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Seasonal differences in energy expenditure, flight characteristics and spatial utilization of Dalmatian Pelicans *Pelecanus crispus* in Greece

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Animals typically adjust their behaviour to their changing environment throughout the annual cycle, modulating key processes such as the timing of breeding and the onset of migration. Such behavioural changes are commonly manifested in the movements and the energetic balance of individuals in relation to their species-specific physiological characteristics, habitat attributes and the environmental properties of their distribution ranges. We used GPS and acceleration data collected using transmitters on free-ranging birds to quantify annual movement patterns and estimate energy expenditure of the Dalmatian Pelican *Pelecanus crispus*, a large, soaring avian species which performs short-distance migration and spends its entire annual cycle in mid-latitudes. To assess the representativeness of our results, the transmitter effect was also tested. We found that daily trends in the overall dynamic body acceleration (ODBA; a proxy for energy expenditure) differed among seasons, with the highest values occurring during spring and the lowest during winter. Long inter-lake flights were very rare in winter, and the number of flights and ODBA during spring was higher than during summer, suggesting greater motivation to move in spring. Although transmitters may have affected the birds, as none of the tagged birds bred, we found seasonal differences in behaviour and activity level. The observed patterns in differences in activity levels, long-distance flights and flight characteristics between seasons suggest an annual rhythm of energy expenditure. These findings allow a better understanding of bird phenology, specifically regarding adaptations to wintering in a cold climate by reducing movement-driven energy expenditure. Finally, the identification of periods with high and low energy expenditure may guide future conservation efforts by adjusting conservation plans in accordance with changing needs during the annual cycle.

Keywords: annual cycle, movement, short-distance migration, soaring.

The behaviour of birds is highly affected by seasonality (Gwinner 2003). The effect of seasonality is mediated by changes in several factors, including weather, feeding opportunities and risks (Nelson *et al.* 1990, Gwinner 2003). In places that are characterized by distinct seasonality, these differences set an annual rhythm of major life-history decisions (e.g. breeding, moulting and migration) that shape the movement and energy expenditure of birds (Gwinner 2003, Newton 2007, Swanson 2010). For example, the energy expenditure of birds is expected to increase due to increased locomotion costs during migration or when rearing chicks, due to increased thermoregulation costs

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during winter, and due to increased costs during production of eggs and moulting of feathers (Gwinner 2003, Swanson 2010). Although there is much evidence to suggest that the events during one period of the annual cycle can carry over and affect subsequent periods and impact many aspects of the animal's life, most studies on vertebrates in general and birds in particular still focus only on one season within the animal's annual cycle (Marra *et al.* 2015). In this study, we investigated the phenology of Dalmatian Pelicans *Pelecanus crispus* by quantifying their behaviour, focusing on their activity-induced energy expenditure, flight characteristics and movements between waterbodies in Greece throughout the annual cycle.

Movement, one of the most important features of life in nearly all organisms, affects many aspects of individual fitness and the dynamics of higher level (population, community) ecological processes (Nathan *et al.* 2008). Birds move mainly by flight, which incurs high energetic costs (Schmidt-Nielsen 1972). These flight locomotion costs change drastically throughout the annual cycle, increasing when flight conditions are less suitable (Hedenström 1993, Sapir *et al.* 2011, Rotics *et al.* 2016). In addition, flight altitude and speed are affected by weather conditions, with lower altitudes and speeds expected during colder weather (Shamoun-Baranes 2006, Horvitz *et al.* 2014). To reduce the energetic costs of flight, birds use different flight modes (e.g. active flapping and passive soaring-gliding) and change their behaviour and physiological state prior to long migratory flights (Alerstam *et al.* 2003, Buehler & Piersma 2008). Birds are also expected to change their daily activity, and thus their energy expenditure, during the annual cycle, for example, increasing expenditure during migration and breeding, and decreasing it during moult (Swaddle & Witter 1997, Dale *et al.* 2006).

Energy expenditure is the sum of two components which can both vary during the annual cycle: (1) the basal metabolic rate (BMR), which is the metabolic rate an adult (non-growing) animal requires for maintenance at rest at thermoneutral conditions, post-absorptive and without breeding-related requirements, and (2) the required metabolic rate for all activities above and beyond BMR, such as flying, feeding and moulting (McNab 1997, Swanson 2010). Energy expenditure typically varies between seasons due to changes in environmental conditions and/or animal behaviour during the annual cycle. Macaroni Penguins *Eudyptes chrysolophus* and Great Cormorants *Phalacrocorax carbo*, for example, show the lowest daily energy expenditure during the first stages of breeding, coinciding with reduced feeding or fasting (Green *et al.* 2009, White *et al.* 2014). In another waterbird, the Common Eider *Somateria mollissima*, annual variation in energy expenditure during rest is not correlated with changes in water temperature but is presumed to be affected by feather moult (Guillemette & Butler 2012). Overall, seasonal changes in the energy expenditure of birds during the annual cycle are rarely studied and the focus has been on a limited range of avian taxa. These studies show no consistent pattern, with some studies supporting the highest energy expenditure during winter, some during spring, and others finding no season-related differences at all (Anava *et al.* 2000, Webster & Weathers 2000). A commonly used method to estimate energy expenditure is the calculation of overall dynamic body acceleration (ODBA; Wilson *et al.* 2006, Halsey *et al.* 2011, Qasem *et al.* 2012). ODBA estimates activity-related energy expenditure and although it cannot estimate energy costs resulting from procedures that do not involve alteration of body posture (e.g. moult or production of eggs), it is highly correlated with more well-established methods and direct measures of energy expenditure, such as oxygen consumption, heart and metabolic rates, and with the doubly labelled water method (Halsey *et al.* 2009, Enstipp *et al.* 2011, Stothart *et al.* 2016).

Here, we used ODBA to estimate seasonal energy expenditure for Dalmatian Pelicans. Dalmatian Pelicans are large, soaring-gliding birds which perform short-distance migrations of a few hundred kilometres at most and which breed in Eastern Europe and Western Asia; their western population spends the entire year at middle latitudes (Crivelli *et al.* 1991, Elliot *et al.* 2017). Dalmatian Pelicans present one of the extreme examples for the study of energy requirements, as these requirements are expected to be higher with increasing body size and colder wintering range (Swanson 2010). Therefore, we predicted that Dalmatian Pelicans will present seasonal variation in energy expenditure and movement with seasonal changes in the interaction between these factors. For the studied Dalmatian Pelicans, climate is considerably colder and food availability lower during winter when many waterbodies freeze. Colder climate also results in less suitable flight conditions for soaring birds, increasing the energetic expenditure in flight and decreasing flight altitude and speed (Shamoun-Baranes 2006, Pennycuick 2008, Horvitz *et al.* 2014), and a decrease in food resources can result in lower energy intake rate. Considering these assumptions, we hypothesized that Dalmatian Pelicans will move less and thus decrease their energy expenditure in colder climates and when food availability is limited. To examine this hypothesis, we focused on movements between waterbodies (inter-lake) throughout the annual cycle, which are significantly longer than movements within waterbodies (intra-lake) and are associated with high energetic demands. We predicted that: (1) ODBA and movement will be lower during winter compared with other periods of the annual cycle; (2) the number of inter-lake flights and the number of visited waterbodies will be lowest during winter and highest during summer; and (3) flight altitude and speed will be lower during winter, while flight energy expenditure will be higher. Addressing questions regarding seasonal energy expenditure and movement could further highlight the consequences of wintering in middle latitudes, provide insights into the evolution of migration and the annual cycle, and aid in the implementation of better, more species-specific and flexible conservation and management plans (Barton *et al.* 2015, Allen & Singh 2016).

METHODS

Study species, study area and data collection

Dalmatian Pelicans typically weigh between 10 and 13 kg, with a wing span between 310 and 345 cm. Dalmatian Pelicans feed almost exclusively on fish, spend most of their time on water and breed on the ground on islands (Elliot *et al.* 2017). The species distribution is wide, ranging from Eastern Europe to Mongolia, and its conservation status was recently downgraded from 'Vulnerable' to 'Near Threatened' following major conservation efforts (Birdlife International 2017). The south-eastern European population consists of over 3000 breeding pairs, *c.* 2000 of them in Greece (G. Catsadorakis pers. obs.). The Greek population includes short-distance migrant sub-populations that winter in the Eastern Mediterranean, mostly along the Greek shore and in Turkey (Onmuş *et al.* 2011, Catsadorakis *et al.* 2015). In 2012–15, these sub-populations bred exclusively in five breeding sites: Lake Mikri Prespa in the north-west is the main breeding site with *c.* 85% of the Greek breeding population, Kerkini Reservoir in the north is a growing breeding colony, and three other smaller breeding colonies are found outside the range of the studied pelicans, two in the western coast of Greece and one 200 km south of Prespa Lakes (Catsadorakis *et al.* 2015). Kerkini Reservoir is also an important site throughout the year, serving as a wintering site and a major stopover site for migrating Dalmatian Pelicans (Crivelli *et al.* 1991, Doxa *et al.* 2012a). Dalmatian Pelicans start breeding at least 3 years after hatching but do not breed every year; the reasons for this and how often they do breed are unknown (Crivelli *et al.* 1997; A.J. Crivelli pers. comm.).

Adult Dalmatian Pelicans were caught at Lake Mikri Prespa using leg traps between June and August of 2012 and 2013 and on 30 May and 1 June 2014, at the end of the breeding season. Age was determined by plumage (Elliot *et al.* 2017, G. Catsadorakis & O. Alexandrou unpubl. data). Movement and acceleration data were collected using solar-powered GPS/GSM transmitters: each Dalmatian Pelican was harnessed with one of seven e-obs GmbH transmitters (Munich, Germany) or seven Vectronic Aerospace transmitters (Berlin, Germany), weighing 90 and 160 g including harness, *c.* 1% and 1.7% of the bird body mass, respectively (see Table S1 for exact timing of capture and transmitter type used for each Pelican). Transmitter dimensions were 66 × 39 × 25 and 110 × 35 × 50 mm for e-obs and Vectronic, respectively, and they were harnessed using silicon encased in Teflon and secured in a permanent backpack configuration. Transmitters collected GPS measurements including location (latitude, longitude and altitude above ellipsoid, with an error < 20 m for 95% of measurements), time and instantaneous speed. The e-obs transmitter duty cycle was set to obtain a GPS measurement every 5, 10, 20 or 60 min, depending on the battery voltage, and the Vectronic transmitter duty cycle was set for every 60 min. The e-obs transmitters also collected tri-axial acceleration data, with a duty cycle of a sample every 2, 5 or 10 min. Acceleration data were sampled at 18 Hz per axis for 4.4 consecutive seconds at first, and then reduced to 10 Hz for 4 s to reduce battery consumption. High-rate acceleration samples (18 Hz) were sub-sampled to 9 Hz to be comparable with low-rate samples (10 Hz).

Tri-axial acceleration data were used to calculate ODBA, which was used as a proxy for energy expenditure (Wilson *et al.* 2006, Qasem *et al.* 2012). ODBA was calculated per measurement by first converting the raw mV data to m/s^2 using tag-specific calibration, then subtracting the static component from the total acceleration value per axis, and finally summing the absolute values of all three axes (Wilson *et al.* 2006). We did not use ODBA to estimate absolute energy expenditure but for comparative purposes, assuming that season-related differences in the match between ODBA and energy expenditure are relatively minor. Transmitter data were downloaded remotely using UHF receivers and automatically through the GSM network; e-obs transmitters only sent partial GPS data with up to five locations per day through the GSM network. Other data gaps (< 1%) occurred as a consequence of low transmitter battery or transmitter failure.

Season comparison

The annual cycle was divided into three parts based on current knowledge about the local Dalmatian Pelican phenology. Spring was defined as the period between 15 January, when courting and mating starts, and 20 April, when egg-laying ends for the vast majority of the population (Doxa *et al.* 2012b, G. Catsadorakis & O. Alexandrou unpubl. data). Summer was defined as the period between 21 April and 9 October, which includes the warmer parts of the year during which breeding birds incubate and rear chicks, and when dispersal from the breeding grounds occurs (Crivelli *et al.* 1998). The winter season was defined as the period between summer and spring; during this time, the Greek population is at its wintering grounds.

The effect of season (spring, summer and winter) on the mean daily ODBA was tested using a linear mixed-effect model (LMM) with individual as a random factor and Tukey honest significant difference (HSD) *post hoc* tests. Mean daily ODBA was calculated by averaging all ODBA measurements of a single day separately for each individual. Daily ODBA curves were plotted by hourly means across all individuals for every season, and an annual ODBA curve was plotted using a running average with a window size of 11 days. The window size was set to prevent masking of the trends by a small window size on the one hand and to allow for within-season trends on the other. We estimated and plotted daily ODBA separately on days with and without inter-lake flights to differentiate between long-distance and local movement energy expenditure. Inter-lake flights were found by mapping the movement of each Dalmatian Pelican or, when data were missing, by comparing locations of a Dalmatian Pelican at the start and end of the day (in this case the flights were only used to count the number of inter-lake flights and not for the flight characteristics analyses). Daily and annual ODBA curves were graphically interpreted for differences in ODBA trends between the seasons, with and without inter-lake flights.

To estimate the effect of seasonality on movement and site use, we compared the number of inter-lake flights, flight routes and flight characteristics during the annual cycle. The number of days Dalmatian Pelicans made an inter-lake flight was counted for each season and the probability of an inter-lake flight occurring was calculated by dividing the number of days with inter-lake flights by the number of days with sufficient data to recognize such a flight; i.e. days that had data before 07.00 h and after 15.00 h, as 95% of the observed inter-lake flights started and ended between these hours. The probabilities of an inter-lake flight occurring were calculated for every Dalmatian Pelican and averaged among all Dalmatian Pelicans by season. These probabilities were then compared between seasons using a generalized linear mixed-effect model (GLMM) with a binomial distribution, individual as a random factor and a Tukey HSD *post hoc* test to compare each pair of seasons. Data from Dalmatian Pelicans that had fewer than 30 relevant days in a certain season were excluded from this analysis. For every inter-lake flight, flapping and soaring-gliding were distinguished using the tri-axial acceleration data by identifying differences in the heave axis (Nathan *et al.* 2012, Resheff *et al.* 2014), and flap rate was calculated by dividing the number of flap events by the total number of acceleration measurements during an inter-lake flight. A comparison of inter-lake flight characteristics between the different seasons was performed by comparing spring and summer season flight characteristics: using GLMM with a binomial distribution to compare flap rate and LMM to compare inter-lake flight displacement (beeline distance between take-off and landing), mean speed and mean altitude above ground-level. All models included individual identity as a random factor. In addition, mean ODBA levels were calculated for each inter-lake flight and tested for correlation with flapping rate using Pearson's correlation coefficient. Altitude was calculated by subtracting the geoid height above the ellipsoid and the ground level (obtained from Movebank's Env-DATA, Dodge *et al.* 2013) from the sampled height above the ellipsoid.

To understand the differences in spatial utilization between the seasons, inter-lake flights were mapped and the relative use of waterbodies in each season was calculated by dividing the number of nights Dalmatian Pelicans spent on each waterbody by the total number of sampled nights in the season. Waterbodies were defined as any place in which the Dalmatian Pelicans landed during the study (which was always on water). The minimal tracking duration for this analysis was 200 days per Dalmatian Pelican, ensuring departure from the capture site (see Table S1 for total tracking times). The altitude of each waterbody was noted and its effect on waterbody choice between seasons was tested using LMM including each individual's identity as a random factor and Tukey HSD *post hoc* tests. An association between the seasons and the proportion of nights spent at the different waterbodies was tested for the 10 most visited waterbodies, using the chi-square test of association.

Transmitter effects

To understand the possible effects of transmitters on the studied Dalmatian Pelicans, we first examined whether Dalmatian Pelicans bred, by mapping their locations during the time that other Dalmatian Pelicans in the population bred. Secondly, the mortality rates of the studied Dalmatian Pelicans were calculated for birds that were tracked for more than 200 days, separately for the first and second year after tag deployment (when data were available).

Data handling and calculation of summary statistics were performed using MATLAB R2013b. GLMMs were performed using the lme4 package (Bates *et al.* 2014) in R 3.4.2 (R Foundation for Statistical Computing, Vienna, Austria). Mapping was done using MATLAB, R and GOOGLE EARTH PRO and other statistical tests were performed using IBM SPSS STATISTICS 21 (IBM Corp, Armonk, NY, USA). Unless otherwise noted, all results are reported as mean ± sd.

RESULTS

General

The following analyses are based on data obtained from 14 adult Dalmatian Pelicans (at least 3 years old) which were tracked between June 2012 and December 2015, with a mean of 288 ± 264 tracking days per individual. Acceleration data were obtained from seven of the Dalmatian Pelicans. Tracking efforts during the annual cycle are presented for every individual in Supporting Information Table S1 and Fig. S1. The most frequent location sample interval was 15–25 min, for which there were 2218 days and 136 381 fixes overall. The number of GPS samples taken at these sample rates differed between seasons and was lower during winter than during the other seasons due to less effective solar charging of tags (Fig. S1).

ODBA seasonal and daily variation

Including days with inter-lake flights, a significant difference was found in daily ODBA between seasons (LMM; $F_{2,2853} = 18.78$, $P < 0.001$) and between each pair of seasons (Tukey HSD; $P = 0.0067$ for spring–summer comparison and $P < 0.001$ for the other comparisons), revealing the highest activity during spring and the lowest during winter. The mean total daily ODBAs were 0.816 ± 0.319 ($n = 572$ days), 0.777 ± 0.224 ($n = 1521$ days) and 0.726 ± 0.229 m/s^2 ($n = 764$ days) during spring, summer and winter seasons, respectively. Daily activity curves for each season were different, with two distinctive activity peaks observed during the spring and summer seasons, at sunrise and 5 h after sunrise; during winter, only a single longer peak appeared (Fig. 1a) between 2 and 5 h after sunrise. ODBA was higher at mid-day during spring and at night during summer (Fig. 1a). Annual activity curves show that during spring, there was an increase in ODBA, followed by two peaks at the start and end of summer and a decrease during winter (Fig. 1b).

When examining days with only intra-lake movements, a significant difference was found in daily ODBA among the seasons (LMM; $F_{2,2768} = 6.0$, $P = 0.0025$); this still showed a

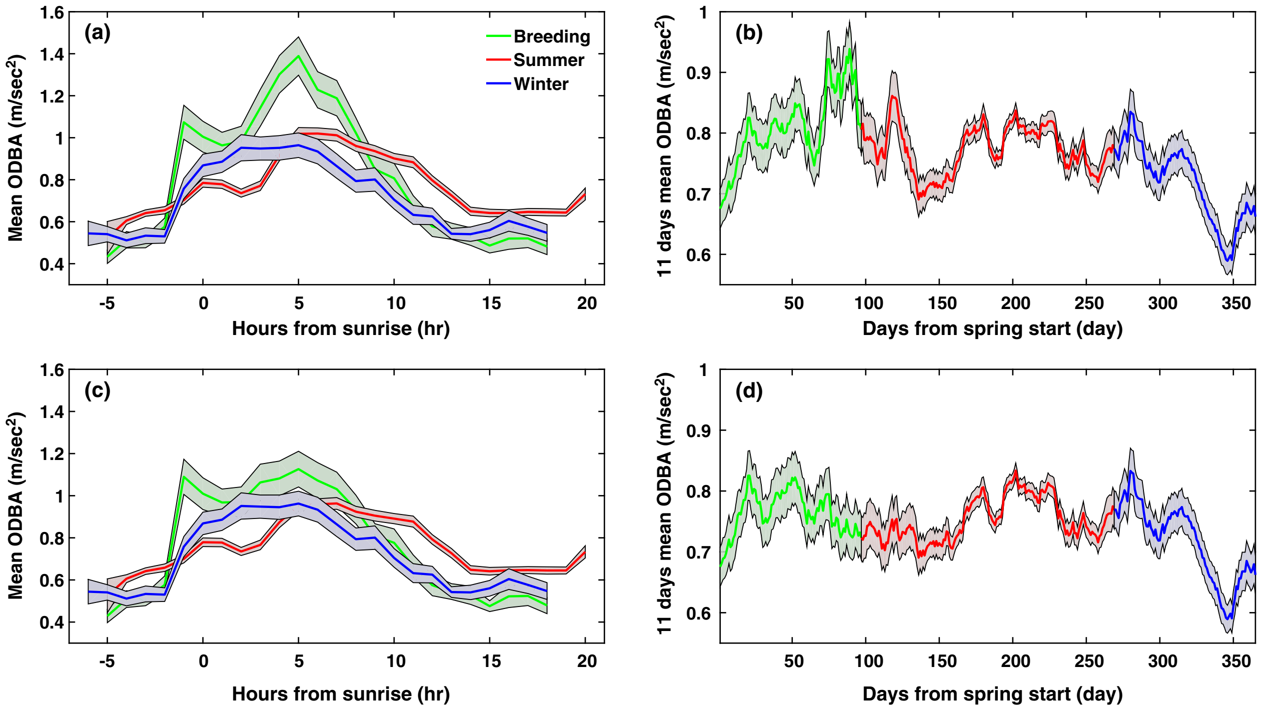

Figure 1. Daily (a, c) and annual (b, d) activity curves are shown for the three seasons, with (a, b) and without days in which inter-lake flights occurred (c, d). Lines represent the mean and the greyish backgrounds represent 95% confidence intervals. In (b) and (d), 0 on the horizontal axis represents the start of the spring season (January 15th).

lower activity during the winter than during other seasons (Tukey HSD; $P = 0.0017$ for winter–spring comparison and $P = 0.012$ for winter–summer comparison), but no significant difference between spring and summer ($P = 0.38$). The mean total daily ODBAs were 0.77 ± 0.224 ($n = 545$ days), 0.756 ± 0.182 ($n = 147$ days) and 0.726 ± 0.231 m/s^2 ($n = 757$ days) during spring, summer and winter seasons, respectively. Daily activity curves in days without inter-lake flights were similar to those with inter-lake flights, with decreased differences during mid-day (Fig. 1c). Neither a gradual increase in ODBA during spring nor a peak in activity during the first part of summer was observed during days with only intra-lake movements (Fig. 1d). Mean ODBA was 1.73 times higher during days with at least one inter-lake flight than was the mean ODBA during days without inter-lake flights.

Inter-lake flights

Overall, Dalmatian Pelicans had 115 days with inter-lake flights out of the 3040 tracking days with available data to identify these flights; thus 3.78% of the days included inter-lake flights. The percentage of days with inter-lake flights averaged across individuals differed significantly between seasons (GLMM; $F_{2,24} = 15.8$, $P < 0.001$) with 5.1 ± 5.7% ($n = 39$ flights of seven pelicans), 3.6 ± 1.9% ($n = 64$ of 10 Pelicans) and 0.66 ± 1.1% ($n = 6$ of nine Pelicans) during spring, summer and winter, respectively. This difference was also significant between each pair of seasons (Tukey HSD; $P = 0.028$ for spring–summer comparison and $P < 0.001$ for the other comparisons). Flight characteristics data were extracted from and analysed for 85 inter-lake flights during spring and summer, as the required data were only available for one inter-lake flight during winter. Significant differences were found between inter-lake flights during spring ($n = 28$) and summer ($n = 57$) seasons in flap percentage (GLMM; $z_{82} = -7.89$, $P < 0.001$) and altitude (LMM; $t_{82} = 3.3$, $P = 0.001$), but no significant difference was found in displacement or speed ($P > 0.28$ for both) (Fig. 2). Flap percentage was positively correlated with ODBA during flight periods (Pearson's correlation, $r = 0.94$, $P < 0.001$).

Flight routes during summer and spring showed that during summer, Dalmatian Pelicans appear to cover a larger area and arrive at more waterbodies compared with during spring (Fig. 3). The proportion of the season Dalmatian Pelicans spent in each waterbody was significantly different between seasons (chi-square test; $\chi^2_{18} = 1318$, $P < 0.001$), with some waterbodies used throughout the year and others mainly in specific seasons (Table 1, Fig. 3). During spring, *c.* 60% of the Dalmatian Pelicans' days were spent in the eastern and north-eastern part of their tracked range, whereas during summer their occurrence in these areas increased to *c.* 80% (Table 1, Fig. 3). However, the Dalmatian Pelicans' inter-lake flights to and along the shoreline were more frequent during summer (Fig. 3). A significant difference was found in the altitude of waterbodies used between seasons (LMM; $F_{2,3646} = 292.4$, $P < 0.001$) and between each pair of seasons (Tukey HSD; $P < 0.001$ for all comparisons), revealing the highest altitude during summer and the lowest during winter, 237 ± 267 m ($n = 732$ days for seven Pelicans), 479 ± 272 m ($n = 1868$ for 14 Pelicans) and 91.9 ± 202 m ($n = 868$ for nine Pelicans) during spring, summer and winter, respectively.

Transmitter effects

None of the studied Dalmatian Pelicans bred during the study. Mortality rates were 22% and 60% during the first and second years, respectively, although five of the six mortality events were related to anthropogenic risk factors (electrification, shooting and fishing nets), and it is possible that the last death was also anthropogenically related (Table S1).

DISCUSSION

In this study, we found differences between seasons in the Dalmatian Pelicans' ODBA, a proxy for energy expenditure, which was highest during spring and lowest during winter. Higher ODBA in spring was associated with higher frequency of energetically expensive inter-lake flights in spring, with a 1.4- and 7.7-fold higher probability of an inter-lake flight occurring during spring compared with summer or winter, respectively. Furthermore, a comparison of ODBA between the seasons disregarding days with inter-lake flights showed no significant difference between spring and summer.

Because none of the Dalmatian Pelicans in this study bred, the higher ODBA during spring and early summer could not be the result of the demands of chick-rearing and may represent the efforts to find mates, as observed in other birds (Guilford *et al.* 2012, Linnebjerg *et al.* 2013). Higher energy consumption due to intensive feeding is not reasonable as, according to observations, feeding is a rare activity for Dalmatian Pelicans during the first stages of the breeding cycle (G. Catsadorakis pers. obs.), and a decrease in body mass has been shown for other large, mid-latitude-wintering birds during this period (Raveling 1979). Studies that examined breeding birds of other species have shown that during the first stages of the

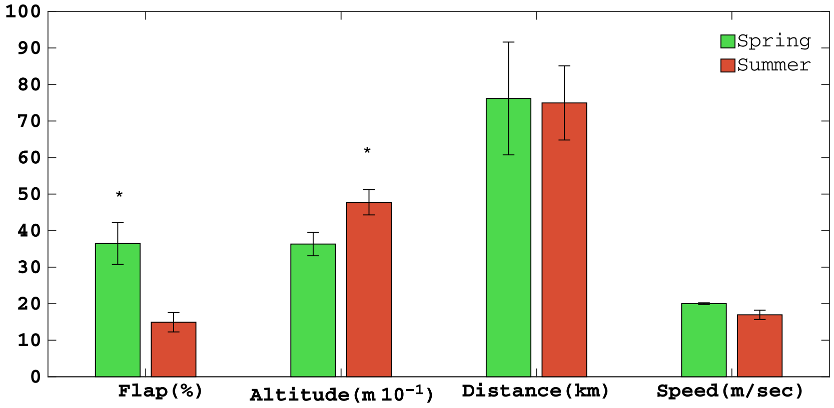

Figure 2. Mean (±se) of inter-lake flight characteristics (flap, altitude, distance and speed) per season (spring and summer). Asterisks represent flight characteristics that differed between spring ($n = 28$) and summer ($n = 57$) (see text). Units of the ordinate axis are given in parentheses under the abscissa axis.

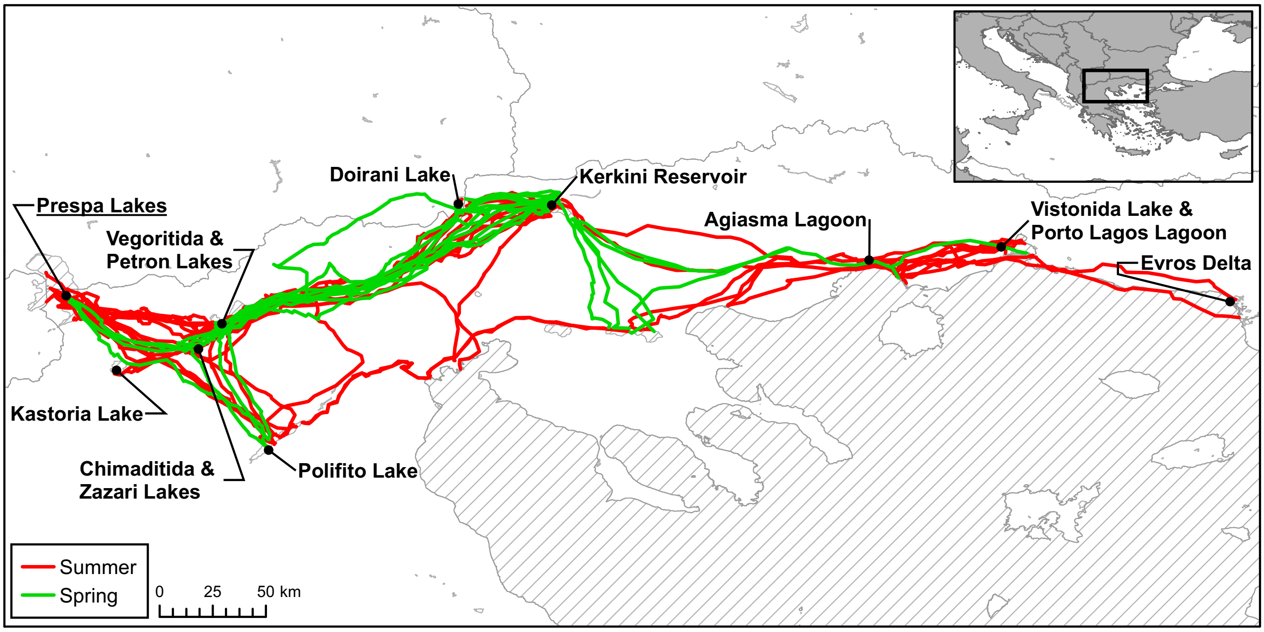

Figure 3. Inter-lake flight routes of GPS-tracked Dalmatian Pelicans across the year. Lines represent inter-lake flights during spring and summer. The tagging site is underlined. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Relative usage of the 10 most frequently used waterbodies.

	Total[a]	Spring	Summer	Winter	Altitude (m)
Prespa Lakes	21.53	6.14	36.08	0.00	850
Evros Delta	16.44	14.29	9.00	25.00	0
Kerkini Reservoir	13.71	14.46	17.01	12.63	30
Vistonida Lake and Porto Lagos Lagoon	11.44	17.00	4.80	23.96	0
Polifito Damlake	11.03	0.63	16.11	0.00	280
Agiasma Lagoon	6.46	2.78	6.27	12.50	0
Kastoria Lake	5.87	16.27	4.82	1.43	625
Doirani Lake	5.70	14.78	1.04	11.96	150
Chimaditida and Zazari Lakes	4.64	6.07	2.27	11.07	620
Vegoritida and Petron Lakes	1.13	3.04	0.99	0.00	520
Other lakes	2.05	4.54	1.61	1.45	

[a] Numbers represent the percentage of the total number of days spent per waterbody during the relevant period. Waterbody locations are shown in Fig. 3.

breeding period, birds expended minimal energy due to minimal movement and reduced feeding or fasting while courting and mating (Green *et al.* 2009, White *et al.* 2014). The finding of minimal energy expenditure during breeding is in disagreement with the results of our study, which show that Dalmatian Pelicans had higher ODBA during this time than during other parts of the annual cycle. It is reasonable to assume that although the studied birds did not breed, their higher ODBA was a result of breeding attempts, whether because they participated in courting and other social interactions during the first stages of breeding or due to increased inter-lake flights aimed at finding new breeding sites or mates in other potential breeding sites. However, this high energy expenditure might also be explained by their lack of success in breeding and might not be found in breeding individuals.

The second peak in activity during summer appears both with and without inter-lake flights and continues through the first stages of winter, which might indicate increased feeding activities aimed at recovering from loss of condition during peak activities earlier in the season or preparing for the less suitable winter conditions, as observed in other large mid-latitude-wintering birds (Owen *et al.* 1992). The high ODBA values during summer nights compared with nights during the rest of the year suggest that Dalmatian Pelicans move more during these nights. Such behaviour has never been described before and might result from night feeding attempts, motivated to increase the energy accumulation rate by the increased mobility of spawning fish at or close to spawning sites (Catsadorakis *et al.* 1996).

During spring, Dalmatian Pelicans made more inter-lake flights than during other seasons. The inter-lake flights during spring were characterized by a higher flap rate and lower flight altitude compared with flights during summer, probably due to less suitable weather conditions (Shamoun-Baranes 2006, Horvitz *et al.* 2014), yet no difference was found in flight distance or speed. Flapping is assumed to consume 5–13 times more energy than gliding (Norberg 1996, Weimerskirch *et al.* 2001, Videler 2006) and can be even costlier due to weather conditions or different decisions made by the flying birds (Hedenström 1993, Horvitz *et al.* 2014). An increase in the number of flights, as well as the energy expenditure of flights, during spring suggests that the Dalmatian Pelicans' incentive to fly during spring was higher than during the rest of the annual cycle, and that the high energy expenditure did not discourage birds from these flights. The finding that Dalmatian Pelicans did not fly faster or cover more distance and that they spent 60% of their days at or close to the breeding grounds during spring suggests that their incentive was not finding food or moving to farther locations but perhaps engaging in social interactions, as they stayed where most of the population was concentrated.

In agreement with our prediction, estimated energy expenditure during winter was very low, and significantly lower than during other seasons, even when disregarding inter-lake flights. Decreased energy expenditure and activity can result from the short days and possibly heightened BMR due to higher thermoregulatory costs, which are characteristics of wintering in middle latitudes (Swanson 2010). Although bigger birds are assumed to be more capable of dealing with colder climates, studies that tested this assumption have produced different results, making this correlation questionable, and there is evidence of increasing BMR due to cold acclimation (McKechnie 2008). Evidence for increasing BMR during winter has been found in other large, mid-latitude-wintering birds (Raveling 1979, Owen *et al.* 1992). In contrast, no significant difference in BMR was found between seasons in captive Great White Pelicans *Pelecanus onocrotalus* (Shmueli *et al.* 2000), although captivity and a low sample size might have affected these results. If the Dalmatian Pelicans' BMR does in fact increase during winter, the lower activity-induced energy expenditure found in this study would imply a trade-off between expending energy to migrate to warmer climates and being limited as to energy expenditure when staying in colder wintering grounds.

Flight routes were also different between seasons. Most of the flights during spring were between the two known breeding sites, Prespa Lakes and Kerkini Reservoir, whereas the routes were more diverse during summer, with more frequent visits to the coastal zone and more eastern locations. The difference in routes between the seasons coincides with the finding that the use of waterbodies was different between seasons; most Dalmatian Pelicans spent almost the entire winter in waterbodies 150 m or less above sea level and a major portion of the summer at the Prespa Lakes; during spring they visited many waterbodies of varying elevations. The difference in use between waterbodies could be explained by three main factors: breeding occurrence, food availability, and air and water temperatures. Prespa Lakes and Kerkini Reservoir host the only breeding colonies among the waterbodies visited by the studied Pelicans, and thus are frequently visited in spring. Food availability changes between seasons and is correlated with weather: high-altitude waterbodies provide an abundance of fish during spring and summer, but in winter these waterbodies freeze, and pelicans move to the coastal wetlands, which are characterized by lower fish densities but do not usually freeze. Lakes Chimaditida and Zazari provide an example of this site preference, being visited frequently during winter despite their relatively high altitude, probably because the winters during this study were mild. During winter 2016–17 these lakes froze and a GPS-tagged Dalmatian Pelican left them at this time (G. Catsadorakis & O. Alexandrou unpubl. data).

Whereas the main increase in energy expenditure during spring and summer is explained by more inter-lake flights, the decrease during winter is explained by a general decrease in activity, a possible way of dealing with the harsh climate at the Dalmatian Pelicans' wintering latitudes. The low ODBA during winter and high ODBA and flight and flap rates during spring point to two sensitive times in the annual cycle of the species. Dalmatian Pelicans significantly reduce their movement-related activity during winter and presumably spend more energy on thermoregulation; they are thus probably sensitive to any disturbance in their wintering grounds that causes them to expend energy by flying. During the period while the birds try to secure a mate and breed, the frequent and low-altitude flights expose the Dalmatian Pelicans to higher risks of collision with wires, hitting wind turbines or being shot. Although data regarding individuals that do breed are missing and should be completed in future research, we suggest that future conservation plans of this vulnerable species take this conclusion into consideration with regard to management plans. For example, management of wind turbine activity times and locations can be guided by the findings regarding use of different routes and waterbodies in different seasons.

Importantly, the fact that none of the tagged birds bred during the study period, together with high mortality rates, suggests that trapping and/or tagging influenced aspects of the Dalmatian Pelicans' behaviour. The observed mortality estimates are higher than the 27.8% found for adults of the closely related American White Pelican *Pelecanus erythrorhynchus* (Ryder 1981). However, the study birds' mortality was almost exclusively caused by anthropogenic risk factors such as electrocution and shooting, which might suggest a high anthropogenic threat to the species; however, tagged birds might be more vulnerable to anthropogenic threats. The study effects on the Dalmatian Pelicans are hard to quantify due to the small sample size and because of natural tendency of Dalmatian Pelicans not to breed every year. In addition, because Dalmatian Pelicans may moult to adult plumage before they start breeding, we cannot be sure whether all of the studied pelicans were already at breeding age. Despite this, we observed our studied birds at the same locations as the rest of the Greek Dalmatian Pelicans population throughout the annual cycle and throughout the study period, and the flight routes taken were ones in which Dalmatian Pelicans are regularly seen, which suggests that aside from not breeding, their movement and behaviour did not differ from that of the rest of the population.

Trapping and tagging of birds can provide invaluable information about their movement and behaviour that cannot be discovered by simply observing them. However, tagging could also have various adverse effects on tagged birds, as shown in many species, with a notable reduction in breeding success in particular (Calvo & Furness 1992, Barron *et al.* 2010, Bodey *et al.* 2017). Barron *et al.* (2010) reviewed the effects of transmitters on birds using 86 studies of different bird species and found similar adverse effects on energy expenditure, regardless of attributes such as sex, age and mass. Overall, proper assessment of the effects of trapping and tagging on movement, behaviour and particularly breeding of GPS-tagged Dalmatian Pelicans will require further studies designed to address such effects directly and to gather independent data on the behaviour of untagged adults and demographic trends in Dalmatian Pelican populations, both of which are critically missing.

To conclude, we observed significant and consistent evidence of differences between the seasons in the behaviour and energy expenditure of Dalmatian Pelicans. Our division of the annual cycle into three seasons on the basis of our previous knowledge yielded several important insights regarding the behaviour of Dalmatian Pelicans during the annual cycle. Some of these insights include higher activity-related energy expenditure during spring and lower expenditure during winter, which may be affected by conspecifics, food availability and climate. Changes in phenology in recent years have been observed in many animals, and ongoing climate change has been proposed as the reason for these changes (Parmesan & Yohe 2002), for example in the Dalmatian Pelican and the closely related short-distance migrant the American White Pelican (Walther *et al.* 2002, Doxa *et al.* 2012b, King *et al.* 2017). Understanding the effects of climate change on the annual cycle of animals is of great interest (Visser *et al.* 2004, Visser & Both 2005) and studying in detail current movement and behaviour patterns during the annual cycle should allow for prediction not only of the time shift of main events but also of the effects climate change and other stressors will have on the animal (Ådahl *et al.* 2006, Marra *et al.* 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Tracking details by individual.

Figure S1. Available daily data.