820 km away). In general, such movements are common among all countries involved (Crivelli *et al.* 1991a, Catsadorakis *et al.* 2015, Catsadorakis 2016), but have not been explored in detail to date, even though there is indirect evidence that the breeding conditions at key colonies may play an important role in the abundance and distribution of wintering pelicans. Indeed, in the Black Sea-Mediterranean Flyway the species' breeding populations have been favoured by successful conservation measures resulting in an increase in breeding numbers in SE Europe and Turkey (Catsadorakis *et al.* 2015) and in the establishment of at least six new colonies (S. Bugariu pers. comm., Bulgarian Society for the Protection of Birds 2016, Society for the Protection of Prespa unpubl. data, Catsadorakis 2019). The apparent increase in the wintering numbers in both the eastern and western subpopulation fits well with the increase of all colonies involved, and mostly in the key breeding colonies, such as those at the Amvrakikos gulf in the western subpopulation and Lake Mikri Prespa in the eastern subpopulation, but also elsewhere (Barov & Derhé 2011, Catsadorakis & Portolou 2018). If carry-over effects can offer a plausible scenario for the observed long-term changes in the wintering population and distribution of Dalmatian Pelicans in our study system, climate change should be reconsidered as a candidate driver according to the results of a recent study exploring the exponential growth of breeding Dalmatian Pelicans in western Siberia (Tarasov & Ryabitsev 2019).

In light of the above, we propose the future implementation of species-specific winter surveys, independently from the IWC. Combined with time-series data on the breeding population size at key colonies and a more detailed description of migratory connectivity, future studies will be able to provide a thorough assessment of the long-term changes and ultimately decipher the interplay of factors affecting the wintering population and distribution of Dalmatian Pelicans along the Black Sea-Mediterranean Flyway.

ACKNOWLEDGEMENTS

We would like to thank Danae Portolou (Hellenic Ornithological Society/BirdLife Greece) and Kiraz Erciyas Yavuz (Ondokuz Mayis University) for their contribution during data compilation from Greece and Turkey, respectively. Special thanks to Alain J. Crivelli who commented on an earlier draft. The work of the Society for the Protection of Prespa for pelicans was supported financially by the MAVA Foundation and after 2018 by the Prespa-Ohrid Nature Trust (PONT).

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SAMENVATTING

Om dierpopulaties op een adequate manier te kunnen beschermen, is kennis over hun dynamiek in ruimte en tijd van doorslaggevende betekenis. Langtermijnreeksen hierover zijn voor de meeste diergroepen schaars. Watervogels vormen daarop een uitzondering, dankzij de midwintertellingen die al meer dan 40 jaar jaarlijks wereldwijd worden georganiseerd. De op wereldschaal bedreigde Kroeskoppelikaan *Pelecanus crispus* is wijdverspreid in Eurazië. Wij onderzochten aan de hand van de midwintertellingen welke veranderingen zich in de loop van de tijd hebben voorgedaan in de winterverspreiding van de vogels van de Zwarte Zee-Mediterrane Flyway, de westelijke van de drie flyways van de soort. Wij presenteren hier regionale en landelijke trends van overwinterende Kroeskoppelikanen in Zuidoost-Europa en Turkije. Uit de analyses blijkt dat de aantallen van de winterpopulatie de laatste dertig jaar in het gehele onderzoeksgebied zijn toegenomen. De toename was het meest opvallend aan de noordrand van de oostelijk subpopulatie en hing samen met een noordoostelijke opschuiving van de winterpopulatie. Een relatie met klimaat hiervoor werd niet gevonden. Voorgesteld wordt om verder onderzoek naar de factoren die voor de veranderingen verantwoordelijk zijn, te overwegen. Aangezien de soort in bijna alle broedlocaties vroeger is gaan broeden, wordt verder voorgesteld om naast de midwintertellingen (die altijd op een vaste tijd in de winter worden gehouden) speciale tellingen in de winter voor deze soort te houden, om meer inzicht te krijgen in de dynamiek van de winterverspreiding.

Corresponding editor: Allert Bijleveld
Received 21 August 2020; accepted 17 May 2021

Supplementary Material is available online
www.ardeajournal.nl/supplement/s109–###–###.pdf

SUPPLEMENTARY MATERIAL

Table S1. Presentation of highest and lowest annual counts per country since 1985 when more systematic surveys began.

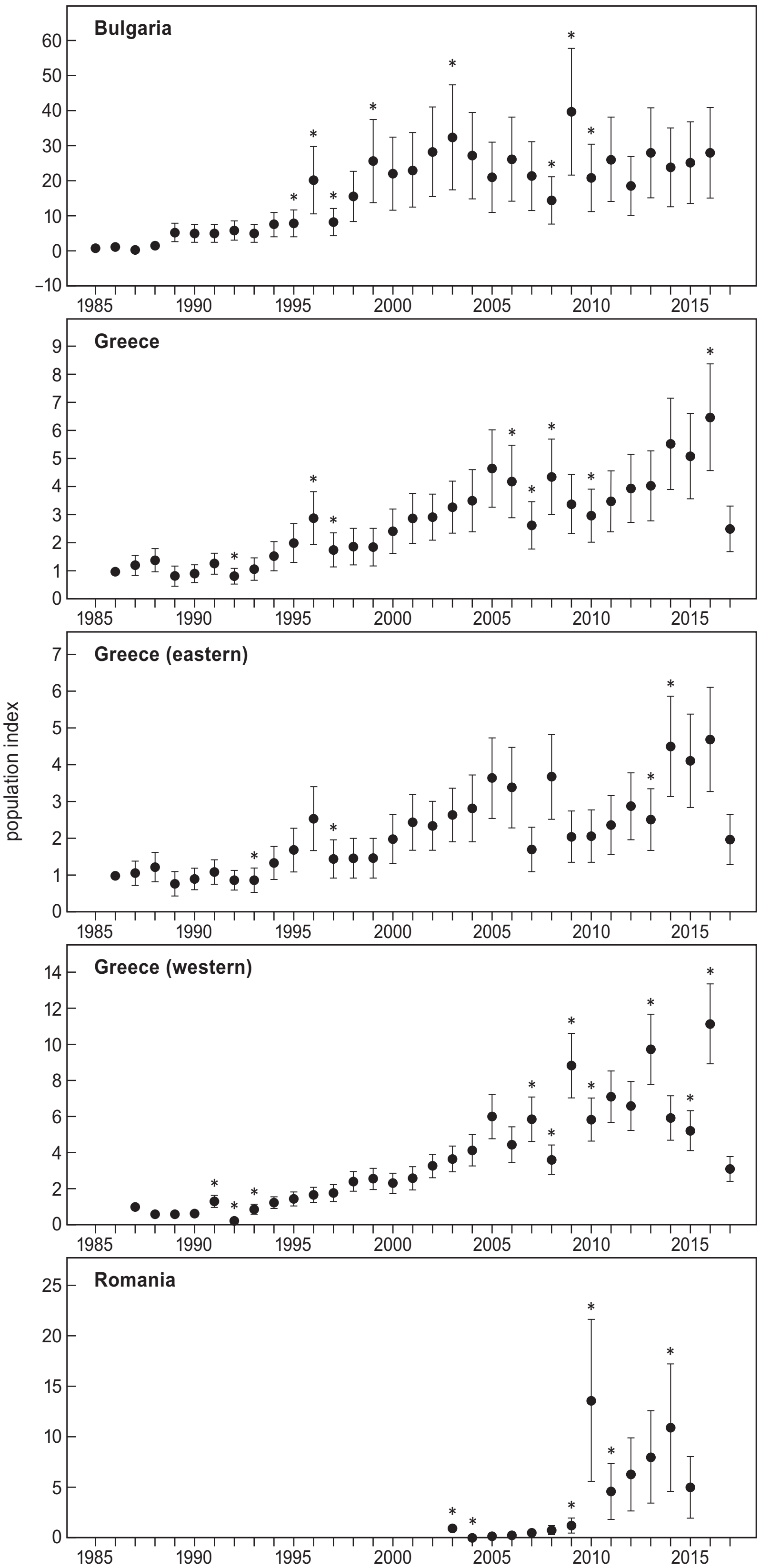
	Year of highest counts (number of individuals)	**Year of lowest counts** (number of individuals)
Bulgaria	2009 (1135)	1987 (1)
Greece (eastern)	2016 (3284)	1992 (119)
Greece (western)	2016 (1005)	1986 (1)
Romania	2010 (563)	2004, 2006 (15)
Turkey	2007 (2332)	1995 (80)
Albania	2013 (245)	2004 (82)
Montenegro	2016 (107)	1991 (4)

Table S2. Spearman correlation coefficients (r^s) for the mean temperature in November–December and January during the period 1985–2017 between pairs of countries comprising the eastern subpopulation. All values were statistically significant ($P < 0.05$).

	Bulgaria	Greece (eastern)	Romania	Turkey
Bulgaria	–			
Greece (eastern)	0.90	–		
Romania	0.82	0.94	–	
Turkey	0.91	0.74	0.67	–

Table S3. Spearman correlation coefficients (r^s) between the annual count and the distribution index (i.e. the ratio of occupied wetlands to the number of surveyed wetlands) for the countries comprising the eastern subpopulation. All values were statistically significant ($P < 0.05$). The survey period and the number of years (n) considered in each case are also given.

	Survey period	r_s	n
Bulgaria	1985–2016	0.59	30
Greece (eastern)	1986–2017	0.61	30
Turkey	1986–2015	0.59	22
Romania	2003–2015	0.71	12
eastern subpopulation	1985–2017	0.83	19


Bulgaria
Greece
Greece (eastern)
Greece (western)
Romania
population index
1985
1990
1995
2000
2005
2010
2015

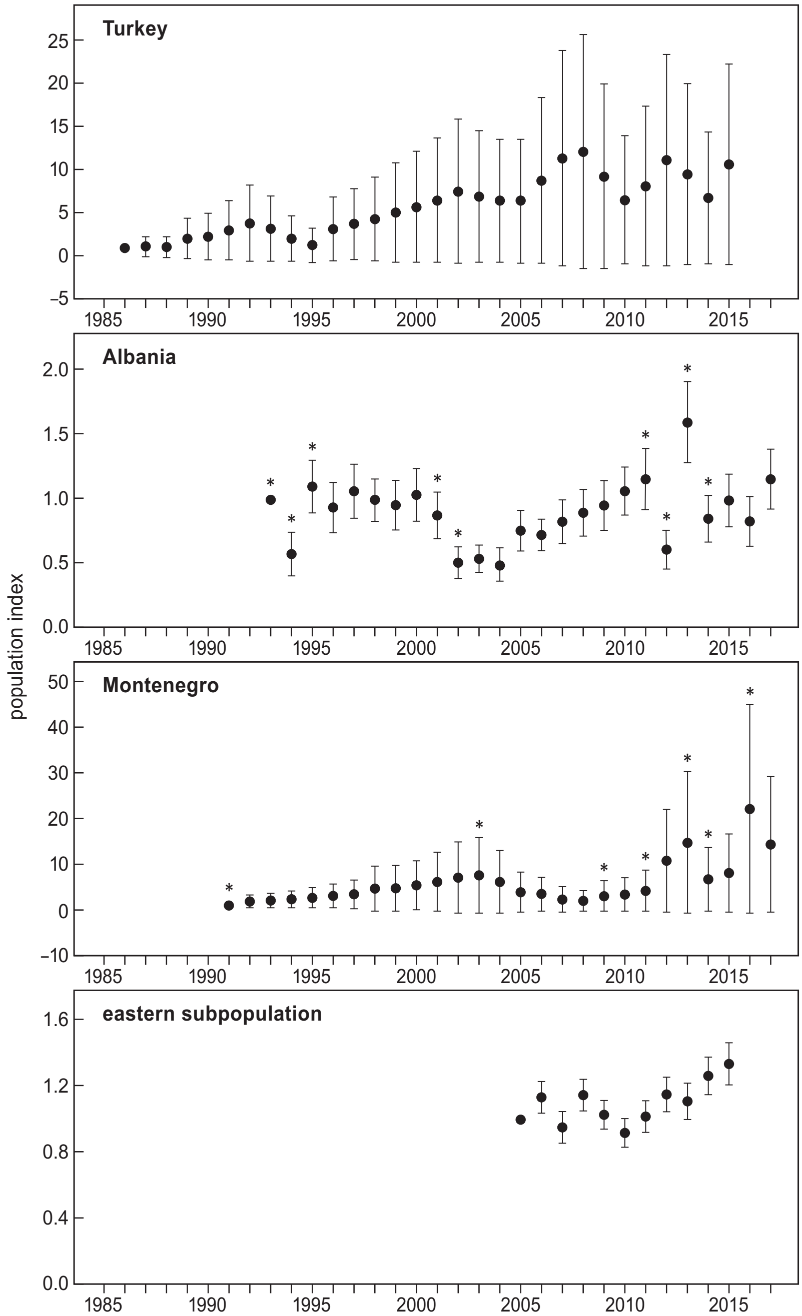
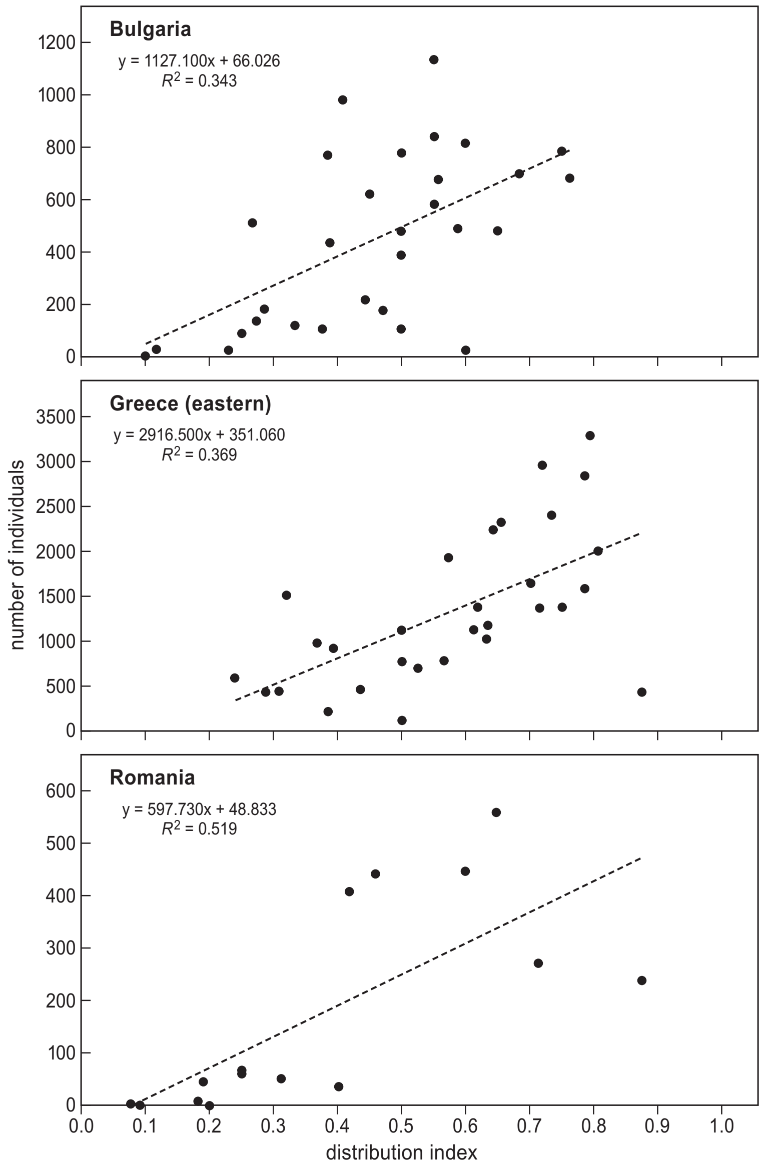


Figure S1. Population dynamics of the wintering Dalmatian pelicans along the Black Sea-Mediterranean Flyway represented by the estimated population index (the first year was considered as the base year) according to the implemented TRIM models. Barplots indicate standard errors. Significant changes in slope ($P < 0.05$) are indicated by asterisks.


Bulgaria
y = 1127.100x + 66.026
R^2 = 0.343
Greece (eastern)
y = 2916.500x + 351.060
R^2 = 0.369
Romania
y = 597.730x + 48.833
R^2 = 0.519
number of individuals
distribution index

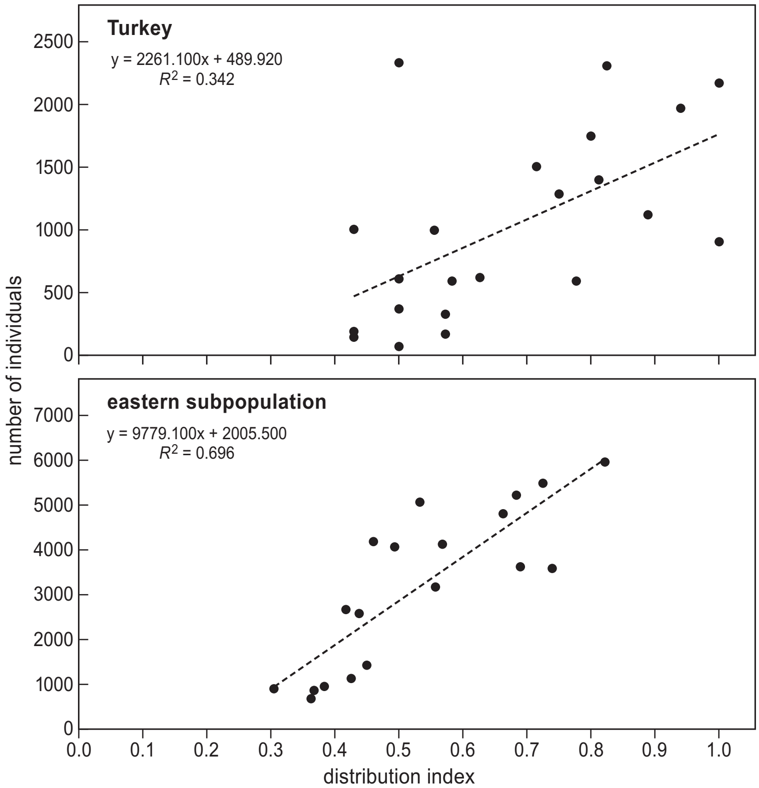
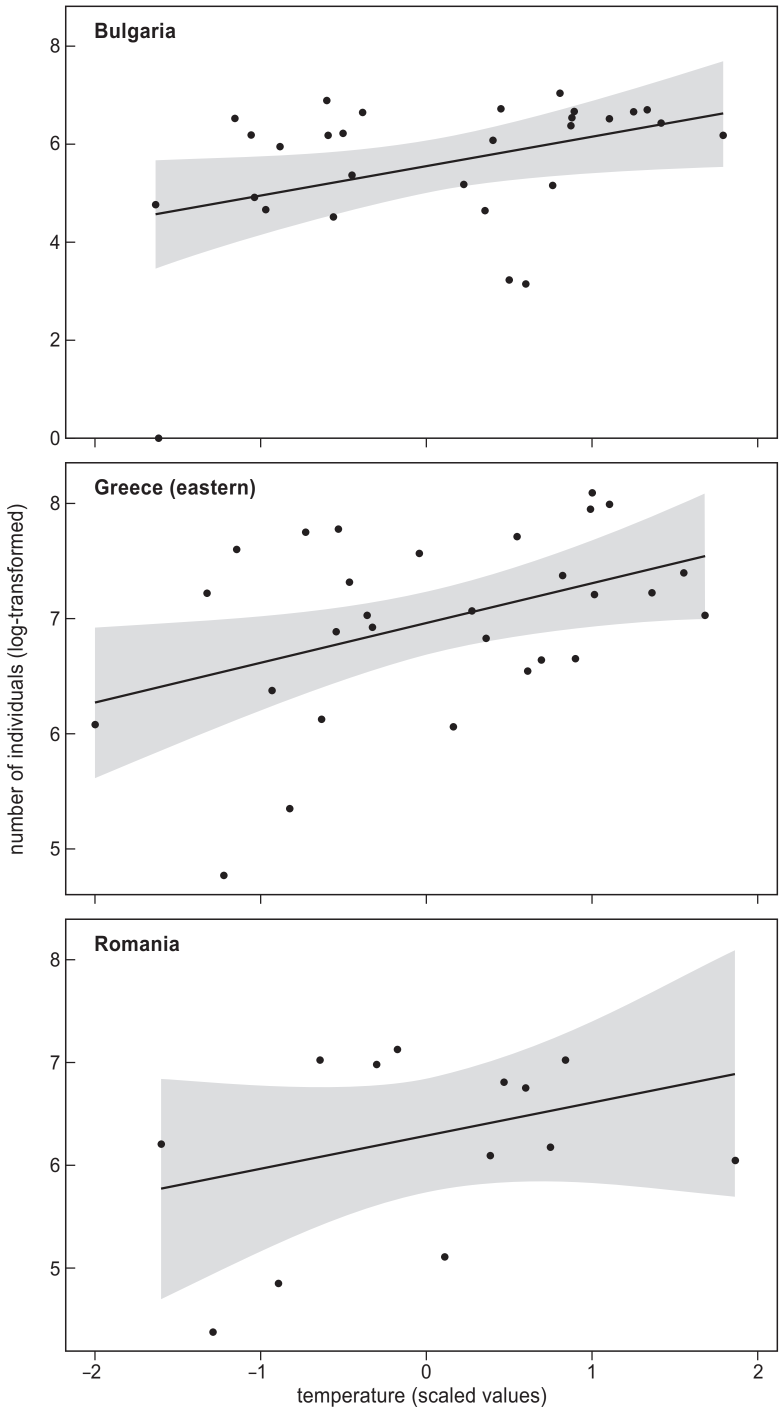


Figure S2. Scatterplots between the annual count and the distribution index (i.e. the ratio of occupied wetlands to the number of surveyed wetlands) within the eastern subpopulation, indicating an increase in the number of counted individuals with an increase in sampling effort. The equation of the linear regression and the R^2 coefficient are given. The trend line (dotted line) is also indicated.


Bulgaria
Greece (eastern)
Romania
number of individuals (log-transformed)
temperature (scaled values)
8
6
4
2
0
8
7
6
5
8
7
6
5
–2
–1
0
1
2

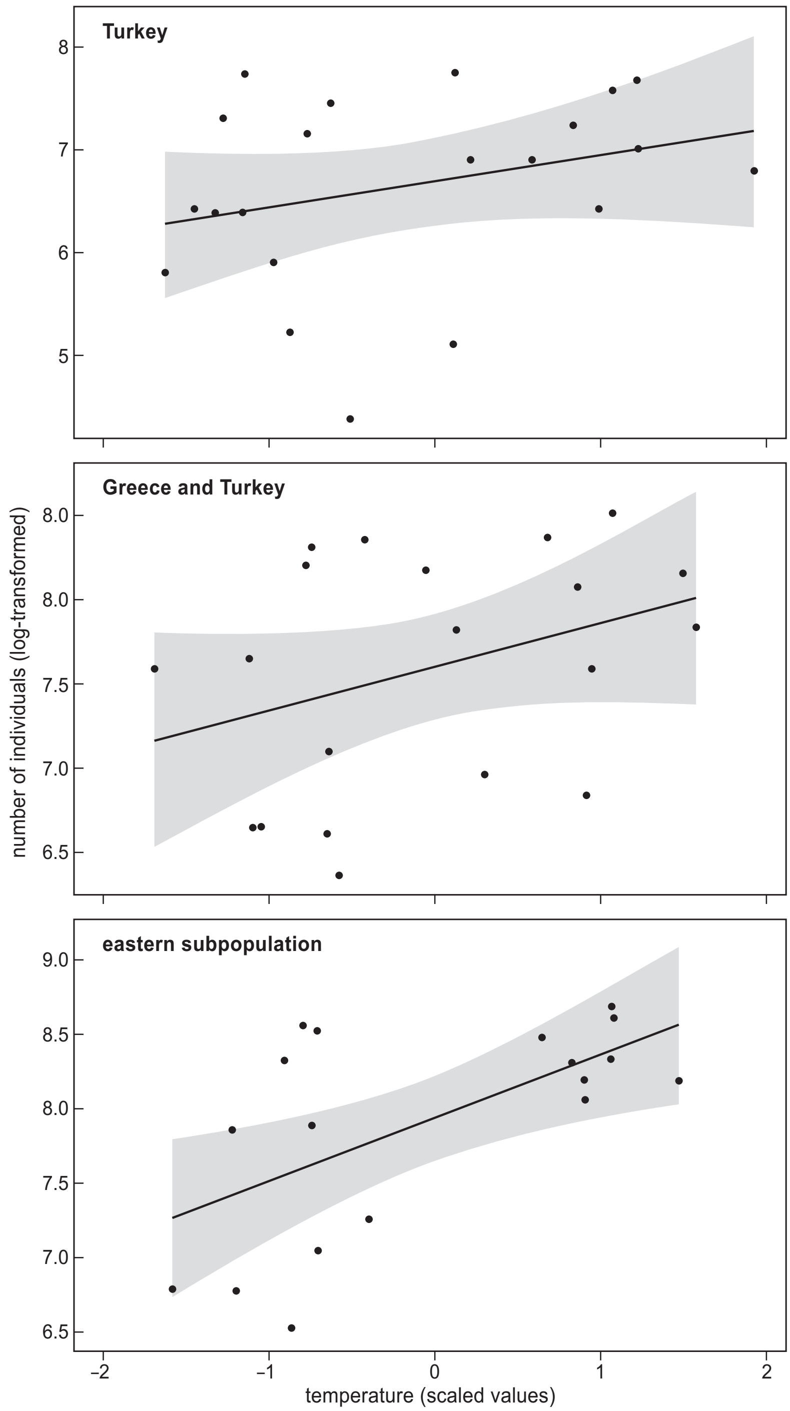


Figure S3. Scatterplots of annual counts (log-transformed) against mean temperature of November–January (scaled) at the national and subpopulation level. The graphs include fitted lines and confidence intervals (grey area) of the linear regression.