THE DEVELOPMENT AND USE OF A METHOD TO FILL TIME GAPS IN MIGRATION COUNTS

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Abstract. In some conservation situations, there is a need for estimates of numbers of seabirds migrating past a specific site, such as sites of proposed offshore wind farms. Migration counts from points strategically located on the coast can be a reliable and effective method of reaching this goal. We propose a consistent and statistically robust method for estimating such numbers by generalized additive modeling of the numbers passing during periods when counts are interrupted. This procedure has the advantage of accounting for the effects of covariates, such as wind, on the counts in a flexible manner, potentially increasing accuracy and precision. We develop a reliable method of estimating precision, based on a parametric bootstrap, and applied a sensitivity analysis to our models to test their accuracy. We demonstrate the method with three species of seabirds migrating through the Strait of Gibraltar. Estimated numbers of the Northern Gannet (*Morus bassanus*) are similar to the estimated Atlantic population that winters in the western Mediterranean Sea, while for both Cory's (*Calonectris diomedea*) and Balearic (*Puffinus mauretanicus*) Shearwaters they are greater than the current population estimates. These results have important implications in conservation and highlight the necessity for reestimation of the latter two species' global population. Potential sources of biases include the constraint on detectability due to distance and the possibility of double counting due to local movements. To avoid overestimates, we suggest that values imputed for the gaps in counts be conservative.

Key words: *bird-migration volume,* Calonectris diomedea*, migration counts, migratory passage,* Morus bassanus*, parametric bootstrap,* Puffinus mauretanicus*, time gaps.*

Desarrollo y Uso de un Método para Llenar Brechas de Tiempo en los Conteos Migratorios

Resumen. En algunas situaciones es necesario obtener estimaciones del número de aves marinas que migran a través de un área específica, como aquellas propuestas para la construcción de parques eólicos marinos. Los censos desde puntos estratégicamente situados en la costa pueden ser un método efectivo y fiable para alcanzar dicho objetivo. En este trabajo proponemos un método robusto y consistente para estimar flujos migratorios, a partir de la estimación del número de aves que pasan en los periodos de tiempo en que los censos son interrumpidos, usando modelos aditivos generalizados. Este procedimiento tiene en cuenta el efecto de diferentes variables en los conteos, tales como el viento, aumentando la exactitud y precisión de las estimaciones. Desarrollamos un método basado en el muestreo repetido paramétrico para estimar la precisión y aplicamos un análisis de sensibilidad a los modelos para testar su exactitud. Probamos el método usando datos de migración de tres especies de aves marinas a través del Estrecho de Gibraltar. Para *Morus bassanus*, los números estimados son similares a la población atlántica que inverna en el Mediterráneo occidental; mientras que para *Calonectris diomedea* y *Puffinus mauretanicus*, los números estimados son superiores a la población estimada en la actualidad. Estos resultados tienen importantes implicaciones en conservación, y resaltan la necesidad de calcular de nuevo las estimaciones poblacionales de estas dos últimas especies. Discutimos potenciales fuentes de error, relacionadas con la pérdida de detección al aumentar la distancia y la posibilidad de dobles conteos debidos a movimientos locales. Finalmente, sugerimos emplear estimaciones conservativas cuando se imputan valores para periodos de tiempo dónde no se han hecho censos, para evitar sobreestimar los flujos migratorios.

INTRODUCTION

Accurate quantitative estimates of the abundance of migrating birds are not only of intrinsic biological interest but are fundamental to conservation planning and action. Such estimates allow identification of species at risk, important sites for birds, potential limiting factors, and feedback for management (e.g., Bart 2005). Furthermore, seabirds are particularly appropriate candidates for monitoring of the biodiversity of marine

ecosystems (see Hunt et al. 1991, Cairns 1992, and Furness et al. 1993 for a review), and they are widely recognized as potentially powerful indicators of changes in marine environments (Kushlan 1993, Furness et al. 1993, Hyrenbach and Veit 2003).

The planned construction of large numbers of offshore wind turbines has highlighted our lack of knowledge of the numbers and distribution of birds at sea, essential to assessing the environmental effects of offshore wind farms (e.g., Camphuysen et al. 2004, Desholm et al. 2006). Thus there is a need for accurate estimates of seabirds' passage across particular areas, such as sites proposed for offshore wind farms. Such estimates should be accompanied by suitable measures of precision (standard error, standard deviation, coefficient of variation, or confidence interval) whenever possible; without these measures, readers may make incorrect conclusions concerning differences among species, sampling units, sampling periods, or other factors of interest (Thompson et al. 1998).

There are well-established techniques for estimating the density of seabirds at sea, from ships or from aircraft. In these surveys, strip transects (Tasker et al. 1984) have been used. Nevertheless, the precise determination of seabirds' density at sea is hampered by several biases such as that due to the movement of the animals being surveyed or the effect of ships on the behavior of birds (Tasker et al. 1984, Garthe and Hüppop 1999, Camphuysen et al. 2004). Moreover, seabirds are often difficult to detect in their nonbreeding range (e.g., Schreiber and Burger 2001) and are usually surveyed from vessels that are at sea for reasons other than bird surveys and may not provide good coverage of the species' range (Clarke et al. 2003). In addition, migration passages are not easily described from moving platforms such as vessels. Detailed studies of seabird passage (e. g., migration or movements for foraging) require more or less fixed (stationary) platforms of observation (Camphuysen et al. 2004).

Land-based counts of migrating pelagic seabirds require an intensive and long-range surveillance of the sea from sites strategically located along the coast, mainly capes, through high-quality telescopes. This intensive effort is difficult to maintain continuously for a long time, so detection efficiency can decline because of the observer's fatigue, requiring two or more observation teams to alternate. Since manpower and funding are usually limited, discrete intervals of intensive observation, followed by gaps without counts, are an alternative for calculating the passage rate (number of birds per hour). The issue becomes to scale up rates based on these intervals into total volume of migration, estimating the number of birds having passed during intervals without counts.

Here, we (1) develop a robust method (accompanied by suitable measures of precision, its accuracy tested with a sensitivity analysis) to infer missing and incomplete values from migration counts, taking into account additional covariates such as weather or date, and allowing estimation of the size of passage from migration counts; (2) use a data set from seabird migration through the Strait of Gibraltar to illustrate the proposed method; and (3) highlight the importance of our results for the conservation of two of the most threatened seabirds in the Mediterranean Sea.

METHODS

One potential framework for estimating the number of birds missed in periods during which counting does not take place, with great flexibility, is generalized additive modeling (GAM, Hastie and Tibshirani 1990; see Wood 2006 for an up-to-date and practical treatment). GAM can be thought of as an extension of the well-known linear framework of least-squares regression in two important respects. First, while linear regression assumes the response variable is normally distributed, GAM allows other distributions such as Poisson, binomial, negative binomial, and gamma. This is useful for count data (such as of migrating birds), which take discrete values and cannot be negative and so are poorly modeled by a normal distribution. Second, while linear regression assumes that the explanatory variables ("covariates") each have a linear effect on the response, GAM allows this relationship to be nonlinear. This is achieved in two ways. First, each covariate is allowed to have a smooth, nonlinear effect, the shape of which is estimated by the data. Second, the sum of these effects is linked to the mean response by a monotonic "link function," which can be nonlinear. For example, for count data, it often makes sense to use a logarithmic link function, i.e., to model the logarithm of the mean response, because this implies the mean response cannot be negative. GAM is also able to deal with autocorrelation (as can generalized additive mixed modeling), which likely is a problem for count data. Many of these features are shared by another framework, generalized linear modeling (GLM), but GLM is more restrictive in that it does not allow for estimation of smooth, nonlinear relationships between covariate and response.

To show the applicability of our method, we analyze data on pelagic birds' migration through the Strait of Gibraltar, one of the hot spots for bird migration in Europe. The Strait of Gibraltar is a bottleneck for pelagic birds, constraining migrants into a narrow front of only 14 km at the closest points of the European and African coasts. It is the only natural connection between the Atlantic Ocean and the Mediterranean Sea (Fig. 1) so concentrates the majority of the seabirds moving in or out the Mediterranean through the year (Hashmi 2000). Our data are for autumn migration (mid-October to mid-November, 2005–2007) of the three most abundant seabirds passing through the strait: the Northern Gannet (*Morus bassanus*), Cory's Shearwater (*Calonectris diomedea*), and Balearic Shearwater (*Puffinus mauretanicus*). These species are not known to migrate through the Strait of Gibraltar at night (e.g., Finlayson 1992, Ruiz and Marti 2004). The counts were made by experienced seabird ornithologists, assisted by trained volunteers during the three species' main periods of passage (Fig. 1).

Observers counted birds hourly during daylight at 10 m above sea level at Tarifa Island (southwestern Spain), the
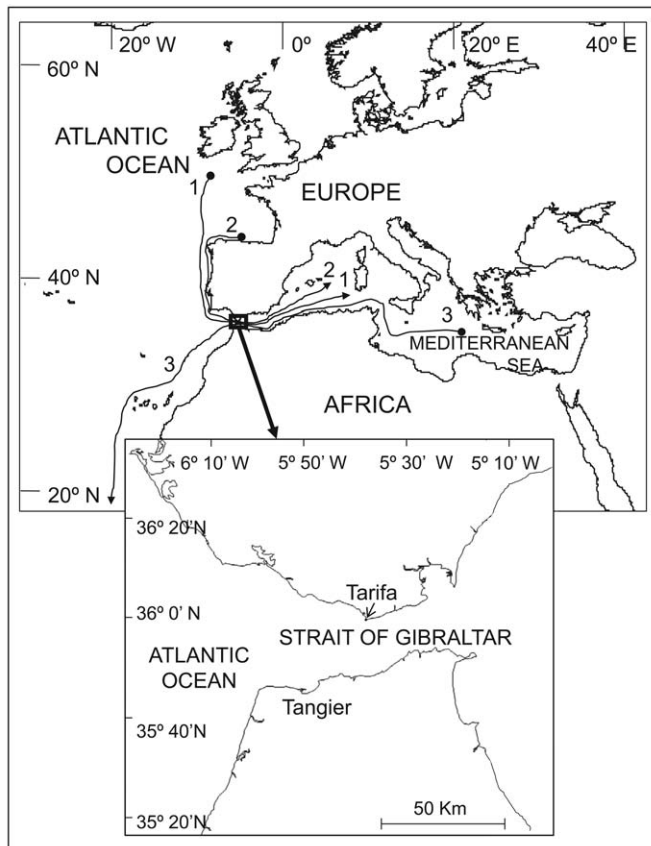
FIGURE 1.   Migration routes of seabirds crossing the Strait of Gibraltar (birds return along the same routes). Line 1: postnuptial migration route of part of the Northern Gannet population, which passes through the Strait of Gibraltar toward the Mediterranean Sea mainly between mid-October to mid-November. Line 2: main prebreeding migration route of the Balearic Shearwater, which passes through the Strait of Gibraltar to the Mediterranean mainly from mid-October to mid-November. Line 3: main postbreeding migration route of Cory's Shearwater, which passes through the Strait of Gibraltar to the tropical Atlantic coast of Africa mainly from mid-October to mid-November (Hashmi 2000). Inset: details of the African and Spanish coastline in the area of Tarifa. Note the funnel shape of the Strait of Gibraltar. Tarifa Island is the most efficient point for surveying seabirds from the coast in the strait (Programa Migres 2009).

TABLE 1.   Total number of days and total number, average, and standard deviation (SD) of 10-min intervals of observation by year, and dates of counts of migrating seabirds from Tarifa Island, Strait of Gibraltar.

Year	Days	Starting date	Ending date	10-min intervals		
				Total	Average	SD
2005	27	10 October	11 November	729	27	8
2006	30	16 October	18 November	698	23	9
2007	30	15 October	17 November	940	31	4

the Atlantic or to the Mediterranean. Simultaneously, a second observer with binoculars (10 × 42) surveyed those seabird flocks flying out of the field of view of the telescope, flying either too close or too high to be registered by the main observer. For each sighting, observers recorded the species, number of birds, and flight direction. We recorded wind data at 10 m hourly at the site of our observations.

The unit for statistical analysis was the 10-min sequence; the response variable was the corresponding count. We assumed that the daily passage occurred during daylight from sunrise to sunset. Thus total hours of observation varied from day to day with the seasons. We counted for a total of 798 hr apportioned among 2367 sequences of 10 min (Table 1).

For the analyses, we used package "gam" in R 2.11.1 (R Development Core Team 2010). Model selection with GAMs involves choosing explanatory variables and their degree of smoothing. The explanatory variables we considered for each model were wind direction and speed and the date variables hour, day, and year. We adopted a forward stepwise procedure, adding new variables to the model one at a time, both as main effects and as interactions with variables already in the model, and we retained the model with the lowest Akaike information criterion (AIC). We entered nonnumerical variables (such as wind direction) as factors, numerical variables (such as day) as smooth terms (thin plate regression splines) with the degree of smoothing determined automatically by the GAM package, by using generalized cross validation (see Wood 2006 for details). Generalized cross validation has some tendency to overfit (i.e., undersmooth) on occasion, so we inflated the penalty associated with the degrees of freedom of the smooth by 1.4, as suggested by Kim and Gu (2004; this is achieved by setting the gamma argument to 1.4 in the GAM package in R, see Wood 2006:224). Furthermore, exploratory analyses showed that, unconstrained, this procedure produced implausibly wiggly relationships between counts and numerical variables, so we constrained the maximum wigglyness by allowing a maximum of three degrees of freedom for the smooth. This is approximately equivalent to allowing at most a cubic relationship between explanatory variable and response, although regression splines have more flexibility to fit the data than do cubic functions. If the estimated degree of smoothing

southernmost point of the north coast of the Strait of Gibraltar (Fig. 1). Observations were made in three 10-min periods per hour, with 10-min gaps between each, 6 days per week (Sundays excluded). Thus we had three units for analysis equally distributed across each hour, totaling 30 min of observation per hour. We extrapolated these units to the other three units (30 min of no observation). We kept to this schedule throughout our study, so the existence of gaps is not related to the intensity of migration. The main observer equipped with a telescope (magnification 20–60×) scanned the area in front of the Tarifa Island, moving the telescope very slowly to the east and west, recording the movements of seabirds passing to

resulted in a model that was close to linear for any covariate (i.e., estimated equivalent degrees of freedom for that variable of 1.1 or less) then we planned to refit the model with a linear term rather than a smooth (Wood 2006); however, this did not happen in practice. As a final check, we used a backward step on the final model, dropping each variable in turn from the model to see if this resulted in a lower AIC.

Count data often are modeled as Poisson random variables, in which the variance is equal to the mean (McCullagh and Nelder 1989). When the individuals occur in clusters, however, the variance of the counts is larger than implied by a Poisson distribution, i.e., the data are "over-dispersed." We modeled these data by using the negative binomial distribution and estimating a dispersion parameter, which we incorporated into the model-selection procedures. We used the log-link function.

Once a final model was chosen for each species, we used it to predict the average number of birds in each time gap. Then we estimated the number of migrating birds as the sum of the predicted numbers over all time gaps plus the number of birds counted directly within the study period.

We used a parametric bootstrap to obtain the standard deviation (SD). In this, we created 10 000 new data sets by simulating new model parameters from a multivariate normal distribution with mean and variance–covariance equal to the fitted values, then using these new parameters to predict data points at the covariates' observed values (Wood 2006). We analyzed these simulated datasets in the same way as the original. We estimated the SD of estimated migratory flow from its empirical SD among the bootstrap samples.

During autumn passage through the Strait of Gibraltar, Northern Gannets and Balearic Shearwaters fly predominantly to the east into the Mediterranean, whereas Cory's Shearwaters fly to the west to the Atlantic (Fig. 1). Nevertheless, we sometimes observed birds flying in opposite direction. Therefore, we counted birds flying in the main and opposite direction separately. Subsequently, we obtained the net passage by subtracting those quantities. We discuss the likely causes of those reverse movements, their potential effects on estimates of totals, and possible solutions.

To validate the models and check its accuracy, we performed a sensitivity analysis by generating a sub-dataset "without gaps" from the original dataset. We deleted one of every three 10-min sequences from the original sample (the second sequence each hour). Our new sample with gaps was therefore one with two 10-min sequences each half an hour. We modeled this sample and used the fitted models to estimate the number of birds passing during the interval that had been deleted. We compared the predicted number of birds of those 10-min sequences with the real counts.

RESULTS

FILLING GAPS IN A REAL MIGRATION: A CASE STUDY

We modeled the counts of each species with GAM (Table 2). AIC differences between the best and next best models were large (>>9) in all cases, and the final backward selection step did not result in any variable dropping out for any species. The final models accounted for a substantial proportion of the deviance (from 28% to 52%, except for Gannets flying west, 17%) Autocorrelation plots (not shown) did not indicate any significant autocorrelation between successive residuals. The date is the most important variable affecting counts in the models for all species (separate smooth and intercept were fitted for each year, Fig. 2). Date adjustment accounted for the largest increase of the amount of variation explained by the models, surpassing the 70% of the total increase. The rest of the deviance explained by the models is due to the adjustment of hour and wind conditions, in different ways depending on the species (Table 2, Fig. 2).

There was a total of 1408 hours of daylight (4224 sequences of 10 min) distributed among all the years, days, and hours, in which we did not count seabirds (1454 sequences in 2005, 1494 in 2006, and 1276 in 2007, Table 3). For those intervals, we used the values generated by the models to predict counts in the missing 10-min sequences. Table 3 summarizes the totals of birds counted and estimated for each year in both directions of flight, including their standard deviation and the final net flow for each species and year. For the Northern Gannet and Cory's Shearwater, the coefficient of variation was 3–5%. For the Balearic Shearwater, it increases to 6 and 9% in 2007 and 2006, respectively, and reaches an anomalous value (192%) in 2005.

Validation of the models with the sensitivity analysis showed how robust and accurate the proposed method is (Table 4). For the Northern Gannet, the mean of the predicted counts is <1% from the mean of the actual counts. For Cory's Shearwater, the mean of the predicted counts is <0.5% from the mean of the actual counts. In the case of Balearic Shearwater, the estimates are a bit worse than for the other two species (see explanation below), but the mean of the predicted counts is still <7% from the mean of the actual counts (Table 4). We selected models in the same way as for the complete data set, and the results are the same for all species and both directions, with the same explanatory variables in each case.

DISCUSSION

The reliability of visual counts for quantifying migrating birds is constrained by several factors producing biases, including birds missed because of observer fatigue or their distance from the observer. In this paper, we have addressed the

TABLE 2.   The six best models (lowest AIC) for predicting numbers of the Northern Gannet, Cory's Shearwater, and Balearic Shearwater in intervals of 10 min of no observation as a function of the date and wind variables. Final models highlighted in **boldface**. All the parameters included in each model are significant ($P < 0.001$). The notation $y \sim x + y$ denotes that y is the explanatory variable and is a function of main effects x and y; $s(x)$ denotes a smooth function of variable x, and $s(x, by = y)$ denotes that there is a separate smooth on x for each level of the factor covariate y (i.e., an interaction between a smooth and a factor). ΔAIC, Akaike differences; %D, percentage of deviance explained by the model; K: the number of parameters in the model (i.e., sum of effective degrees of freedom for smooth terms and number of parameters for the other terms).

Species and flight direction	Model structure	ΔAIC	%D	K
Northern Gannet				
East	**count ~ s(day, by = year) + s(hour, by = year) + wind speed**	**0**	**28.2**	**23**
	count ~ s(day, by = year) + s(hour, by = year) + wind speed + wind direction	12	28.2	26
	count ~ s(day, by = year) + s(hour, by = year) + wind direction	57	26.4	21
West	**count ~ s(day, by = year) + wind speed + s(hour, by = year)**	**0**	**17.6**	**23**
	count ~ s(day, by = year) + wind speed + s(hour, by = year) + wind direction	9	17.6	26
	count ~ s(day, by = year) + wind speed + wind direction	44	15.4	17
Cory's Shearwater				
West	**count ~ s(day, by = year) + s(hour, by = year) + wind direction**	**0**	**39.1**	**21**
	count ~ s(day, by = year) + s(hour, by = year) + wind direction + wind speed	10	39.1	26
	count ~ s(day, by = year) + s(hour, by = year)	148	37.7	18
East	**count ~ s(day, by = year) + s(hour, by = year) + wind direction**	**0**	**46.7**	**21**
	count ~ s(day, by = year) + s(hour, by = year) + wind direction + wind speed	76	46.7	26
	count ~ s(day, by = year) + s(hour, by = year) + wind speed	188	45.9	23
Balearic Shearwater				
East	**count ~ s(day, by = year) + s(hour, by = year) + wind speed + wind direction**	**0**	**38.0**	**26**
	count ~ s(day, by = year) + s(hour, by = year) + wind speed + wind direction + wind speed × wind direction	61	38.0	34
	count ~ s(day, by = year) + s(hour, by = year) + wind speed	71	36.4	23
West	**count ~ s(day, by = year) + wind direction + s(hour, by = year)**	**0**	**52.0**	**21**
	count ~ s(day, by = year) + wind direction + s(hour, by = year) + wind speed	47	52.0	26
	count ~ s(day, by = year) + wind direction + wind speed	116	50.0	17

first factor; the importance of the others, with potential solutions, is discussed later in this section.

To avoid observer fatigue reducing the quality of the observations, it is usual for intensive observations to be divided into discrete sequences, followed by gaps without counts. We have demonstrated a robust method to fill time gaps in the counts, including measurements of precision. Validation revealed the models' accuracy for the Northern Gannet and Cory's Shearwater, the mean of the predicted counts of those species being <1% from the mean of the actual counts. An issue often ignored is that the precision of the estimates should be estimated (Stratoudakis 1999). We used a parametric bootstrap to translate uncertainty in the fitted model of the count into uncertainty in estimates of missed birds. It is worth emphasizing that the estimated precision was high, with standard deviation that did not surpass 10% of the estimated total, except for the Balearic Shearwater in 2005 (see below). This might be expected given such intensive sampling and models that explain reasonably high proportions of the variability in counts.

One must be cautious when interpreting data from migration counts because an unknown number of birds might be "invisible" to the observer because they are flying too high to be seen with binoculars or telescope (Alerstam 1978, Kerlinger 1989). In the case of counts of migrating seabirds passing appropriately chosen coastal viewpoints, such problems are reduced because most seabirds, such as shearwaters, most likely migrate at very low altitudes above the sea (e.g., Gudmundsson
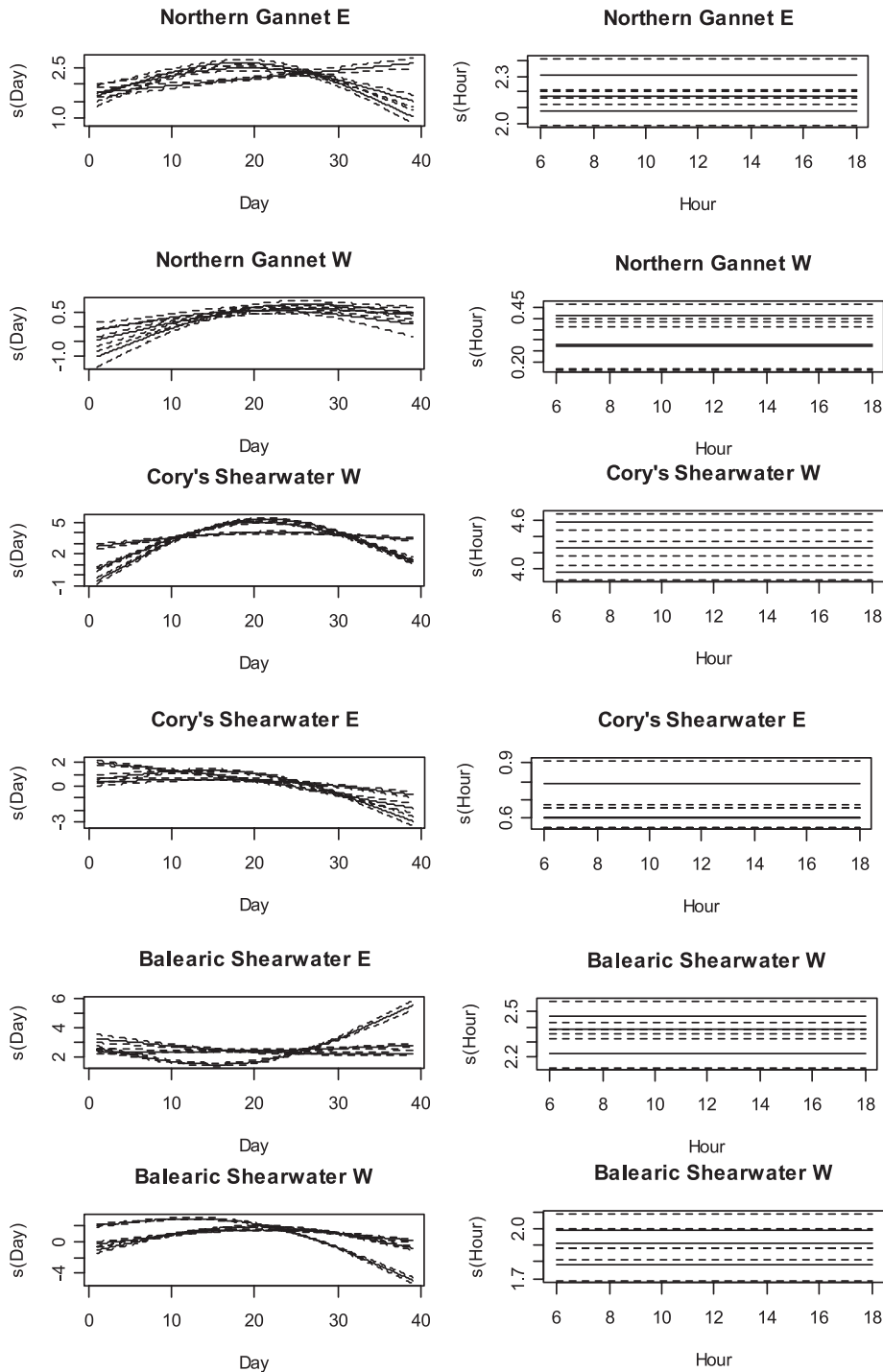
FIGURE 2. Fitted smooth terms (solid lines) for each final model (Table 2), for each species and flight direction (E, east; W, west), plotted on the scale of the link function (i.e., the log scale). Where there are three solid lines per plot, the final model includes an interaction with year. Dashed lines represent approximate 95% confidence intervals (±2× SE).

et al. 1992, Alerstam et al. 1993). This agrees with our observation that the vast majority of seabird flocks fly below our position (10 m above sea level) or slightly higher (Mateos 2009).

The reliability of land-based counts for quantifying seabirds at sea is constrained by the distance at which birds can be detected. In the case of the Strait of Gibraltar, migrating birds generally concentrate near the coast: the majority of birds fly nearer than 3000 m, and almost all birds up to 3000 m are seen (Mateos 2009, Mateos et al. 2010, Mateos and Arroyo 2011, thus confirming Christensen et al. 2003). Even if our

TABLE 3.   Total birds counted and estimated each year in both directions of flight with their standard deviation (SD) and the final net flow for each species and year.

Species and year	Counts			Estimates					Total				
	East	West	n^a	East	SD	West	SD	n^a	East	West	Net flow	SD	n^a
Northern Gannet													
2005	5756	954	729	10 743	432	1945	110	1454	16 499	2899	13 599	542	2183
2006	7321	995	698	19 728	1158	1981	109	1494	27 049	2976	24 073	1267	2192
2007	8704	1659	940	13 300	469	2139	93	1276	22 004	3798	18 206	562	2216
Cory's Shearwater													
2005	2586	62 987	729	7376	693	100 960	4713	1454	9962	163 947	153 985	5405	2183
2006	1732	58 307	698	3444	267	150 590	9982	1494	5176	208 897	203 721	10 249	2192
2007	651	36 227	940	1096	69	70 305	5148	1276	1747	106 532	104 785	5217	2216
Balearic Shearwater													
2005	9245	8181	729	14 894	758	15 080	931	1454	24 139	23 261	878	1689	2183
2006	6760	1717	698	17 014	1331	4073	277	1494	23 774	5790	17 985	1608	2192
2007	10 603	3572	940	17 154	804	4963	271	1276	27 757	8535	19 222	1076	2216

[a]Number of 10-min counts.

TABLE 4.   Validation of the models of seabird migration through the Strait of Gibraltar.

| Species and year | Counted birds[a] | | | Counted vs. estimated birds | | | | | | | Total | | | | | | | | | |
| | | | | East | | | West | | | | East | | West | | Net flow[e] | | | | Obs − Est[f] | %[g] |
	East	West	n^b	Obs[c]	Est[d]	SD	Obs[c]	Est[d]	SD	n^b	Obs[c]	Est[d]	Obs[c]	Est[d]	Obs[c]	Est[d]	SD	n^b		
Northern Gannet																				
2005	3953	629	499	1803	1838	97	325	318	18	230	5756	5791	954	947	4802	4844	115	729	−42	−0.9
2006	5012	676	475	2309	2299	111	319	317	18	223	7321	7311	995	993	6326	6318	129	698	8	0.1
2007	5878	1112	633	2826	2865	120	547	546	29	307	8704	8743	1659	1658	7045	7085	149	940	−40	−0.6
Cory's Shearwater																				
2005	2025	42 240	499	561	572	62	20 747	20 508	1125	230	2586	2597	62 987	62 748	60 401	60 151	1187	729	250	0.4
2006	1131	38 538	475	601	510	42	19 769	19 682	1510	223	1732	1641	58 307	58 220	56 575	56 579	1552	698	−4	0.0
2007	335	24 243	633	316	269	11	11 984	11 842	915	307	651	604	36 227	36 085	35 576	35 481	926	940	95	0.3
Balearic Shearwater																				
2005	6157	5786	499	3088	3022	191	2395	2400	221	230	9245	9179	8181	8186	1064	993	412	729	71	6.7
2006	4383	1293	475	2377	2257	112	484	563	44	223	6760	6640	1777	1856	4983	4784	156	698	199	4.0
2007	6806	2307	633	3797	3782	203	1265	1195	62	307	10 603	10 588	3572	3502	7031	7086	265	940	−55	−0.8

[a]Total birds counted each year in the 10-min intervals of observation modeled in both directions of flight.
[b]Number of 10-min counts.
[c]Number of birds actually counted in the 10-min intervals of observation by year and direction of flight.
[d]Total birds estimated by year and direction of flight.
[e]Final net flow by species and year.
[f]Difference between the observed and estimated passages.
[g]Percentage of difference with respect to the total observed passage.

study is applied to greater distances, at which detection is assumed to decrease with increasing distance, bias caused by the decreasing probability detection could be corrected by the methods of distance sampling (Buckland et al. 2001, 2004), although it is necessary to account for the fact that the density of birds is not uniform at all distances, as assumed by standard distance-sampling methods. Preliminary investigations have demonstrated that it is possible to combine an estimate of the density gradient, based on modeling of sightings from ferries crossing the Strait of Gibraltar, with distances of sightings from Tarifa Island o obtain reliable estimates of detection probability. This is the subject of continuing research.

Another source of bias is that birds may pass the same observation point multiple times, resulting in double or even

triple counts that bias the results. Since a visual observer can cover a limited range from our observatory (maximum 7000 m, mean 1438 ± 978 m, n = 1173 flocks; Mateos et al. 2010), more than half of the channel of the Strait of Gibraltar remains invisible from the north coast, and seabirds could fly back without being seen. However, oblique ship transects across the Strait of Gibraltar from commercial ferries between Algeciras and Tangier from 2002 to 2006, from the project "Migres Marinas" (Arroyo and Cuenca, unpubl. data; see fig. 5 in Mateos and Arroyo 2011), did not reveal those species flying in the direction opposite that expected from their pattern of migration, either through the center of the strait or along the south coast. In addition, as far as we know, reverse migration of pelagic seabirds has never been reported, and several studies tracking Cory's Shearwaters (Ristow et al. 2000, González Solís et al. 2007) showed that this species migrates rapidly and directly through the strait in autumn. Thus reverse migration of seabirds migrating through the Strait of Gibraltar is likely to be minimal. Nevertheless, we did record movements in the direction opposite that expected. These movements were not relevant in autumn for Cory's Shearwaters or the Northern Gannet but were marked for the Balearic Shearwater. The main period of migration of the Balearic Shearwater through the Strait of Gibraltar is from mid-May to mid-July (Finlayson 1992, Hashmi 2000, Programa Migres 2009). In autumn, days when Balearic Shearwaters fly into the Mediterranean regularly alternate with days when they fly into the Atlantic (pers. obs.). We suggest that when the relative magnitude of movement in the opposite direction is low (as in the case of the Northern Gannet and Cory's Shearwater), the probability of double counting is reduced by considering the net passage, defined as the result of subtracting of the total count of birds flying in the opposite direction from the total count of those flying in the main direction. In the case of the Balearic Shearwater, to reduce the probability of double counts due to local movements, we recommend surveys during to the main period of migration (mid-May to mid-July), when reverse movements will be reduced to the minimum.

An alternative to estimating the numbers of birds could be doubling the staffing of observation stations to permit continuous observation without gaps by alternating observers. Nevertheless, other problems could reduce the quality of the observations, mainly by increasing the variability in the data due to differences between observers (e.g., different degrees of experience, variation in visual acuity).

ESTIMATES OF MIGRATORY PASSAGE

The date appeared to be the most important factor influencing our counts, as expected for both extrinsic and intrinsic reasons; migration is normally confined to segments of the annual cycle (Newton 2008). The precise timing of migration partly determined by weather (e.g., Elkins 2004, Newton 2008).wind speed and direction in particular have been cited as important factors (e.g., Alerstam 1978, Kerlinger 1989). Our results support the importance of wind on the precise timing of migration.

A comparison of estimates of the passage from the north side of the Strait of Gibraltar with the existing estimates of populations of seabirds in the Mediterranean Sea is particularly relevant. The number of pairs of Cory's Shearwater breeding in the Mediterranean has been estimated to be around 30 360–42 530 (BirdLife International/EBCC 2000). The breeding individuals make up 45% of the species' population of the species in the Mediterranean (Tellería 1980, Yésou 1982, Mayol 1991), so the total population in this sea could be roughly estimated as 100 000–140 000. In 2005 and 2006 the number of migrating Cory's Shearwaters estimated from European side of the Strait of Gibraltar slightly surpassed the estimated Mediterranean population; in 2007 it was similar (Table 3). A substantial portion of the birds leaving the Mediterranean enters the Strait of Gibraltar along the African side (Navarrete 2008), and only a variable fraction crosses the Strait of Gibraltar along the European side, where a percentage, but never the total, can thus be seen from Tarifa Island (Hashmi 2000, pers. obs.). Thus our estimate from the Spanish coast should be considered an underestimate of the total movement.

The Balearic Shearwater is endemic to the Balearic archipelago (western Mediterranean) and is considered one of the rarest and most critically endangered seabirds in the world (Birdlife International 2000, Oro et al. 2004), being categorized by the Internation Union for the Conservation of Nature as critically endangered (IUCN 2010). The breeding population has been estimated at 2000–2400 pairs (Ruiz and Martí 2004, Arcos and Oro 2004), the total population (including nonbreeders) at about 8000–10 000 (Oro et al. 2004, BirdLife International 2010). A major part of the population leaves the Mediterranean each year, mostly from May to October (Mayol et al. 2000, Yésou 2003). Although reverse movements in autumn may confound the results of total counts (see above), the net passage of the Balearic Shearwater was 17 985 in 2006 and 19 222 in 2007, leading us to suspect that current published estimates of the species' population size could be low.

Our results reveal the necessity of updating the estimates of these two species' breeding populations, since the numbers of birds migrating along the north side of the Strait of Gibraltar, even if likely underestimated, are higher than those reported in the literature to date.

It is thought that around 20 000 Northern Gannets, approximately 4% of the Atlantic population, pass the winter in the western Mediterranean (Finlayson 1992, Paterson 2002). The net passage of Northern Gannets we observed heading east along the north side of the Strait of Gibraltar falls in a range consistent with the previous population estimates (13 599–24 073 birds).

That our estimates of the numbers of two shearwaters migrating through the Strait of Gibraltar exceed other population

estimates for the Mediterranean might suggest that we are overestimating migratory passages. However, all known potential sources of bias tend to underestimate rather than overestimate actual passage rates. Therefore, we believe our estimates of these species' abundance are conservative.

Our method provides a reliable, accurate, and statistically consistent method for converting passage rates based on incomplete counts into volumes of migration, including estimates of precision and considering covariates such as date or wind. This method is applicable to all kind of bird censuses that require intensive and/or long-range surveillance, circumstances that make it particularly difficult to maintain an intensive effort for a long time, and thus where discrete sequences of intensive observation are commonly followed by gaps without (such as monitoring of migration, foraging movements, or local displacements through areas of interest). An application relevant to conservation is to estimate the relative importance of migratory pathways for seabirds in quantitative terms, which allow testing of the criteria for the definition of areas to be protected like the Special Protected Areas for birds defined by the European Commission directive on the conservation of wild birds (79/409/EEC).

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