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Forum

Welcome aboard: are birds migrating across the Mediterranean Sea using ships as stopovers during adverse weather conditions?

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Birds use stopovers during migration to interrupt endurance flight in order to minimize immediate and/or future fitness costs. Stopovers on ships is considered an exceptional and anecdotal event in the ornithological literature. This does not match the experience we had in the summer of 2021, during an oceanographic campaign in the Central Mediterranean, when we regularly observed on average 2.8 birds, of at least 13 species, stopping on board during the 25 days of the campaign. The median stopping time was 42 min, ranging from a few minutes to overnight stays on board. The probability of finding a bird stopping aboard increased with wind force and cloud cover. Birds also stopped more often in a headwind and did not stop when the wind came from different directions other than the headwind. The Central Mediterranean is one of the busiest sea routes in the world, combining the mean daily number of birds on board with the thousands of ships that pass through it during the 3 months of summer migration; we estimate that nearly 4 million birds could use ships as stopover sites. This behaviour may represent a modern-day strategy that uses ships as stopovers in the event of adverse weather conditions or could act as an ecological trap, increasing the mortality of migrants. This phenomenon deserves more research attention and further studies recording body condition and tagging of individuals on board would be informative.

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The numbers of migrating birds are staggering from any perspective you want to analyse. Around 5 billion land birds of nearly 200 species breeding in Eurasia migrate every year, half of which are passerines and related groups (Hahn *et al.* 2009). These movements include medium- or long-range round trips of thousands of kilometres; flight performance in terms of distance, height or speed can be truly remarkable (Newton 2010, Elphick 2011). Migration is the most energy-consuming stage in the life cycle of these birds and can cost up to 50% of an individual's annual energy balance (Drent & Piersma 1990). Evidently this is a winning strategy that has an important adaptive value, because bird species with regular long-distance movements or greater diversity of migratory phenology seem more resilient to extinction than sedentary ones or those that only undertake post-fledging dispersal (Sekercioglu *et al.* 2004, Gilroy *et al.* 2016). However, birds pay significant costs during their migration which are not incurred during their stationary periods in both breeding and non-breeding areas or not experienced by resident species. There are many inherent risks associated with each journey, which at least in the short term can have an effect on population size and dynamics, thus leading to different migration strategies (Richardson 1990, Newton 2010). These strategies vary not only between species (e.g. Saino *et al.* 2010, Deppe *et al.* 2015) and populations (e.g. Gilroy 2017, Sarà *et al.* 2019) but also between age groups and sexes (e.g. Kjellén *et al.* 2001, Vansteelant *et al.* 2017, Santos *et al.* 2020) and between the same individuals crossing different routes in consecutive years (e.g. Mellone *et al.* 2011, Agostini *et al.* 2019). The migratory journey includes long flights without water and food, during which the risks of energy deprivation and dehydration are always present, together with the risks of predation and loss of the route due to headwinds and storms, and all these risks increase dramatically when crossing barriers, such as the Mediterranean Sea. It is therefore not surprising that despite the fact that the migrants carefully negotiate the conditions for crossing the sea barrier (e.g. Vansteelant *et al.* 2017, Santos *et al.* 2020), in many species, migration leads to the death of more individuals than at any other time of the year (Sillett & Holmes 2002, Klaassen *et al.* 2014), and sometimes to mass mortality (Zu-Aretz & Leshem 1983).

Migratory stopovers are the prime example of the flexible behaviour used by migratory individuals, be they large soaring Accipitrids or small broad-front passerines, to adapt to the changing conditions encountered en route or to cross barriers (Schmaljohann *et al.* 2007, Mallon *et al.* 2021, Roques *et al.* 2021). Stopovers have multiple functions that change depending on the ecological and physiological needs of individuals, are related to the life history of species and are also context-dependent (reviewed in Linscott & Senner 2021, Schmaljohann *et al.* 2022). They have been recently defined as 'an interruption of migratory endurance flight to minimise immediate and/or delayed fitness costs' (Schmaljohann *et al.* 2022). Accordingly, the use of stopovers takes place to refuel reserves necessary to continue the journey (e.g. Fusani *et al.* 2009, Aamidor *et al.* 2011, Smith & McWilliams 2014), for physiological recovery (Fuchs *et al.* 2006, Ferretti *et al.* 2021), to wait for the passage of inclement weather (e.g. Smith & McWilliams 2014) or for the arrival of optimal flight conditions, such as the rise of thermal updrafts strong enough to sustain the flight of soaring birds (Vansteelant *et al.* 2015, Shamoun-Baranes *et al.* 2017, Mallon *et al.* 2021).

Behavioural decisions made for stopping (i.e. where to land, when to land and depart, how long to stop, etc.) and the ecology of stopping sites (weather conditions, habitat composition, physical characteristics, etc.) greatly influence efficiency and migration success (Smith & McWilliams 2014), interacting with the selection of favourable winds (Erni *et al.* 2005) or with the rainfall regime (Halupka *et al.* 2017) to determine the survival rates of individuals. Therefore, the location and the network of stopover sites (coastal islands, coastal wetlands, desert oases, etc.) experienced en route, and the behavioural decisions on their use have cascading effects on the regulation of population size of migratory species. Research is showing the key role that understanding these factors plays in improving conservation actions for migratory birds (Mackell *et al.* 2021). The Mediterranean Sea is crossed by numerous routes of Eurasian migratory birds that fly over the marine barrier with multiple strategies; the Strait of Sicily in Central Mediterranean is a crossroads of this traffic (Hahn *et al.* 2009, Elphick 2011, Panuccio *et al.* 2021). The Mediterranean Sea is also one of the busiest shipping route in the world, accounting for 20% of seaborne trade, 10% of world container quantity and over 200 million passengers (REMPEC 2008) and the Strait of Sicily within the Central Mediterranean is one of the core lanes of this traffic (Deidun *et al.* 2018). If we leave out the significant pollution from oil spills and ballast water and the enormous environmental impact of this maritime traffic for Mediterranean wildlife (MED QSR 2017), this brief description gives an idea of the enormous extent of shipping that passes through the routes of Eurasian birds at each migratory season and which could be used as stopover sites. The ornithological literature seems to have neglected the occurrence of birds stopping aboard ships, relegating it to an occasional behaviour (e.g. Newton 2010). There is a long tradition of migration studies conducted at vantage points on the mainland and islands, but migration studies aboard ships are much less numerous and are generally done with the aid of radar (e.g. McClintock *et al.* 1978, Larkin *et al.* 1979, Schmaljohann *et al.* 2008, Hedenströum *et al.* 2009). This phenomenon of onboard stopovers may have been overlooked due to logistical challenges and costs of avian research on vessels.

Scientific articles that report birds stopping on ships are scarce. Paynter (1953) recorded Barn Swallows *Hirundo rustica* that rested on his ship, but did not give weight to the observations, because he was focused on demonstrating the existence and regularity of migration in the open sea across the Gulf of Mexico (debated at the time). Several years later, Szent-Ivány (1959) wrote a short article on House Sparrows *Passer domesticus* that travelled on his ship en route from Bremerhaven (Germany) to Melbourne (Australia), and noticed the group of birds in the Suez Canal (Egypt), the only stop of the ship, and reported that the sparrows landed in Australia at the end of the journey. Vansteelant *et al.* (2017) mentioned a case of a tagged juvenile European Honey Buzzard *Pernis apivorus* roosting on a sailing ship which later died. Indeed, seabirds often use offshore oil and gas platforms for roosting at night and during the day, while landbirds are known to stop on such platforms during migration (reviewed in Ronconi *et al.* 2015). Additionally, dispersed on the world-wide web there are anecdotal observations of birds stopping on sailboats or commercial ships (e.g. Papageorgiou 2019).

During an oceanographic campaign in the Central Mediterranean, we regularly observed several birds stopping on board; below we report a brief description of this. In more detail, we have listed the species and the occurrence of their stops encountered during the oceanographic campaign and we have tried to answer the basic question of whether weather conditions cause an increase in the number of birds that stop on the ship.

DATA SAMPLING

The oceanographic campaign in the Strait of Sicily (Central Mediterranean Sea, Fig. 1), held from mid-August to early November 2021, was divided into three legs; however, constant ornithological sampling took

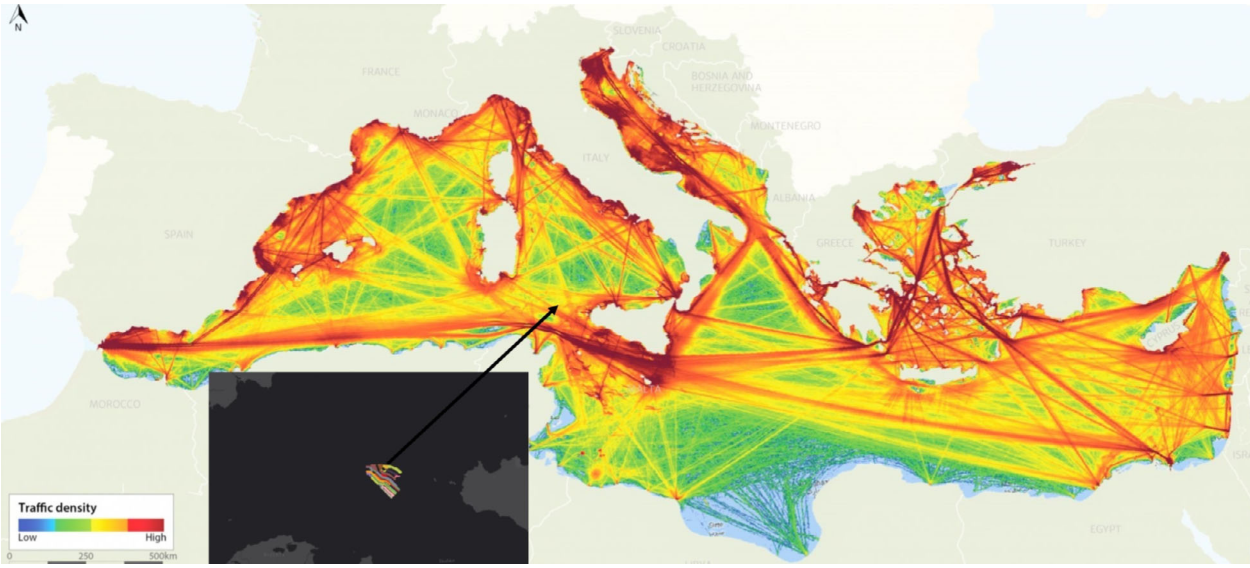

Figure 1. The study area of the marine campaign held in summer 2021 in the Strait of Sicily within the Central Mediterranean Sea. The inset shows the transects of the ship, with the arrow indicating the position on the map with respect to the density of maritime traffic in the Mediterranean Sea. Modified from MED QSR 2017.

place only during the first leg (16 August to 9 September) and was sporadic in the next two. The first leg of the campaign was aimed at describing the geomorphology of the seabed with a multibeam scanner plus the migration of birds and the occurrence of other marine wildlife (seabirds, turtles and cetaceans, large pelagic fishes) in the study area. The observations were made aboard an offshore supply ship (gross tonnage: 1240 t; current draught: 4.2 m; length overall x breadth extreme: 50 × 13.5 m; crew 14 people), built in 2015. Cruising navigational speed was 7–8 knots/h; however, the ship's cruising speed during data acquisition and processing was 2–4 kn/h, due to geological prospecting, which requires low speed. The ship made transects of varying length, back and forth, in the study area (inset of Fig. 1). Seven marine wildlife researchers scanned the study area for marine traffic, litter, migratory birds and other marine animals from 06:30 to 18:30 h (UTC + 1) on the bow deck of the ship. They alternated in shifts of two to four people to cover the 12 h of daily observation. The position on the bow deck allowed a clear view in an arc of 180° from east to west or vice versa depending on the ship heading. The observations were performed with professional optical instruments (Ultravid Leica 10 × 52, Nikon Aculon 7 × 50 WP Global compass and Steiner Navigator PRO 7 × 50 binoculars; Leica Apo Televid 10×–50× telescope; Nikon Coolpix P900 and Canon EOS 5D cameras with telephoto lens Canon – EF 70-200 mm f/2.8). Maritime traffic was recorded using binoculars and telescope and with the onboard radar, which with the aid of dedicated apps (www.marinetraffic.com, www.vesselfinder.com) made it possible to identify the characteristics of the ships (name, type, heading, destination, distance, gross tonnage, cruising speed, etc.). The position and route of the ship at the time of each animal observation and the sea and weather conditions (Beaufort, Douglas and cloud cover scales) were recorded every 15 min with digital equipment and then calibrated with the onboard instruments. Garmin GPS was used for position and routes, and smartphone apps (e.g. www.windfinder.com or www.lamma.rete.toscana.it/en/sea/wind-sea.php) for sea and weather conditions. The total coverage of the sky that took into account all the cloud cover present (low, medium or high clouds) was measured by eye according to the following scale: clear (zero coverage, 0%), little or moderately cloudy (25–50% coverage), cloudy (62–75%), very cloudy (88%), cloudy (100%). Visual assessment of bird distances was standardized in progressive bands (A = 0–50 m, where 0 equals individual on board; B = 51–100 m; C = 101–200 m; D = 201–300 m; E = 301–500 m; F > 500 m), by measuring distances to ships, buoys, etc., with an HK Uineye laser rangefinder (measure range up to 2000 m) and the marine binoculars provided with graduated lenses; distances were then calibrated with the onboard radar. For the purposes of the study, however, only the observations of birds that approached the sides of the ship trying to land or arrived on board (0 distance of A band) have been considered here. The stopover time was measured in minutes from arrival to the observed or inferred (individual no longer seen) time of departure. Some stops of seconds have been standardized as 1 min. Crew operations often disturbed the birds by forcing them to fly away; in addition, some small passerines disappeared among the cables and stern machinery and then flew away unnoticed. When a bird spent the night on board and was not seen the next day, its departure time was conventionally estimated at 06:00 h (around sunrise). Therefore, the stopover time must be considered as an indicative reference value, because in the cases indicated above, it may have been different from that calculated.

DATA ANALYSIS

Birds that landed on board during the first leg (16 August to 9 September 2021) were identified to species level, except in two cases of individuals identified as passerines. They ranged in size from small passerines to medium-sized herons and gulls. This constituted the stopover sample ($n = 52$ records with 58 individuals) that included the same taxa of birds that did not approach the ship (control sample, $n = 142$ records with 234 individuals). The control sample was also mostly identified to the species level, with the exception of 19 records of passerines, four of small waders and two records of medium-sized Ardeids flying too far from the ship. Swifts and seabirds, such as shearwaters and petrels, which usually do not rest on ships, were excluded from the analysis, along with other species larger than the size of the largest bird observed on board. We have excluded large birds (gulls, terns, herons, hawks) because we believe that, for a bird, the ease of stopping depends on the size of the ship. Large birds tend not to land on small or medium-sized ships such as ours, where there is not a sufficient safe distance (or height of towers and antennas) from the crew and operators. This was corroborated by the observation of some small birds that tried to get on board but were unintentionally dislodged by the crew working in their potential landing area.

The stopover sample was analysed with univariate non-parametric statistics (Mann–Whitney U-test for equal medians, Kolmogorov–Smirnov D test) to describe the duration of the stops between similar species and to verify whether the size of the bird predicted the duration of the stopover. For this reason, the birds on board were sized as small (≤ 25 cm, e.g. passerines) or medium (> 25 cm, e.g. doves).

The effect of meteorological conditions on the probability of stopover was evaluated using a generalized linear model (GLZ) with a logit link function and a binomial distribution of the error (McCullagh & Nelder 1989). In this model the response variable was binomial, i.e. present/not present on board (1/0), and the predictors were the wind force on the Beaufort scale (ratio variable on a 0–12 scale), the direction of the wind blowing from the eight cardinal directions of the wind rose (categorical variable with North = 1, North-East = 2, East = 3, etc.) and the presence (continuous variable range 0.0–1.0) of cloud cover. Wind force (WF) and cloud cover (CC) were modelled as continuous and the direction of wind (WD) was entered in models as categorical. The single effects of the predictors and the two interactions (WF × WD and WF × CC) were modelled to test the hypothesis that the probability of stopping on board depends on the meteorological conditions. The predictors were standardized (mean = 0, sd = 1) to eliminate the effect of differences in the original scale of measurement, and were previously subjected to verification of multi-collinearity. This test checked the interdependence between explanatory variables, using the variance inflaction factor (VIF). The rejection threshold of a variable was conservatively considered at VIF < 2.5 (Johnston *et al.* 2018). The procedure rejected the sea force on the Douglas scale (0–9) and the wave height in metres, as these variables were significantly collinear between them and with the force of the wind.

The explanatory power of all possible models predicting the probability for a bird to land on board was evaluated by Akaike's information criterion corrected for small sample (AICc). All models were evaluated by ranking those from the lowest (best) to the highest (worst), computing the ΔAICc difference between each model's AICc value and that of the lowest model. The models that differed by less than two AICc points were considered to receive nearly identical support from the data (Burnham & Anderson 2002). Finally, the Akaike model weight (AICw), which averages the ranked models, so that the sum of weights over the set of candidate models is 1 (Conroy & Carroll 2009), was obtained.

To assess the classification accuracy of the models, the values of a confusion matrix were used to calculate the correct classification rate (CCR), sensitivity (the ratio of correctly predicted presences to the total number of presences) and specificity (the ratio of correctly predicted absences to the total number of absences). The two latter quantities combined in the area under the curve (AUC) of the receiver operating characteristic provided an aggregate measure of the model's performance. The goodness of fit of the resulting models predicting the probability for a bird to land on board was evaluated with the Nagelkerke generalized coefficient of determination. The latter adjusts between 0 and 1 the Cox–Snell coefficient of determination calculated from the ratio between the likelihood of the intercept-only model ($L0$) and that of the specified model ($L\beta$) raised to the power of $2/n$.

We also used circular statistics (Batschelet 1981, Kovach 2011) to analyse whether the degree of wind directions (azimuth with respect to geographical north) occurring when the birds landed (stopover sample) or not (control sample) on board were different from a uniform Van Mises dispersion and differed from each other in their distributions and means. The concentration of data (k value) can increase from 0 (uniform dispersion of the data around the whole circular range of 360°) to > 1 (progressive concentration in one or more directions, with bimodal or multimodal distributions). As unknown distributions can be different from unimodal ones, we used statistics such as the Watson's U^2-test, which in the case of data with both bimodal or multimodal distributions has the ability to control a Type-I error rate near the nominal value and has good statistical power for detecting mean differences (Landler *et al.* 2021). In the test of mean direction, we generated random datasets (with $n = 52$ for the stopover sample, and $n = 142$ for the control one) corresponding to the southern headwind encountered en route during autumn migration in the Strait of Sicily. The random samples fitted a von Mises distribution with mean of 180° and increasing concentration of observation ($k = 2$ and $k = 3$), and were compared with the observed means of stopover and control samples using the Watson–Williams F-test.

Statistical significance was set in all analyses at $P < 0.05$. Statistics were computed in Statistica 10.0 (www.statsoft.com), PAST 4.07b (Hammer *et al.* 2001) and Oriana 4.02 (Kovach 2011).

RESULTS

During the first leg of the campaign, we recorded 58 cases of birds stopping or attempting to stop on board (Table 1). We counted 46 individuals belonging to 13 identified species plus one unidentified passerine that used the ship as a stopover for a recorded time, and another 12 individuals (two Ruddy Turnstones *Arenaria interpres*, eight Western Yellow Wagtails *Motacilla flava* and two passerines) that repeatedly tried to get on board but were dissuaded by human presence (Table 1). They were, however, considered to be on board for modelling purposes, which do not need to use the time spent on board (see GLZ below). The median stopover length was 42.5 min (range: 1–1765 min; Q25–Q75: 5–293 min; $n = 46$) and we recorded seven cases of overnight stay on board (Table 1), and also two cases of a Spotted Flycatcher *Muscicapa striata* and an Eastern Subalpine Warbler *Curruca cantillans* preying upon flies

Table 1. List of birds recorded during the summer survey in the Strait of Sicily within the Central Mediterranean Sea with an indication of those that stopped on board and their median stopover time and lower and upper quartiles (Q25–Q75). In parentheses, individuals that repeatedly tried to get on board but were dissuaded by human presence.

		Stopover time (min)			On board	Overnight	Not on board	% on board
English name	Species	Q25	Median	Q75	*n*	*n*	*n*	F%
European Turtle Dove	*Streptopelia turtur*	16	35	70	6		7	46.2
Eurasian Collared Dove	*Streptopelia decaocto*		1343		1	1	0	100.0
Black-crowned Night Heron	*Nycticorax nycticorax*						8	0.0
Squacco Heron	*Ardeola ralloides*		1680		2	2	1	66.7
Western Cattle Egret	*Bubulcus ibis*						10	0.0
Little Egret	*Egretta garzetta*						30	0.0
Small Herons	Not identified Ardeidae						15	0.0
Ruddy Turnstone	*Arenaria interpretes*				(2)		0	100.0
Waders	Not identified						16	0.0
Common Redshank	*Tringa totanus*						1	0.0
Mediterranean Gull	*Ichthyaetus melanocephalus*		2		1		1	50.0
Eurasian Hoopoe	*Upupa epops*	122	351	580	2		11	15.4
Great Reed Warbler	*Acrocephalus arundinaceus*		5		1		0	100.0
Barn Swallow	*Hirundo rustica*						5	0.0
Eastern Subalpine Warbler	*Curruca cantillans*	40	230	465	13	3	14	48.1
Spotted Flycatcher	*Muscicapa striata*		1765		1	1	3	25.0
European Pied Flycatcher	*Ficedula hypoleuca*						2	0.0
Common Redstart	*Phoenicurus phoenicurus*	4	33	54	3		1	75.0
Whinchat	*Saxicola rubetra*		227		1		0	100.0
African Stonechat	*Saxicola torquatus*						1	0.0
Northern Wheatear	*Oenanthe oenanthe*		5		1		8	11.1
Meadow Pipit	*Anthus pratensis*		45		1		0	100.0
Western Yellow Wagtail	*Motacilla flava*	2	12	41	12 (8)		79	20.2
Passerines	Passeriformes		1		1 (2)		21	12.5
Total		5	42.5	293	46 (12)	7	234	19.9

and moths, a not-unusual behaviour among birds stopping aboard (*cf.* Papageorgiou 2019). There is no difference in the duration of the stopover made by 34 small and 12 medium-size birds (Mann–Whitney test for equal medians $U_{12,34} = 137$; $Z = 1.665$; $P = 0.093$) and the two samples statistically belong to populations with an equal distribution (Kolmogorov–Smirnov test $D = 0.328$; $P = 0.263$). However, some interspecific differences can be noted, as the stopover median times of the 13 Eastern Subalpine Warblers were significantly longer that those of the 12 Western Yellow Wagtails ($U_{12,13} = 30.5$; $Z = 2.560$; $P = 0.007$) and these samples are not taken from populations with equal distribution ($D = 0.596$; $P = 0.022$). During the same period, another 234 birds were observed in flight and not landing on board (Table 1). Other ornithological data collected occasionally during the second and third legs added further individuals and species. These were not taken into consideration in the statistical analysis but used to confirm the migratory phenomenon and the stop on board until the end of October (Fig. 3).

In the first leg, we recorded 13 species with a daily mean of 2.80 ± 2.42 individuals on board (range: 0–9; $n = 20$ days) compared with 11.70 ± 10.11 (range: 1–43; $n = 20$ days) individuals that did not make a stopover; this was a statistically significant difference in favour of non-stopping birds (Wilcoxon matched pairs $Z_{20} = 3.85$, $P = 0.0001$), certainly inflated by flocks of waders, herons and other birds observed away from the ship. However, even the most conservative test comparing the daily mean of the cases with stopped birds (2.55 ± 1.91 cases; range: 0–6; $n = 20$ days) with that of not-stopped birds (7.10 ± 5.60; range: 1–27; $n = 20$ days) provided a statistically significant difference (Wilcoxon matched pairs $Z_{19} = 3.74$, $P = 0.0002$). The GLZ showed that the probability of finding a bird stopping on board depends on the interaction between wind strength and cloud cover (Table 2). In fact, even the second model, classified within the < 2 AICc values and therefore with the same data support, highlighted this interaction together with the fixed effect of cloud cover. This model has a non-significant likelihood ratio and only about one-third of the weight of the first mode; however, the evidence ratio for model 1 to model 2 is only 1.64, indicating relatively weak support for the best model. The model uncertainty in favour of alternative hypotheses including also the CC (and WF) fixed effects is thus quite high. The CCR is 0.751, which is fairly good, but this correct classification rate originates from a very good specificity (0.965) and a very low sensitivity (0.173). In practice, the accuracy of the model is biased towards true-negatives; modelling for sensitivity correctly assigned as true-positives only nine of 52 presences on board, predicting the remaining 43 as false-negatives. Accordingly, the AUC is 0.716, a barely acceptable value, and the Nagelkerke generalized coefficient of determination is low ($R^2 = 0.178$).

The mean (± sd) vector of wind direction of the stopover sample was 161.7° ± 97.4° (bootstrapped 95% confidence interval: 105.8–210.8°; $n = 52$), whereas that of the control sample was 231.2° ± 95.2° (bootstrapped 95% confidence interval: 205.4–255.6°; $n = 142$). The length of the two mean vectors is equivalent ($r_{stopover} = 0.235$ vs. $r_{control} = 0.252$), indicating that the observations are loosely clustered around the mean (r ranges from 0 to 1), with the control sample slightly more clustered than the stopover one (Fig. 2). According to the Watson's U^2-test, each of the two samples had a different distribution than the uniform one ($U^2_{stopover} = 0.230$; $P < 0.025$ and $U^2_{control} = 0.833$; $P < 0.005$). The two samples had different mean values ($F_{1,192} = 14.465$; $P = 0.0002$) under the same distribution of observation ($U^2_{52,142} = 0.180$; $0.1 > P > 0.05$). The mean wind direction that blows when birds stop on board is not statistically different from a headwind generated after random sampling ($F_{1,102} = 0.225$; $P = 0.636$; $k = 2$); by contrast, the mean wind direction blowing when the birds do not stop on board is statistically different from the same random headwind sample ($F_{1,282} = 25.320$; $P = 0.000$; $k = 2$). The same result (not reported for brevity) is obtained by increasing the concentration of the random observations to $k = 3$.

A total of 112 ships of variable tonnage were recorded during 16 days of counting, with a daily mean of 7.0 ± 2.5 (range: 3–11) ships. Of these ships, 60% were commercial, such as oil tankers and cargo ships, while the remaining 40% were local traffic, fishing boats, cruise ships, ferries, military ships and others. Figure 1 shows a representation of the density of marine traffic lanes in the Mediterranean Sea (MED QSR 2017). In

Table 2. Parameter estimates of the first three independent subsets, as obtained from generalized linear models, showing predictors that significantly influence the probability of birds stopping on board. The first two models with ΔAICc < 2 support the data. WF = wind force on the Beaufort scale, CC = cloud cover.

Rank	Variable		df	AICc	Likelihood ratio	P	ΔAICc	Model weight
1	WF × CC		1	224.508	4.538	0.033	0.000	0.339
2	CC	WF × CC	2	226.503	4.629	0.099	1.995	0.125
3	WF	WF × CC	2	226.589	4.543	0.103	2.081	0.120

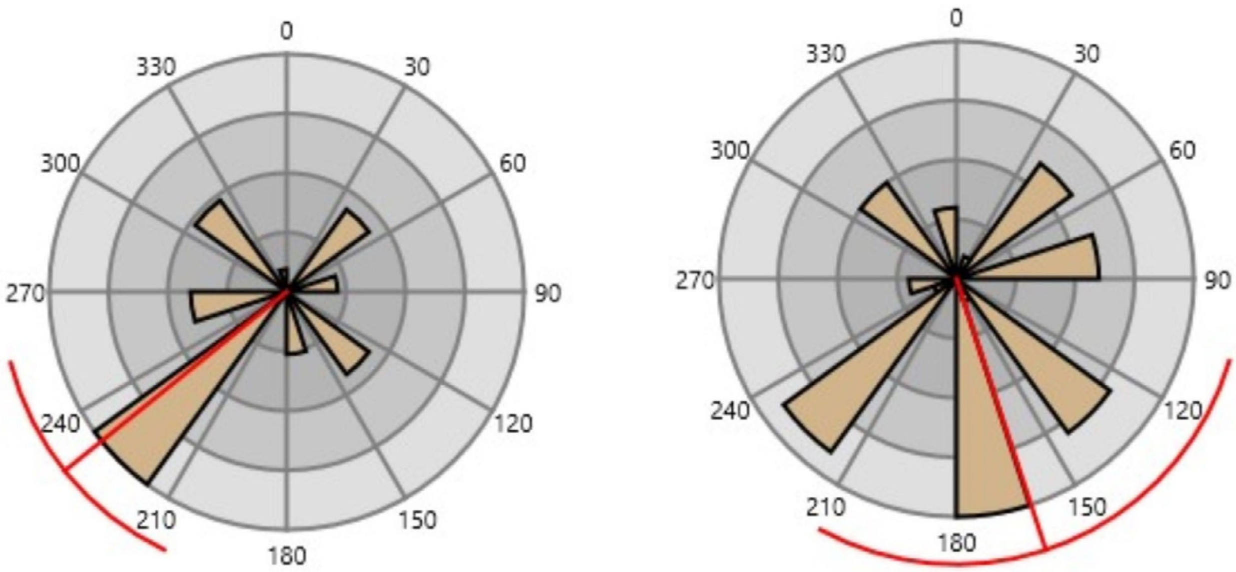

Figure 2. Rose diagram of wind directions blowing during cases of birds stopping (right) and not stopping (left) on board. The mean direction with confidence limits is indicated in red.

2014, some 63 000 AIS (automatic identification system, Le Tixerant *et al.* 2018) signals of commercial vessels and EU fishing boats over 15 m were recorded in the Strait of Sicily. This is an underestimation, as it excludes all local traffic (MED QSR 2017) and the hidden trawling activity which, when included, would increase total fishing activity in the area by around 20% (Ferrà *et al.* 2020). Moreover, since 2015, expansion of the capacity of the Suez Canal has increased the number of cargo and commercial ships crossing the Mediterranean Sea. Although underestimated (Le Tixerant *et al.* 2018), a mean monthly passage of nearly 5500 commercial ships through the Strait of Sicily would produce at least 16 000 ships in transit during the 3 months (August–October) of post-reproductive migration. According to the daily mean of birds stopping on board in the days of the first leg (2.80 ± 2.42), during the 3 months of autumn migration (*cf.* Fig. 3), 252 birds (range: 34–470) could have landed for a variable amount of time on a single ship. This leads to an estimated potential figure of about 4 million birds (ranging from at least half a million to > 7 million birds) that could stop on board the above 16 000 commercial ships. The 4 million we recorded represent about 0.2% of the estimates of birds in transit between Europe and Africa (Hahn *et al.* 2009), with a good correspondence between some of the more frequent species (e.g. Western Yellow Wagtail, Northern Wheatear) observed both on board and listed in Hahn *et al.* (2009). Although it might appear to be tossing up some figures in the air (Moreau 1972 in Hahn *et al.* 2009), our extrapolation is plausible if a series of average conditions occur. For instance, we assumed that the meteorological conditions of the campaign are equivalent to those of the other years and that AIS signals coverage showed an almost constant monthly value for commercial ships, as occurs for fishing vessels (*cf.* Ferrà *et al.* 2020).

DISCUSSION

Throughout our oceanographic campaign we observed a constant flow of birds on board involving at least 18 species, and continuous sampling during the second and third legs would certainly have increased the list. Literature examination on this subject revealed a surprising lack of published articles. Nonetheless during the web search we found several anecdotal observations. Having birds on board was a trivial matter for the crew of our ship, who have experienced them sailing all the seas of the world. For example, the second shipmate showed a video of a Snowy Owl *Bubo scandiacus* staying 3 days in winter 2019 aboard a cargo during a snowstorm in the North Sea. This coincided with the seven Snowy Owls observed for nearly a week aboard a container ship from Canada to France in December 2013 (www.researchgate.net/post/Are_birds_using_ships_for_longer_sea_crossings). These anecdotal records and the past experience of one of us who observed several cases of small birds aboard trawlers in the Strait of Sicily during autumn 1982 (Sarà 1983), but above all the short film that shows about 70 species aboard freighters, oil tankers and other commercial ships (Papageorgiou 2019), made it possible to verify that the cruising speed of a ship does not prevent the birds from stopping. Trawlers

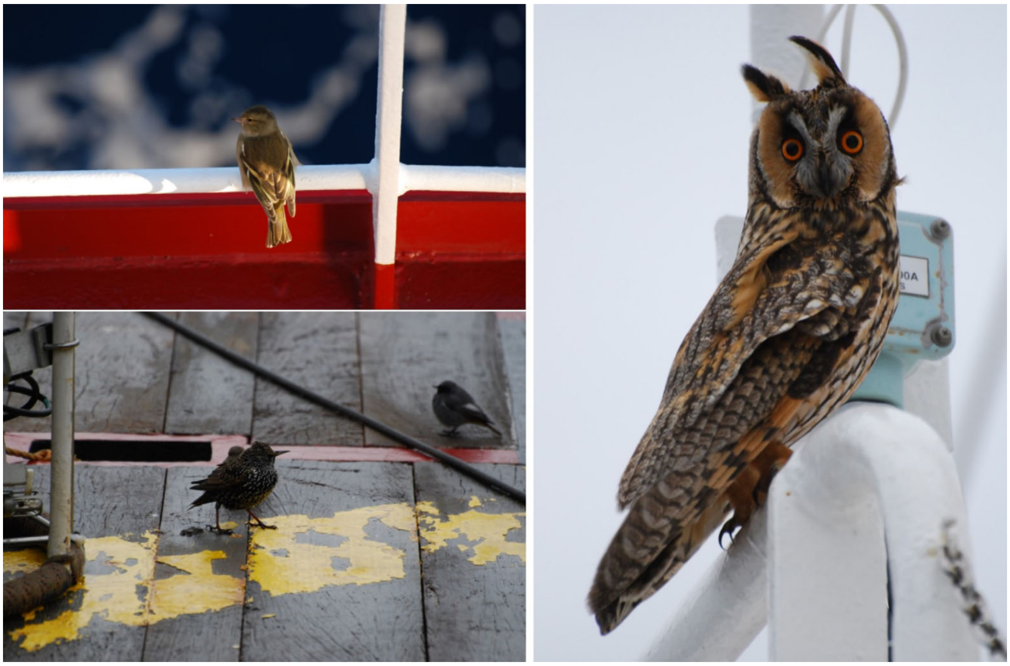

Figure 3. The lack of ornithologists on board prevented the orderly collection of bird data during the other oceanographic legs. Birds on board were, however, photographed until 29 October: (clockwise) Common Chaffinch, Long-eared Owl, Common Starling and Black Redstart. Photo credits: Francesco Stenico.

sail at 0.5–6 kn/h depending on the fishing phase (Sarà 1983) and commercial vessels sail at an average of 10–15 kn/h and oil tankers even faster, at 20–25 kn/h (www.marinetraffic.com). Therefore, the birds are able to stop aboard ships of different types that travel even at quite high speeds.

The most common explanations made by commentators of the anecdotal observations is that birds stop on ships because they: (1) want to escape bad weather during sea crossings, (2) are in poor body condition or tired and energy-depleted, or (3) they have lost their route. The last is relevant for major oceanic journeys and probably does not apply to the relatively short Mediterranean Sea crossing. These explanations are congruent with what we know about stopover ecology. Currently it is thought that the stopover and its duration depend on the combined effect of environmental factors, endogenous programmes and physiological conditions. Indeed, there are two major lines of evidence – first, the effect of weather on stopovers, especially during autumn migration (*cf.* Brust *et al.* 2019, Mallon *et al.* 2021) and secondly, the importance of energy reserves, hence pointing to the physiological condition of individuals (*cf.* Fusani *et al.* 2009, Lupi *et al.* 2016).

Overall, the duration of land and island stopovers is short, with only a small fraction of birds staying longer than 24 h (Newton 2010, Maggini *et al.* 2020, Mallon *et al.* 2021). The median length of stopover in our sample was approximately 42 min, which is much less than the mean of 9 and 41 h calculated on island sites for fat and lean birds, respectively (e.g. Goymann *et al.* 2010). This low value probably occurred because there were no refuelling possibilities on the ship. Certainly, a short stop can be enough to avoid the most tiring part of traversing a low atmospheric pressure cell, or to recover from the physiological stress that the migratory flight entails (Jenni & Schaub 2003, Maggini *et al.* 2020).

Analysis of our data suggested that the interaction between cloud cover and wind force, and possibly cloud cover itself, predicted the probability of stopping on the ship. Most interestingly, the direction of the wind that blew during the stopover cases was different from the direction in the sample of non-stopping birds, with headwinds blowing from the south as a possible cause for stopping. Research has already shown that wind direction is of primary importance, and that departure decisions from stopover locations and sea barrier crossings are greater with increasing tailwinds and smaller with cross- and adverse winds (Brust *et al.* 2019, Haest *et al.* 2019). Low cloud cover is another favoured meteorological factor during migration (Newton 2010, Packmor *et al.* 2020, Roques *et al.* 2021). Adverse and/or unpredictable weather conditions can increase the risk of mortality and therefore more individuals stop on board to avoid it or at least to recover slightly. Avoiding adverse environmental conditions during the migratory endurance flight and physiological recovery (Schmaljohann *et al.* 2022) are certainly among the main causes, probably difficult to untangle from each other, in determining the probability of onboard stops. Further research is needed to discover the mechanisms involved and their causal links in this peculiar form of stopover. However, first it seems crucial to ask whether this phenomenon deserves to be studied and whether it could contribute to our understanding of the ecology of stopovers and bird migration in general. We answer this question with a firm yes, as we believe that the phenomenon is much less occasional than generally assumed. We have extrapolated an impressive estimate of about 4 million birds potentially stopping on ships crossing the single lane of the Sicilian Strait in autumn. Although these numbers may appear to be speculation, they are far from representing an exhausted minority (Newton 2010) and make us think of the potential number of birds that stop on board ships crossing their migratory routes. Maritime traffic is likely to have a considerable impact on migration, with effects that may be more diverse and important for some species than for others. In our opinion, stopover on board ships deserves more attention in ornithological research. Undoubtedly, before deciding whether we are faced with a new migration strategy favoured by maritime traffic, we need more precise numerical estimates and mapping of the presences between the marine subdivisions of the Mediterranean Sea (Barale 2018, GFCM 2018). Furthermore, it would be interesting to know whether this phenomenon is also occurring during pre-breeding migration or whether the duration of the stop is related to the distance from the coast or to the intersection between the direction of the ship and the migratory route of the birds. As life history (e.g. r/K selected species) is expected to affect the fitness consequences of stopovers (Schmaljohann *et al.* 2022), it is worth asking which species, if any, benefit from it. In reality we do not yet know whether a stopover can harm the birds and constitutes an ecological trap. Ronconi *et al.* (2015) listed a number of negative bird interactions with offshore oil and gas platforms and in fact we know nothing of the potential interference that onboard instrumentation or night lighting of ships can have on birds by causing disorientation and route loss. We have observed that some birds on board dirty their feathers with oil and grease from machinery, which could damage their flight and affect their survival.

Recently, Schmaljohann *et al.* (2022) highlighted that research on stopover ecology focuses more on the analysis of departure decisions, and they propose to investigate further the reasons why migratory flights are interrupted, leading to the landing of birds. Certainly, a standardized capture and manipulation protocol of the birds arriving on board ships can offer an interesting sample in which the arrival and departure times are known with greater certainty and can also be experimentally manipulated with respect to stopovers at other sites (e.g. Goymann *et al.* 2010). Bio-logging birds on board would allow data to be collected on their fate (e.g. survival, travel speeds and timing, future stopover sites), while sampling of blood or other tissues will provide information on hormonal regulation processes necessary for avian migration (e.g. Bauer & Watts 2021) and the oxidative stress due to sea crossing (e.g. Owen & Moore 2006). Other useful information could be obtained by checking whether stopping birds are lean or fat, and whether lean individuals stay longer than fat individuals (*cf.* Fusani *et al.* 2009, Goymann *et al.* 2010). Is it possible to carry out ornithological research on board ships? Again, the answer is yes. In Italy, to cite one example, there is a long-term monitoring project for cetaceans, turtles and marine litter based on fixed-line transects (Arcangeli 2010). Ornithologists could easily work alongside marine biologists who carry out these investigations on ferries and ships in transit between Italian ports and between these and neighbouring countries (Tunisia, France).

Regardless of the weather upon departure, migratory birds can encounter unfavourable conditions along the way that require immediate decisions to overcome the risks of continuing their journey in poor weather. The obvious reaction is to land and wait for conditions to improve, but when over sea they cannot stop. Intense maritime traffic across the world's seas is perhaps offering them a new opportunity, mimicking the role small islands play as stepping-stones for most migratory birds after or before crossing sea barriers (Maggini *et al.* 2020, Ferretti *et al.* 2021). The paradigm shift invoked in the research on the ecology of the stopover (see Schmaljohann *et al.* 2022) could perhaps start from targeted projects undertaken by ornithologists on board ships that cross the trade routes of the Mediterranean Sea during avian migration periods.

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AUTHOR CONTRIBUTIONS

Maurizio Sarà: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (equal); methodology (lead); writing – review and editing (lead). **Roberto Firmamento:** Conceptualization (supporting); data curation (equal); investigation (supporting); methodology (supporting). **Giuseppe Cangemi:** Data curation (equal); investigation (supporting). **Luca Pagano:** Conceptualization (supporting); data curation (equal);

investigation (supporting). **Martina Genovese:** Data curation (supporting); investigation (supporting). **Teresa Romeo:** Project administration (lead); resources (supporting); supervision (equal). **Silvestro Greco:** Project administration (lead); resources (lead); supervision (lead).

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Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

REFERENCES

Aamidor, S.E., Bauchinger, U., Mizrahy, O., McWilliams, S.R. & Pinshow, B. 2011. During stopover, migrating blackcaps adjust behavior and intake of food depending on the content of protein in their diets. *Integr. Comp. Biol.* **51**: 385–393.

Agostini, N., Prommer, M., Vaczi, M. & Panuccio, M. 2019. Repeated large scale loop migrations of an adult European Honey Buzzard. *Avocetta* **43**: 13–21.

Arcangeli, A. 2010. ISPRA cetacean monitoring network along fixed transect. *Biol. Mar. Mediterr.* **17**: 400–401.

Barale, V. 2018. A supporting marine information system for maritime spatial planning: the European atlas of the seas. *Ocean Coastal Manag.* **166**: 2–8.

Batschelet, E. 1981. *Circular Statistics in Biology*. New York: Academic Press.

Bauer, C.M. & Watts, H.E. 2021. Corticosterone's roles in avian migration: assessment of three hypotheses. *Horm. Behav.* **135**: 105033.

Brust, V., Michalik, B. & Hüppop, O. 2019. To cross or not to cross - thrushes at the German North Sea coast adapt flight and routing to wind conditions in autumn. *Mov. Ecol.* **7**: 32.

Burnham, K. & Anderson, D. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Conroy, M.J. & Carroll, J.P. 2009. *Quantitative Conservation of Vertebrates*. Oxford: Wiley-Blackwell.

Deidun, A., Gauci, A., Azzopardi, J., Camilleri, C., Cutajar, D., Chalabreysse, M. & Trinquard, F. 2018. Development of a novel tool for the monitoring of shipping traffic within the strait of Sicily (Central Mediterranean): the BIODIVALUE AIS vessel tracker. *J. Coastal Res.* **85**: 1356–1360.

Deppe, J.L., Ward, M.P., Bolus, R.T., Diehl, R.H., Celis-Murillo, A., Zenzal, T.J., Moore, F.R., Benson, T.J., Smolinsky, J.A., Schofield, L.N., Enstrom, D.A., Paxton, E.H., Bohrer, G., Beveroth, T.A., Raim, A., Obringer, R.L., Delaney, D. & Cochran, W.W. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proc. Natl Acad. Sci. USA* **112**: E6331–E6338.

Drent, R. & Piersma, T. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders. In Gwinner, E. (ed) *Bird Migration*: 399–412. Berlin: Springer-Verlag.

Elphick, J. 2011. *Atlas of Bird Migration. Tracing the Great Journeys of the World's Birds*. Richmond Hill: Firefly Books Ltd.

Erni, B., Liechti, F. & Bruderer, B. 2005. The role of wind in passerine autumn migration between Europe and Africa. *Behav. Ecol.* **16**: 732–740.

Ferrà, C., Tassetti, A.N., Armelloni, E.N., Galdelli, A., Scarcella, G. & Fabi, G. 2020. Using AIS to attempt a quantitative evaluation of unobserved trawling activity in the Mediterranean Sea. *Front. Marine Sci.* **7**. https://doi.org/10.3389/fmars.2020.580612

Ferretti, A., Maggini, I. & Fusani, L. 2021. How to recover after sea crossing: the importance of small islands for passerines during spring migration. *Ethol. Ecol. Evol.* **33**: 307–320.

Fuchs, T., Haney, A., Jechura, T.J., Moore, F.R. & Bingman, V.P. 2006. Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*. *Anim. Behav.* **72**: 951–958.

Fusani, L., Cardinale, M., Carere, C. & Goymann, W. 2009. Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. *Biol. Lett.* **5**: 302–305.

GFCM 2018. *GFCM Data Collection Reference Framework (DCRF). Version 21.2*. Available at: https://www.fao.org/gfcm/data/dcrf (accessed 24 April 2022).

Gilroy, J.J. 2017. Stay-at-home strategy brings fitness benefits to migrants. *J. Anim. Ecol.* **86**: 983–986.

Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. 2016. Migratory diversity predicts population declines in birds. *Ecol. Lett.* **19**: 308–317.

Goymann, W., Spina, F., Ferri, A. & Fusani, L. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole-Island telemetry. *Biol. Lett.* **6**: 478–481.

Haest, B., Hüppop, O., van de Pol, M. & Bairlein, F. 2019. Autumn bird migration phenology: a potpourri of wind, precipitation and temperature effects. *Glob. Chang. Biol.* **25**: 4064–4080.

Hahn, S., Bauer, S. & Liechti, F. 2009. The natural link between Europe and Africa - 2.1 billion birds on migration. *Oikos* **118**: 624–626.

Halupka, L., Wierucka, K., Sztwiertnia, H. & Klimczuk, E. 2017. Conditions at autumn stopover sites affect survival of a migratory passerine. *J. Ornithol.* **158**: 979–988.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **4**: 1–9.

Hedenströum, A., Alerstam, T., Báckman, J., Gudmundsson, G.A., Henningsson, S., Karlsson, H., Rosén, M. & Strandberg, R. 2009. Radar observations of arctic bird migration in the Beringia region. *Arctic* **62**: 25–37.

Jenni, L. & Schaub, M. 2003. Behavioural and physiological reactions to environmental variation in bird migration: a review. In Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*: 155–171. Berlin, Heidelberg: Springer-Verlag.

Johnston, R., Jones, K. & Manley, D. 2018. Confounding and collinearity in regression analysis: a cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. *Qual. Quant.* **52**: 1957–1976.

Kjellén, N., Hake, M. & Alerstam, T. 2001. Timing and speed of migration in male, female and juvenile ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *J. Avian Biol.* **32**: 57–67.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Bairlein, F. & Alerstam, T. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Anim. Ecol.* **83**: 176–184.

Kovach, W.L. 2011. *Oriana – Circular Statistics for Windows, ver. 4*. Pentraeth, Wales, UK: Kovach Computing Services.

Landler, L., Ruxton, G.D. & Malkemper, E.P. 2021. Advice on comparing two independent samples of circular data in biology. *Sci. Rep.* **11**: 20337.

Larkin, R.P., Griffin, D.R., Torre-Bueno, J.R. & Teal, J. 1979. Radar observations of bird migration over the Western North Atlantic Ocean. *Behav. Ecol. Sociobiol.* **4**: 225–264.

Le Tixerant, M., Le Guyader, D., Gourmelon, F. & Queffelec, B. 2018. How can automatic identification system (AIS) data be used for maritime spatial planning? *Ocean Coast. Manag.* **166**: 18–30.

Linscott, J.A. & Senner, N.R. 2021. Beyond refueling: investigating the diversity of functions of migratory stopover events. *Condor* **123**: duaa074.

Lupi, S., Goymann, W., Cardinale, M. & Fusani, L. 2016. Physiological conditions influence stopover behavior of short-distance migratory passerines. *J. Ornithol.* **157**: 583–589.

Mackell, D.A., Casazza, M.L., Overton, C.T., Donnelly, J.P., Olson, D., McDuie, F., Ackerman, J.T. & Eadie, J.M. 2021. Migration stopover ecology of cinnamon Teal in western North America. *Ecol. Evol.* **11**: 14056–14069.

Maggini, I., Trez, M., Cardinale, M. & Fusani, L. 2020. Stopover dynamics of 12 passerine migrant species in a small Mediterranean Island during spring migration. *J. Ornithol.* **161**: 793–802.

Mallon, J.M., Bildstein, K.L. & Fagan, W.F. 2021. Inclement weather forces stopovers and prevents migratory progress for obligate soaring migrants. *Mov. Ecol.* **9**: 39.

McClintock, C.P., Williams, T.C. & Teal, J.M. 1978. Autumnal bird migration observed from ships in the Western North Atlantic Ocean. *Bird-Banding* **49**: 262–277.

McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models*. London: Chapman and Hall/CRC.

MED QSR 2017. *Mediterranean quality status report of the Mediterranean action plan system*. Available at: https://www.medqsr.org/ (accessed 9 November 2021).

Mellone, U., Lopez-Lopez, P., Limiñana, R. & Urios, V. 2011. Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor. *Int. J. Biometeorol.* **55**: 463–468.

Newton, I. 2010. *New Naturalist Bird Migration*. London: Harper Collins.

Owen, J.C. & Moore, F.R. 2006. Seasonal differences in immunological condition of three species of thrushes. *Condor* **108**: 389–398.

Packmor, F., Klinner, T., Woodworth, B.K., Eikenaar, C. & Schmaljohann, H. 2020. Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? *Mov. Ecol.* **8**: 6.

Panuccio, M., Mellone, U. & Agostini, A. 2021. *Migration Strategies of Birds of Prey in Western Palearctic*. Boca Raton, FL: CRC Press.

Papageorgiou, O.F. 2019. *Bird migration on merchant ships*. Available at: https://www.youtube.com/watch?v=arJenBAVr10. (accessed 7 November 2021).

Paynter, R.A. 1953. Autumnal migrants on the Campeche Bank. *Auk* **70**: 338–349.

REMPEC 2008. *Study of maritime traffic flows in the Mediterranean sea, final report*. Available at: http://www.rempec.org/admin/store/wyswigImg/file/Prevention/Maritime%20Study/Study%20of%20Maritime%20Traffic%20Flows%20in%20the%20MedSea_Unrestricted.pdf (accessed 9 November 2021).

Richardson, W.J. 1990. Timing of bird migration in relation to weather: updated review. In Gwinner, E. (ed) *Bird Migration*: 78–101. Berlin, Heidelberg: Springer-Verlag.

Ronconi, R.A., Allard, K.A. & Taylor, P.D. 2015. Bird interactions with offshore oil and gas platforms: review of impacts and monitoring techniques. *J. Environ. Manag.* **147**: 34–45.

Roques, S., Lank, D.B., Cam, E. & Pradel, R. 2021. More than just refuelling: lengthy stopover and selection of departure weather by sandpipers prior to transoceanic and transcontinental flights. *Ibis* **163**: 519–535.

Saino, N., Rubolini, D., Von Hardenberg, J., Ambrosini, R., Provenzale, A., Romano, M. & Spina, F. 2010. Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds. *Funct. Ecol.* **24**: 658–669.

Santos, C.D., Silva, J.P., Muñoz, A.-R., Onrubia, A. & Wikelski, M. 2020. The gateway to Africa: what determines sea crossing performance of a migratory soaring bird at the strait of Gibraltar? *J. Anim. Ecol.* **89**: 1317–1328.

Sarà, M. 1983. Osservazioni sulla consistenza numerica e l'alimentazione della Berta maggiore (*Calonectris diomedea*) nel Canale di Sicilia. *Riv. Ital. Orn.* **53**: 183–193.

Sarà, M., Bondì, S., Bermejo, A., Bourgeois, M., Bouzin, M., Bustamante, J., de la Puente, J., Evangelidis, A., Frassanito, A., Fulco, E., Giglio, G., Gradev, G., Griggio, M., López-Ricaurte, L., Kordopatis, P., Marin, S., Martínez, J., Mascara, R., Mellone, U., Pellegrino, S., Pilard, P., Podofillini, S., Romero, M., Gustin, M., Saulnier, N., Serra, L., Sfougaris, A., Urios, V., Visceglia, M., Vlachopoulos, K., Zanca, L., Cecere, J.G. & Rubolini, D. 2019. Broad-front migration leads to strong migratory connectivity in the lesser kestrel (*Falco naumanni*). *J. Biogeogr.* **46**: 2663–2677.

Schmaljohann, H., Eikenaar, C. & Sapir, N. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. *Biol. Rev.* **97**: 1231–1252.

Schmaljohann, H., Liechti, F., Bächler, E., Steuri, T. & Bruderer, B. 2008. Quantification of bird migration by radar – a detection probability problem. *Ibis* **150**: 342–355.

Schmaljohann, H., Liechti, F. & Bruderer, B. 2007. Songbird migration across the Sahara: the non-stop hypothesis rejected! *Proc. R. Soc. B* **274**: 735–739.

Sekercioglu, C.H., Daily, G.C. & Ehrlich, P.R. 2004. Ecosystem consequences of bird declines. *Proc. Natl Acad. Sci. USA* **101**: 18042–18047.

Shamoun-Baranes, J., Liechti, F. & Vansteelant, W.M. 2017. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A* **203**: 509–529.

Sillett, T.S. & Holmes, R.T. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* **71**: 296–308.

Smith, A.D. & McWilliams, S.R. 2014. What to do when stopping over: behavioural decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. *Behav. Ecol.* **25**: 1423–1435.

Szent-Ivány, J. 1959. The House Sparrow being shipped to Australia. *Aquila* **66**: 324–325.

Vansteelant, W.M., Bouten, W., Klaassen, R., Koks, B., Schlaich, A., Van Diermen, J., Van Loon, E. & Shamoun-Baranes, J. 2015. Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. *J. Avian Biol.* **46**: 25–39.

Vansteelant, W.M., Kekkonen, J. & Byholm, P. 2017. Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proc. R. Soc. Lond. B* **284**: 20170387.

Zu-Aretz, S. & Leshem, Y. 1983. The sea – a trap for gliding birds. *Torgos* **50**: 16–17.

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