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RESEARCH

Home range of the Dalmatian pelican in south-east Europe

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Abstract

Delineating an animal's home range is crucial for understanding its spatial ecological requirements and vital for management and conservation decisions. We applied a dynamic Brownian Bridge Movement Model to investigate the movements, annual home range (HR) and core area (CA) size of eleven Dalmatian pelicans *Pelecanus crispus* fitted with satellite transmitters in northern Greece. The average monitoring period per bird ranged from 126 to 365 days, but tracking duration was unrelated to the overall distance covered by the birds. Altogether tracked pelicans visited 31 water bodies. The average home range (95% utilisation distribution) was estimated at ca. 461 km^2 while the core area (50% utilisation distribution) was estimated at ca. 14.4 km^2, representing 3.12% of the former. The home range size of the studied birds varied widely between individuals, ranging from 43 to 1533 km^2. Home ranges were not single areas but on average consisted of 4.1 different nuclei (range = 1–8), often more than one in a single wetland. Sex did not have an effect on the annual HR (or CA) size of the species. There were no similar or comparable patterns of seasonal movements between the pelicans monitored, and no statistically significant seasonal variation was found in HR and CA sizes. The conservation of Dalmatian pelican populations in south-east Europe depends not only on good habitat conditions prevailing in individual breeding wetlands but also on a wider network of water bodies in the region.

Keywords Utilisation distribution · Core areas · Dynamic Brownian Bridge Movement Model · Waterbirds · Space use · Seasonal and annual movements

Introduction

The concept that individual animals restrict their movements to finite areas known as home ranges and use resources disproportionately to their availability for meeting their ecological requirements has been fundamental in conservation biology (Manly et al. 2002). Furthermore, most animals tend to exploit one or more regions within their home range, i.e. core areas, more frequently than others during their regular annual or daily movements (Hodder et al. 1998).

Home range analysis is central to many ecological studies and a crucial step for understanding the spatial ecology of animals and the mechanisms of their response to environmental change (Akçakaya 2000; Thomas and Taylor 2006; Cummings and Cornelis 2012). Mcloughlin and Ferguson (2000) claim that the central problem of what determines home range size is the integrative nature of the home range. Although various ecological and physiological factors influence home range size, such as climate, abundance and distribution of food, social organisation, population density and risk of predation, there is no consensus as to which factors are primary in determining home range size (see review in Mcloughlin and Ferguson 2000). Variation of HR size is a scale-dependent issue and factors that influence home range size at the individual level include food availability, patchiness in the environment, density, predation and sex (Mcloughlin and Ferguson 2000).

There are eight species of pelicans in the world (Kennedy et al. 2013) but the home range has been studied only for two of the three New World species, namely the Brown pelican (*Pelecanus occidentalis*) (King et al. 2013; Lamb et al. 2019, 2020) and the American white pelican (*P. erythrorhynchos*) (Sovada et al. 2013; King et al. 2016). In the Old World, the Dalmatian pelican (*P. crispus*) is an iconic soaring waterbird

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distributed from Montenegro to China (Crivelli and Vizi 1981; Catsadorakis and Portolou 2018). In Europe, Dalmatian pelicans behave as short-distance migrants as they migrate only for short distances, staying mostly in the eastern Mediterranean region (Crivelli et al. 1991a; Barboutis et al. 2021).

In Greece, our knowledge of the species' biology and ecology has been substantially improved due to long-term research and conservation programmes (Crivelli 1987; Crivelli et al. 1991a, b; Catsadorakis et al. 1996; Crivelli et al. 1997). Dalmatian pelicans (DPs) tend to use various wetlands with different characteristics during their annual cycle (Efrat et al. 2018); however, data on the species home range size is still lacking (Catsadorakis and Portolou 2018; Efrat et al. 2018). It is also not known whether there is intra-population variation in home range sizes and whether sex plays a role in individual variation of home range sizes. DPs are gregarious colonial birds that migrate, move, and rest in groups; they fish both singly and in groups and they nest in clumped aggregations. They do not defend territories other than around their nests, and they are not threatened by avian predators. Their overall life histories present a lot of similarities to seabirds, and they are frequently treated as such. The challenges of the definition and metrics of the species' home range become even more intriguing taking into consideration that DPs repeatedly visit certain wetlands at a distance from their breeding colonies during their annual cycle (Crivelli et al. 1991a; Efrat et al. 2018).

In this study, we developed a GPS telemetry scheme to investigate the annual home range of DPs in northern Greece. We aimed to obtain an insight into the species' ranging behaviour and improve our knowledge on its movement ecology. Our goal was to quantify both the species' home range size (HR) and core areas (CA) of intense use (Kie et al. 2010), and to distinguish temporal usage (e.g. summer and winter, breeding, dispersal). We anticipate that the DPs HR and CA will include wetlands often visited by the birds during their annual cycle.

Methods

Fieldwork and data collection

The ranging behaviour of the species was investigated by monitoring 11 DPs during 2013–2019. The birds were captured using leg-hold traps at the end of the breeding season at Lake Mikri Prespa ($n=7$) and just at the beginning of the breeding season in the Kerkini Reservoir ($n=4$). Traps in Prespa were placed in June–July, close to the colonies, on small, floating, reed-rhizome islands, used by the birds for resting. Traps in Kerkini were put in February, in shallow water (< 20 cm) close to the coastline, far from the nesting platform and birds were attracted by throwing dead fish in the water. All the pelicans were aged as adults according to their plumage (Elliot et al. 2017, G. Catsadorakis & O. Alexandrou unpubl. data). Their sex was determined a few months after capture by molecular techniques, namely, analysis of DNA extracted from blood samples (Griffiths et al. 1998) and morphometric measurements. All birds captured in Prespa were sexed as males and all birds captured at Kerkini were sexed as females. All pelicans were marked with yellow PVC engraved rings and handmade patagial wing tags (14 cm × 10 cm) made from white vinyl-covered nylon and painted with black ink. Rings and tags were placed on both legs and wings respectively. The birds were additionally equipped with solar-powered GPS/GSM transmitters (e-obs GmbH, Germany) that weighed ca. 1% of their body mass (i.e. 90 gr) including the attachment material. The transmitters were backpack-harnessed on the pelicans using silicon strings encapsulated in tubular Teflon ribbon (Thaxter et al. 2014). Lamb et al. (2016) concluded that Brown pelicans fitted with GPS transmitters exhibit comparable behaviours to untagged individuals within a day of capture and that GPS tracking is a viable technique for studying behaviour and demography in the Brown pelican. We have not systematically checked for transmitter effects on DPs but as we have not observed any strange behaviour, we assumed that they have remained unaffected. Tags were programmed to collect data on time, position (i.e. GPS fixes of latitude and longitude ± 5 m according to the manufacturer specifications for the estimated spatial error), flight height (i.e. metres above ellipsoid with an error < 20 m for 95% of measurements) and instantaneous speed (Km/h). Before used in any of the subsequent analyses, the data were checked, and any outlying radiolocations caused by transmitters' error were removed. Their duty schedule was set to operate 24 h/day and to obtain GPS locations and relevant measurements every 5, 10, 20 or 60 min, depending on the battery voltage. Nevertheless, some time gaps did occur due to low battery power.

Data curation

In an effort to explore the temporal variation of the species' spatial utilisation pattern, the annual cycle of DPs was divided into four stages, namely the breeding period including courtship, pair formation and egg laying for the vast majority of the population, i.e. 15th December–20th April; the post-breeding period including brooding and chick rearing for breeders and dispersal for non-breeders, i.e. 21st April–31st July; the pre-winter period that includes the dispersal phase for all birds, i.e. 1st August–10th October, and the wintering period, i.e. 11th October–14th December.

The temporal resolution of the data for all individuals was also standardised by retaining the first radiolocation point in each hour (see also Buechley et al. 2018). The duration of the observation period for each individual ranged from 126 to 1994 tracking days. However, as our goal was to explore the annual movement pattern of the Dalmatian pelicans, we kept the latest 365 tracking days of the monitoring period for those tracks exceeding one calendar year (Table 1). All data were stored in the Movebank database (https://www.movebank.org/).

Statistical analysis

The utilisation distribution (UD), which is commonly expressed by a density function that provides the probability of finding an animal's position in a plane or its relative space use within its home range (Anderson 1982; Worton 1989), was estimated by applying the dynamic Brownian Bridge Movement Model (dBBMM) (Horne et al. 2007; Kranstauber et al. 2012). The method estimated the UD for each individual pelican, based on the study of its movement tracks and behaviour (e.g. movement, rest) (Kranstauber et al. 2012). The model applies a conditional random walk-(Brownian bridge) in order to approximate the bird's trajectory and estimates in particular its UD by taking into consideration the sequence of locations, the distance and the time between two successive locations (Horne et al. 2007). Basic assumptions are a constant movement between sequential locations and the uncertainty in the bird's movement path expressed as the variance of the Brownian motion (σ2m) and the location errors (Horne et al. 2007). The σ2m describes the deviation from a straight-line movement in the path of each pelican (Horne et al. 2007; Kranstauber et al. 2012). The dBBMM has the ability to estimate a varying σ2m, which in turn allows the identification of changes in a pelican's movement pattern; thus, it was regarded as ideal for understanding the complex movement behaviour patterns of the species (e.g. breeding, foraging, flying, resting) (Kranstauber et al. 2012; Palm et al. 2015; Buechley et al. 2018). The varying σ2m is estimated within a sliding window (w) of locations (≥ 3) and a margin of size (m) at the start and the end of each window (Kranstauber et al. 2012) that are relevant to the species biology (Kranstauber et al. 2012; Byrne et al. 2014; Palm et al. 2015; Buechley et al. 2018).

Preliminary data exploration revealed that the mean and median distances between consecutive points were between 328.4 m and 1838.3 m and between 21.7 m and 187.6 m, respectively. This implied that the birds flew over small distances within an hour and thus a grid size of 100 m^2 resolution was considered appropriate for the calculation of their UDs using the dBBMM. A window size of 25 locations and a margin of 9 locations were used, corresponding to a temporal window of approximately one day for hourly observations (Kranstauber et al. 2012; Buechley et al. 2018). The choice of window and margin aimed to encompass the daily activity of the Dalmatian pelican, as for diurnal soaring birds one should successfully identify both daily and across-day changes in the σ2m within each individual's trajectory. The dBBMMs were generated using the library "move" in the R package v. 4.0.6 (Kranstauber et al. 2020).

Sex-related differences in the annual 95% UD (HR in this study) and 50% UD (CA in this study) sizes were examined by applying univariate analyses, i.e. Mann–Whitney *U* Test. Spearman correlation analysis was applied in order to explore the relation between the number of wetlands visited by the DPs and their 95% UD size. Differences in the seasonal 95% UD and 50% UD sizes were examined by applying non-parametric Kruskal–Wallis rank sum tests with a Bonferroni correction for multiple comparisons. Seasons refer to the four stages of the annual cycle (see section "Data curation").

Table 1 Tracking data of 11 Dalmatian pelicans monitored by GPS/GSM telemetry during 2013–2019 in south-east Europe. The area (in km^2) of the utilisation distribution (UD) 95% and 50% of Dalmatian pelicans radio-tracked is provided. They are ordered from smaller to larger UD 95% area

Pelican ID	Sex	Monitoring period	Tracking days	UD 95%	UD 50%
K1	F	11/02/2016–12/01/2017	336	1533.16	23.88
K3	F	12/02/2016–08/03/2017	365*	909.08	18.73
P06	M	22/06/2013–02/02/2014	225	714.57	29.1
K4	F	13/02/2016–18/06/2016	126	609	13.69
P09	M	23/07/2013–07/01/2019	365*	439.13	36.88
P05	M	21/06/2013–10/02/2015	365*	369.01	14.1
K2	F	11/02/2016–03/07/2017	365*	144.91	11.25
P08	M	20/07/2013–16/09/2014	365*	138.65	2.61
P10	M	01/06/2014–17/12/2015	365*	98.95	4.57
P14	M	01/06/2014–04/01/2015	217	73.21	2.22
P13	M	30/05/2014–22/07/2015	365*	42.41	1.53

*Only the last 365 tracking days were considered

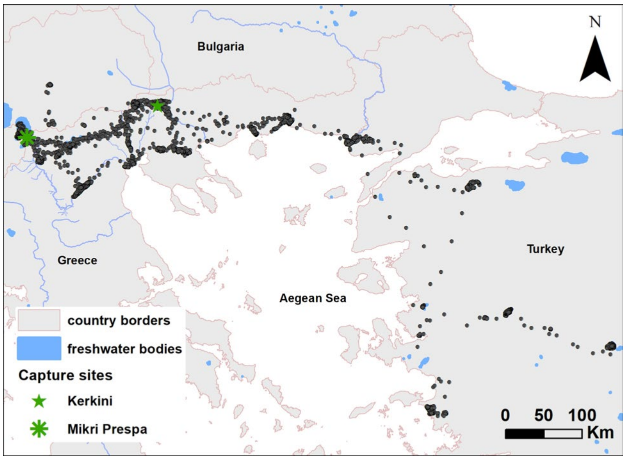

Fig. 1 Locations of Dalmatian pelicans ($n=11$) captured at Lakes Kerkini and Mikri Prespa in northern Greece. Shapefiles of large rivers and lakes were downloaded from https://www.eea.europa.eu/data-and-maps/data/wise-large-rivers-and-large-lakes and shapefiles of Greek rivers and lakes were downloaded from http://geodata.gov.gr/en/

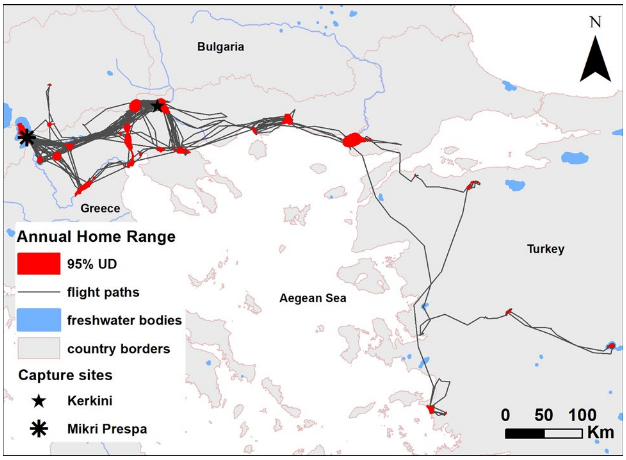

Fig. 2 Overview map of the 11 individuals' trajectories. The red areas depict the 95% of the utilisation distribution (UD) of all individuals. Individuals ranged from northern Greece (Great Prespa Lake) to Turkey (Lake Işıklı)

Results

A total of 58,369 GPS locations were collected from 21st June 2013 to 07th January 2019 (Fig. 1, Table 1). The average monitoring period per bird was 314 ± 84 tracking days (range = 126–365) whereas the mean number of radiolocations was 5306 ± 2205 per bird (range = 1959–8524) (Table 1).

The home ranges of the 11 Dalmatian pelicans included in total of 31 water bodies distributed in the broader Balkan region including wetlands and lakes in North Macedonia and in Turkey (Fig. 2), in addition to all the large wetlands of northern Greece, from the Prespa lakes in the west (Greece-Albania-North Macedonia) to the Evros/Meriç delta in the east (Greece-Turkey). The threefold difference observed in the 95% UD between males/captured at Prespa and females/captured at Kerkini, was not significant (Prespa males mean 95% UD = 268.0 km^2 vs. Kerkini females mean 95% UD = 799.0 km^2, Mann–Whitney U Test $P > 0.05$). Similarly, the 50% UD did not differ between sexes/capture sites (Prespa males mean 50% UD = 13.0 km^2 vs. Kerkini females mean 50% UD = 16.9 km^2, Mann–Whitney U Test $P > 0.05$).

The 95% UD was estimated for all individuals at 461.1 ± 458.9 km^2 (range = 42.4–1533.2) and the 50% UD at 14.4 ± 11.8 km^2 (range = 1.5–36.9) (Table 1). The number of water bodies visited by each bird was positively related to the DPs 95% UD (Spearman $r = 0.79$, $P < 0.05$).

The home range size of the breeding period is larger than the other three seasons both for the 95% UD and 50% UD, but differences were not statistically significant between seasons for either of the 95% UD and 50% UD sizes (Kruskal–Wallis test with Bonferroni corrections $P > 0.05$) (Fig. 3).

Discussion

Annual HR and CA

The HR and CA of the Dalmatian pelicans were estimated for the first time. Results from the study of 11 radio-tagged individuals showed that the birds travel thousands of kilometres away from and back to their capture site within a year (see Figs. 1 and 2). Many factors are known to directly affect the spatial organisation and movement of animals (McNab 1963; Mace et al. 1983; Weimerskirch et al. 2000; Rolando 2002). In particular, HR is primarily determined by the underlying distribution of food resources, both general abundance and spatio-temporal predictability (Brown 1975; Schoener 1983; McLoughlin and Ferguson 2000; McLoughlin et al. 2000; Rolando 2002; Legagneux et al. 2009). In the case of Dalmatian pelicans, the dBBMM results indicate that the birds spend considerable amounts of time in most of the wetlands they visit.

Furthermore, HR and CA of Dalmatian pelicans exhibited manifold differences between individuals. This is something observed for both American white pelican (King et al. 2016) and brown pelican (King et al. 2013; Lamb et al. 2019). The former species is mainly a migrant and less so a partial migrant while the latter is a partial migrant, although some methodological differences between studies in HR estimation may exist. Within-population variation in HR size is observed in many animals, although the underlying processes have not been well understood yet (Rühmann et al. 2019; Seigle-Ferrand et al. 2021). For example, the black-backed woodpecker is known to have HR sizes varying several orders of magnitude, although the ecological factors explaining the variation have not been adequately explored (Tingley et al. 2014). Amongst the main drivers

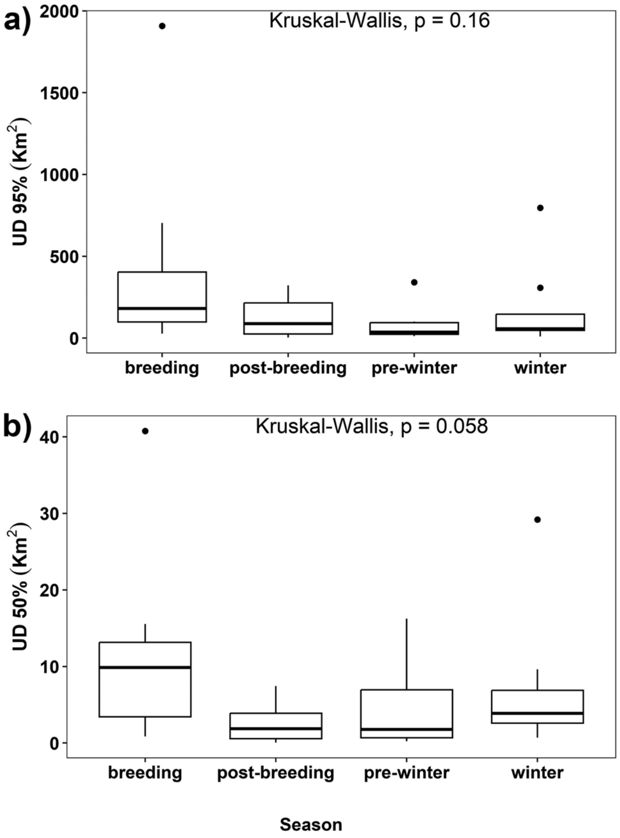

Fig. 3 Boxplots depicting the mean **a** 95% utilisation distribution (UD) and **b** 50% UD sizes during breeding, post-breeding, pre-winter and winter stages. The means were not significantly different (Kruskal–Wallis rank sum test with Bonferroni correction, $P > 0.05$)

of within-population variation in HR are resource availability, landscape heterogeneity, life traits (e.g. body mass) and individual attributes, such as age and sex (McLoughlin and Ferguson 2000; Rolando 2002; Ruhmann et al. 2019; Seigle-Ferrand et al. 2021). The underlying causes for the 36-fold and 24-fold (in HR and CA respectively) individual differences between the studied pelicans may be attributed to physical condition, breeding propensity, time spent in trying to secure a mate and a nesting place, temporal variations in abundance and availability of food, several trade-offs on energy matters and possibly other social factors that remain obscure (Mcloughlin and Ferguson 2000). We assume that depending on the cumulative effect these factors have, each individual follows a different strategy, resulting in manifold differences between the estimated HR and CA (King et al. 2013, 2016, 2017). The fact however that all tracked pelicans exhibited different use patterns of the 31 wetlands used in total, is an indication that irrespective to resource availability, social factors may also play a very important role in the exploitation of the wetlands' spectrum available to pelicans.

No differences in the HR sizes between sexes were detected, although females in this study tended to have larger home ranges than males. However, the fact that all male birds were captured at Lake Mikri Prespa and all females at Lake Kerkini, created an unexpected confounding effect of sex and capture site. Some studies of the brown pelican have shown that male individuals have almost 3 times larger HR than females (King et al. 2013), but more recent studies (Lamb et al. 2020) have found no sex effects. However, differences in the models used, or/and different time intervals studied, can be related to the species ecological preferences (breeding, feeding, etc.) and might also play an important role in the demonstration of sex effects. In any case, we avoid to draw any conclusions based on our results because of the confounding effect of sex and capture site.

The number of wetlands visited was positively associated with the estimated annual HR size. Given the fact that DPs are inshore feeders, spending most of their foraging time in or around wetlands, this pattern could be related to food availability and water level fluctuations in the wetland system of northern Greece. Home ranges are primarily driven by the underlying distribution of food resources (Brown 1975; Schoener 1983; Legagneux et al. 2009). Unfortunately, there were no available data on fish stock sizes for the wetlands, which could be accounted for as a resource availability metric. Moreover, no age comparison could be made, as all the individuals studied were adults.

Additionally, as Kerkini Lake is the major staging site where DPs stop on their way to Prespa and additionally they visit Kerkini from Prespa to feed, it is not clear whether the capture site and capture method may associate with our results because the exact relation of the captured birds to the capture site is not clear. Thus, HR size of different individuals captured at the two different sites cannot be correlated to the colony sizes to check whether there are density-dependent effects on HR or CA. Nevertheless, individuals captured at the two different colonies overlapped in their space use during the year and the breeding period. If we hypothesise that individuals captured at each site are indeed connected to this site, then a negative effect of density on HR is suggested, as the average HR of Kerkini birds was 3 times larger than that of the Prespa birds. This is the inverse observed for Brown pelicans in the Gulf of Mexico (Lamb et al. 2020).

King et al. (2013) showed that the HR of brown pelicans in the northern Gulf of Mexico consisted of many different parts in several wetlands. They also showed that CA (50% UD) represented 0.85–5.34% of the total HR (99% UD). Furthermore, King et al. (2016) showed that core HR for the American white pelicans was also spatially unconnected and comprised 7.1–9.9% of the total HR. Very similarly, for the Dalmatian pelican in SE Europe CAs represented ca 1.55–8.4% (average 3.91%) of the total HR and generally, they were not single areas but consisted of an average of 4.1

different nuclei (range = 1–8), often more than one in a single wetland. It seems that in large colonial waterbirds such as pelicans, whose main activity is confined in wetlands, the ratio between CA and HR is much smaller than that of territorial species, which are central place foragers and use confined areas around their nests. For example, for Marsh Harriers *Circus aeruginosus*, Cardador et al. (2009) found that CA represented 10–28% of HR. However, like other large waterbirds, pelicans tend to intensively use specific sub-areas of wetlands which contain their main roosting and resting areas, where they spend almost 70% of their daily time budget (unpublished field observations; see also del Hoyo et al. 1992; Nelson 2006). Besides, in contrast to territorial species, pelicans often forage communally in loose or dense groups, concentrating their fishing activities in areas with high prey density (unpublished field observations; see also Nelson 2006).

Seasonal HR and CA

We did not detect seasonal variation in the HR (and CA) of the Dalmatian pelicans. Efrat et al. (2018), however, working with the same population, showed that during spring, Dalmatian pelicans appear to perform more inter-lake flights and use more water bodies compared with summer or winter. For the American white pelican, King et al. (2016) found that summer HR tended to be 3–4 times larger than winter HR. Our contrasting findings may be explained by the fact that apparently none of our monitored pelicans bred during the examined annual cycles. But higher spring HRs might be related to higher mobility of pelicans amongst sites prior to breeding to inspect possible nest locations and mating possibilities or efforts for re-nesting after early nest failure (Haig et al. 1998).

As Dalmatian pelicans in SE Europe are short-distant migrants, the environmental conditions they encounter in several parts of their annual cycle only differ radically during the breeding season, given the specific requirements for nesting habitats and the very limited number of breeding wetlands. Other species, such as ducks for example (Scott and Rose 1996; Guillemain et al. 2005), are long-distance migrants known to use very distinctive habitats and have different ecological requirements in winter compared to the breeding season, with presumably completely different spatial use due to divergent energy (reproduction vs. survival) and social requirements (Legagneux et al. 2009). In our case, we may hypothesise that there are two crucial conditions for DPs: the possibility to breed, and food and related energetics, but other factors might also play a role (e.g. social factors, such as the formation of groups of peers). Birds visit breeding colonies in search of opportunities to breed and at a certain threshold of time investment, if they have failed, they quit and start wandering (unpublished field observations). In the same line of argument, Efrat et al. (2018) showed that long inter-wetland flights were very rare in winter, and the number of flights during spring was higher than during summer, suggesting greater motivation to move in spring, i.e. to search for mates and a mating site (Efrat et al. 2018), as observed in other birds (Guilford et al. 2012; Linnebjerg et al. 2013). In fact, higher mobility in spring (Efrat et al. 2018) does not necessarily correspond to a larger spring HR.

Conservation and management implications

Dalmatian pelicans use annually a number of different wetlands across northern Greece, SE Europe and Turkey (see also Efrat et al. 2018; Catsadorakis 2019). Our results suggest that there might be intra-population differences in the extent of the seasonal HRs and confirm the continuous intersite movements of the species, a behavioural trait also characteristic of other waterbirds (Haig et al. 1998). The conservation of the breeding populations of DPs in SE Europe depends not only on good habitat conditions prevailing in individual wetlands, but also on a wider network of water bodies extending from the Prespa lakes to eastern Anatolia in Turkey, and from Lake Karla in the south (Catsadorakis 2019) to the Danube Delta in the north (unpublished data). As in the case of other short- or long-distance migrants, transboundary and/or even intercontinental conservation efforts are needed (Haig et al. 1998) to secure the species survival. Dalmatian pelicans and other pelican species have population dynamics that require the use of multiple wetlands but this aspect of their life history has often been ignored in planning their conservation (Haig et al. 1998). As in other pelican species (cf. Lamb et al. 2020), individuals from different colonies overlap in the use of wetlands away from their capture sites. Thus, in case of an acute stress event, the probability of an individual interacting with that stressor will also relate to the distribution of colonies in the region. Although our data and methods of spatial analysis did not show that flight paths or flight corridors connecting the various wetlands used by the birds were a part of the HR or CA of Dalmatian pelicans, a simple examination of the movement itineraries of the studied birds (Figs. 1 and 2) rather advocates for the existence of such corridors. It is apparent that conservation measures should be taken to ensure that the frequent movements of pelicans between CAs of their HRs in NW Greece are made safe and risk free, for example not obstructed by wind energy facilities and other infrastructure that may threaten pelicans. Within that framework, to propose effective conservation measures, we should further explore and better understand the modes in which pelicans make use of each separate wetland, and which parts of the wetlands they use per season to cover their needs and activities (feeding, resting, roosting).

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Author contributions G.C. and O.A. collected and provided the data. E.G. and G.C. wrote the main manuscript text and E.G. prepared all figures and tables. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the authors on reasonable request. The data include the latest 365 tracking days of the monitoring period (for each Dalmatian pelican) for those tracks exceeding one calendar year.

Declarations

Conflict of interest The authors declare no competing interests.

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