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STOPOVER ECOLOGY OF PASSERINE BIRDS ON AN ISLET IN THE BAY OF BISCAY IN AUTUMN REVEALS A PATTERN SIMILAR TO THEIR USE OF SMALL MEDITERRANEAN ISLANDS IN SPRING

LA ECOLOGÍA DE PARADA DE DESCANSO MIGRATORIO DE LAS AVES PASERIFORMES EN UN ISLOTE DEL GOLFO DE VIZCAYA EN OTOÑO REVELA UN PATRÓN SIMILAR AL USO DE LAS PEQUEÑAS ISLAS MEDITERRÁNEAS EN PRIMAVERA

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Summary.—During migration, landbirds normally need to stop-over in order to rest and/or acquire fuel stores that power their flight. Refuelling strategies become particularly evolutionarily relevant when birds must cross broad geographic barriers, where the chance to land and get food is nil, such as when crossing oceans. Our objective was to learn more about the use of the small islands located close to the mainland coast as stopover areas by small migratory birds that cross the Bay of Biscay. Using data collected in a constant-effort mist-netting programme conducted on Izaro Island (northern Spain) during autumn migration (years 2018 to 2021), we aimed to determine (1) which species land on the island and for how long they stay there, and (2) their fuel load and fuel deposition rate. Structurally, the assemblage was dominated by Willow Warblers *Phylloscopus trochilus*, which on average accounted for 84% of the abundance. Clustering analyses reveal that the assemblage was rather homogeneous across the four study years. Most birds probably stayed on the island for less than 24 hours, with fewer than 5% being recaptured one or more days after their first capture. The first-capture-event body mass of Willow Warblers captured only once (8.0g, 95%CI 7.8-8.4g) did not differ from the initial body mass of those captured two or more times within a season (8.0g, 95% CI 7.0-9.0g), and those stopping over on Izaro had a negative mean fuel deposition rate of –0.2g/day (SE = 0.1g/d). Overall, Izaro was used as an emergency stopover site during the course of this study, where exhausted birds

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landed after sea-crossings. From a conservation standpoint, and as compared to other stopover sites used as 'emergency' stopover sites, results suggest that Izaro is of little value for replenishing the fuel stores of these small birds during autumn migration.—Betanzos-Lejarraga, L., Guzmán, I., Escandell, R., Unamuno, E. & Arizaga, J. (2023). Stopover ecology of passerine birds on an islet in the Bay of Biscay in autumn reveals a pattern similar to their use of small Mediterranean islands in spring. *Ardeola*, 70: 241-255.

Key words: Basque coast, fuel, Izaro, ringing, stopover, Willow Warbler *Phylloscopus trochilus*.

RESUMEN.—Durante la migración, las aves terrestres normalmente necesitan detenerse para descansar o adquirir las reservas que después consumirán durante el vuelo. Las estrategias para ganar estas reservas se vuelven particularmente relevantes desde el punto de vista evolutivo cuando las aves han de cruzar grandes barreras geográficas en las que la posibilidad de aterrizar y alimentarse es nula, como ocurre al atravesar océanos. El objetivo de este artículo es profundizar en el uso de las pequeñas islas situadas cerca de la costa por las pequeñas aves migratorias que cruzan el golfo de Vizcaya. Utilizando los datos que fueron recolectados mediante un programa de anillamiento científico desarrollado en la isla de Izaro (norte de España) durante el periodo de paso posnupcial (años 2018 a 2021), se pretendió identificar (1) cuáles son las especies que usan la isla y cuánto tiempo permanecen allí, y (2) cuál es su cantidad y tasa de deposición de reservas. Estructuralmente, el ensamblado estuvo dominado por el mosquitero musical *Phylloscopus trochilus*, que en promedio representó el 84% de la abundancia. Los análisis de *clusters* revelaron un ensamblado muy homogéneo a lo largo de todo el periodo de estudio. En general el periodo de estancia en la isla fue de un día para la mayoría de los ejemplares capturados para anillamiento, y de ellos menos del 5% fueron recapturados uno o más días después de su primera captura. La masa corporal de la primera captura no varió entre mosquiteros musicales capturados una sola vez en la isla (8,0 g, IC 95 % 7,8-8,4 g) y capturados dos o más veces en la temporada (8,0 g, IC 95 % 7,0-9,0 g). La tasa de ganancia de reservas de los recapturados fue negativa (–0,2 g/d; SE = 0,1 g/d). En general, nuestros resultados sugieren que Izaro es usada como punto de parada migratoria de emergencia por las aves que, tras cruzar el Cantábrico, llegan exhaustas a la costa del norte de España. Desde el punto de vista de la conservación, y en comparación con otros sitios de parada migratoria utilizados, Izaro parece tener poco valor como punto de ganancia de reservas durante el periodo de paso posnupcial.—Betanzos-Lejarraga, L., Guzmán, I., Escandell, R., Unamuno, E. y Arizaga, J. (2023). La ecología de parada de descanso migratorio de las aves paseriformes en un islote del golfo de Vizcaya en otoño revela un patrón similar al uso de las pequeñas islas mediterráneas en primavera. *Ardeola*, 70: 241-255.

Palabras clave: anillamiento, costa vasca, Izaro, mosquitero musical *Phylloscopus trochilus*, parada migratoria, reservas de fuel.

INTRODUCTION

During migration, most terrestrial birds normally need to land multiple times to make 'stopovers', which, according to a recent review, can be defined as 'an interruption of migratory endurance flight to minimise immediate and/or delayed fitness costs' (Schmaljohann *et al*., 2022). Stopovers, therefore, are not only made to rest and/or gain fuel stores that they will burn aloft (Newton, 2008; Chernetsov, 2012), but can have other functions, including avoiding adverse weather in flight, minimising risk of predation, recovery from physical exhaustion or making spatio-temporal adjustments during the course of migration (Schmaljohann *et al*., 2022). Refuelling strategies become particularly important when birds must cross broad geographic barriers where there is little or no chance to land and acquire food, as with desert and ocean crossings respectively

(Schmaljohann *et al*., 2006). Sea crossings impose the need to gain as much fuel as necessary before the crossing (Rubolini *et al*., 2002). But, evolutionary speaking, this fuelling is the result of a compromise between gaining as much fuel as the bird can acquire, while simultaneously avoiding putting on so much weight that it increases energetic and predation costs by being too heavy (Lindström y Alerstam, 1992; Hedenström & Alerstam, 1997; Lind *et al*., 1999; Kullberg *et al*., 2000). Quantitatively, the necessity of fuelling before a sea crossing is to some extent shaped by the chance to replenish the energy consumed during the flight afterwards (Moore & Kerlinger, 1987; Spina *et al*., 1993; Pilastro & Spina, 1997; Arizaga *et al*., 2012). Stopover ecology studies after sea crossings are in this context necessary to understand how birds face such a hazardous challenge (Moore & Kerlinger, 1987; Moore *et al*., 1990; Pilastro & Spina, 1997; Yong & Moore, 1997; Spina & Pilastro, 1999; Barboutis *et al*., 2022; Gutiérrez Ramírez *et al*., 2022).

The Bay of Biscay, in the Atlantic Ocean, is big enough to be a geographical barrier that many migratory landbirds tend to avoid, both in autumn and spring (Tellería *et al*., 2009; Weisshaupt *et al*., 2018). However, this water body is not completely impassable for avian migration and some trans-bay passage occurs, especially under good meteorological conditions (Weisshaupt *et al*., 2016). In autumn, the Basque coast is one of the two main entry routes of migratory birds into Iberia (Tellería *et al*., 2009; Weisshaupt *et al*., 2016), the other route being in the eastern Pyrenees (Galarza & Tellería, 2003). It is relatively well known that, at least under certain meteorological circumstances, such as on days with strong southerly winds, many birds arrive exhausted at the southern end of the Bay of Biscay, stopping at the first piece of land they find. The landing of birds on islands during migration is a well-known phenomenon elsewhere, such as in the Mediterranean, where these small pieces of land in the vast sea constitute migratory stopover points for numerous species (Pilastro *et al*., 1998; Rubolini *et al*., 2005; Gargallo *et al*., 2011; López-Iborra *et al*., 2022). Often, and especially on smaller islands, these stopovers last no more than a few hours and their only function is for resting and recovery from physical exhaustion (Gargallo *et al*., 2011), acting as a 'rescue boat' (Sarà *et al*., 2023). Studying this phenomenon, however, is useful to deepen our understanding of migratory strategies and the role of seas as ecological and evolutionary drivers of migratory bird populations. In the case of the Bay of Biscay, very little is still known about how, when and under what conditions birds cross this barrier (Weisshaupt *et al*., 2016; Weisshaupt *et al*., 2018). The stopover ecology of migrant birds on islands or on the coastline is also a subject that has not been studied in the Bay of Biscay, for several reasons. Firstly, the Bay is a deep sea with few islands, especially off the coast of northern Spain, where they are practically reduced to a handful of small islets close to the coast. Secondly, there are few ringing stations along the coast. Previous research on the stopover ecology of small migratory birds along the coast of northern Spain is scarce and has primarily focused on wetland-associated (mostly reed-bed) passerines (González *et al*., 2007; Andueza *et al*., 2013; Andueza *et al*., 2014a; Andueza *et al*., 2014b; Arizaga *et al*., 2014a; Arizaga *et al*., 2014b; Unamuno *et al*., 2014; Arizaga *et al*., 2019).

Results from previous studies, e.g., within the Mediterranean, suggest that small islands along the Bay of Biscay offering (apparently) relatively limited feeding opportunities (Gargallo *et al*., 2011; Arizaga *et al*., 2012) are primarily used as opportunistic or emergency stopover sites (*sensu* Overdijk & Navedo, 2012) by birds exhausted after the sea crossing (Schmaljohann *et al*., 2022; Sarà *et al*., 2023). We therefore predict that most indi-

viduals stopping on small islands in the Bay of Biscay make short stopovers (< 24 h) and have modest fuel deposition rates (Gargallo *et al*., 2011).

In order to test this prediction and to learn more about the use of the coastline and particularly the small islands close to the coast as stopover sites for the small migratory birds that cross the Bay of Biscay, a constant-effort based ringing station was operated during four consecutive autumns on Izaro islet (Bermeo, northern Spain) to determine (1) which species land on the island and for how long they stay, and (2) their fuel load, fuel deposition rate and the effect of weather on capture rates.

Material and methods

Study area and data collection

Izaro Islet (hereafter, Izaro; 43º 25' N, 02º 41' W) is a 3.2ha island situated 3km to the east of the town of Bermeo, Bizkaia, northern Spain (Figure 1). The island ranges up to 44.5m high, and to some extent has the form of a plateau, bounded by rather steep cliffs with the centre comprising a relatively structurally simpler zone of bare soil together with some patches of grass, nitrophile plants (mostly mallow *Lavatera* spp. and beet *Beta vulgaris*) and a small zone with tamarisks (*Tamarix* spp.). The island lacks fresh water

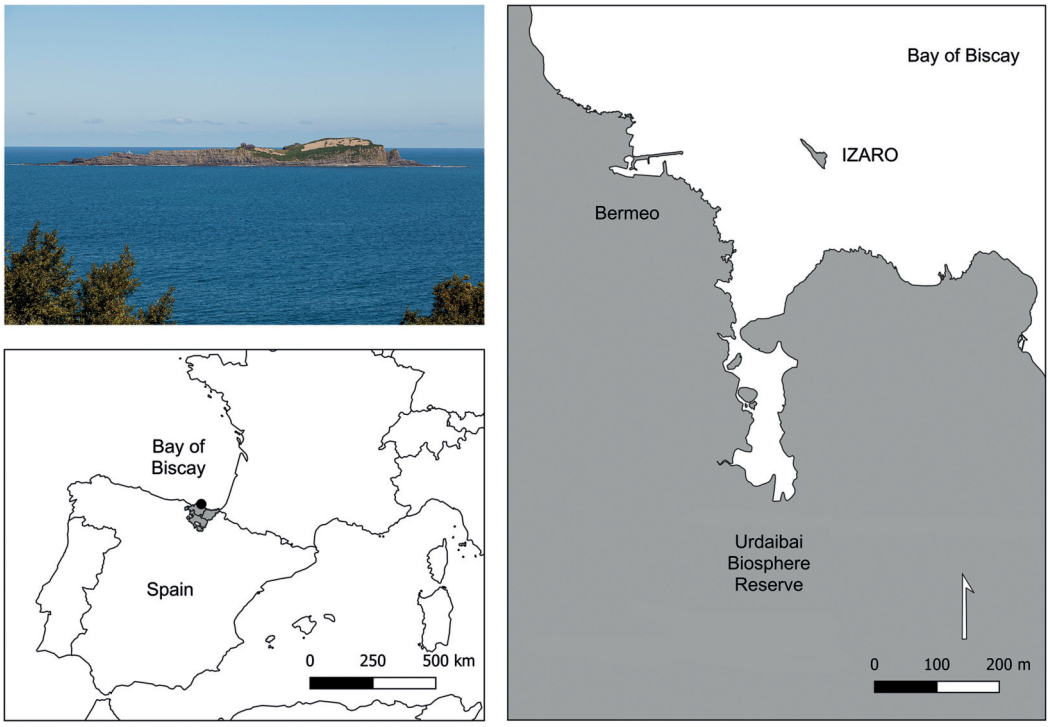

Fig. 1.—View and location of Izaro island, situated at the mouth of the Oka River (Urdaibai estuary), near the town of Bermeo, Biscay province, Basque Country (shaded area in the map of the bottom left panel).
[Isla de Izaro, situada en la desembocadura del río Oka (estuario de Urdaibai), cerca de la villa de Bermeo, provincia de Bizkaia, Euskadi (área en gris del mapa inferior a la izquierda).]

but was populated from 1422 to 1719 by a few monks who built a small monastery, today in ruins. Since 1719 the island has been uninhabited and today hosts a large Yellow-legged Gull *Larus michahellis* colony (*c*. 310 adult breeding pairs) (Arizaga *et al*., 2022), together with an egret heronry (Galarza & Arizaga, 2014), a small European Storm-petrel *Hydrobates pelagicus* colony, a pair of resident Peregrine Falcons *Falco peregrinus,* and a few pairs of small, presumably resident, passerines, mostly Eurasian Blackbirds *Turdus merula* and Black Redstarts *Phoenicurus ochruros*. These last two species are also represented by passage migrants.

Fieldwork was carried out from August until 8 September (at the latest) annually, from 2018 to 2021. The protocol used was a constant effort monitoring site, comprising a fixed number (117m in total) of five-shelf mist nets with a mesh size of 16mm (optimal for small passerine birds and allies, such as some woodpeckers, e.g., the Eurasian Wryneck *Jynx torquilla*, placed at fixed sites during the whole study period (for details see Betanzos *et al*., 2019). Sampling occurred daily from dawn to dusk. The nets were only closed at times of extreme weather, such as heavy rain or strong winds.

Once captured, all birds were ringed (or the ring was read if a bird was recaptured) and aged and the wing length (method III by Svensson, 1996; 0.5mm accuracy) and body mass were measured (with a digital balance, 0.1g accuracy). The mist nets were checked hourly, or every 30 minutes during high temperatures. Birds were aged according to their moult patterns and plumage characteristics (Svensson, 1996), and classified as either adults (EURING code 4) or young (first-year birds; EURING code 3).

Meteorological data were obtained from Matxitxako Cape Meteorological Station (source: Euskalmet), situated 5.5km from Izaro. The data provided by this station were daily means of the direction and intensity of the wind and precipitation. This last variable was codified as a binary variable (rain or no rain). The tailwind component, b, was estimated as: $b = V \times \cos\left[\alpha_T - (180 + \alpha_W)\right]$ (Andueza *et al*., 2013), where V is wind velocity (m/s), α_T is the angle at which the birds would hypothetically depart from Izaro in autumn, and α_W is the wind direction angle; α_T was assumed to be 225°, since most migrants in this part of Europe move along a NE-to-SW axis (Franks *et al*., 2022). High positive values of b indicate a strong tailwind (thus favouring active migration), whilst high negative values correspond to a strong headwind (which could detain birds at stopovers).

Data analyses

Each bird was considered only once per unit of analysis (e.g., once per year to estimate the contribution of each species, in terms of captures). Large species, like some waders, herons or seabirds, were anecdotal in the sample and, therefore, excluded from the analyses, that were limited to passerines, the Common Kingfisher *Alcedo atthis* and the Eurasian Wryneck (Table 1).

Co-occurrence analyses were done by estimating the percentage of captures of each species. We also conducted a hierarchical cluster analysis to estimate bird assemblage similarity among years using the UPGMA method with the Jaccard similarity index based on species' presence/absence (Sneath & Sokal, 1973).

The only species providing sufficient recaptures to address robust models on factors shaping fuel load and fuel deposition rate was the Willow Warbler *Phylloscopus trochilus* (Table 1). We assessed fuel load using body mass, with wing length as an offset variable, whilst fuel deposition rate was calculated on an individual basis, as the difference in body mass between the last and

TABLE 1

Number of birds never recaptured, recaptured only once or recaptured more than once within a single season on Izaro island during the autumn migration (2018-2021). The last column shows the percentage of individuals of each species recaptured (once or more). Species are listed alphabetically by generic name and classified as long-distance (L) or short-distance (S) migrants, or residents (R) (Tellería *et al*., 1999). Rec. = recaptured.
[Número de ejemplares capturados una sola vez y recapturados una o más de una vez en cada temporada en la isla de Izaro, durante el periodo de paso posnupcial (2018-2021). La última columna indica el porcentaje de individuos recapturados en la isla una o más veces. Especies ordenadas alfabéticamente siguiendo su nombre en latín, y clasificadas como migrantes de larga (L) o corta (S) distancia o como residentes (R) (Tellería et al*., 1999).]*

	Type	No rec.	Rec. once	Rec. > once	Sample size	% rec.
Sedge Warbler *Acrocephalus schoenobaenus*	L	3	2		5	40.0%
Common Reed Warbler *Acrocephalus scirpaceus*	L	32			32	0.0%
Common Sandpiper *Actitis hypoleucos*	S	2			2	0.0%
Common Kingfisher *Alcedo atthis*	S	1			1	0.0%
Greater Whitethroat *Curruca communis*	L	82	6	3	91	9.9%
Sardinian warbler *Curruca melanocephala*	R	1			1	0.0%
European Robin *Erithacus rubecula*	S	14	2		16	12.5%
Pied Flycatcher *Ficedula hypoleuca*	L	171	6		177	3.4%
Icterine Warbler *Hippolais icterina*	L	2			2	0.0%
Melodious Warbler *Hippolais polyglotta*	L	60	6		66	9.1%
Eurasian Wryneck *Jynx torquilla*	L	1			1	0.0%
Red-backed Shrike *Lanius collurio*	L	3			3	0.0%
Common Grasshopper Warbler *Locustella naevia*	L	3			3	0.0%
Common Nightingale *Luscinia megarhynchos*	L	7	4		11	36.4%

TABLE 1 (cont.)

	Type	No rec.	Rec. once	Rec. > once	Sample size	% rec.
Bluethroat *Luscinia svecica*	S	1			1	0.0%
Western Yellow Wagtail *Motacilla flava*	L	3			3	0.0%
Spotted Flycatcher *Muscicapa striata*	L	45			45	0.0%
Northern Wheatear *Oenanthe oenanthe*	L	153	2		155	1.3%
Black Redstart *Phoenicurus ochruros*	S/R	39	46	31	116	66.4%
Common Redstart *Phoenicurus phoenicurus*	L	20	2		22	9.1%
Willow Warbler *Phylloscopus trochilus*	L	3868	58	23	3949	2.05%
Whinchat *Saxicola rubetra*	L	8			8	0.0%
European Stonechat *Saxicola rubicola*	S	1			1	0.0%
Eurasian Blackcap *Sylvia atricapilla*	S	1			1	0.0%
Garden Warbler *Sylvia borin*	L	8	2		10	20.0%
Common Blackbird *Turdus merula*	S/R	3	8	13	24	87.5%
Song Thrush *Turdus philomelos*	S	1			1	0.0%
Eurasian Hoopoe *Upupa epops*	L	10			10	0.0%
Total		**4543**	**144**	**70**	**4757**	

first capture event, divided by the number of days elapsed between these dates. Within-day recaptures are not considered, so percentage recaptures and fuel deposition rate refers to birds recaptured after one or more days.

To estimate body mass, we only considered those birds for which we had measured body mass and wing length. General Linear Models (GLM) were run to analyse the physical condition of Willow Warblers stopping over on Izaro. We first tested whether the initial body mass (as an object variable) of individuals that were never recaptured differed from those that were recaptured once

or more within the season, controlling for age (as a factor), using hour and wing length as offset variables. We then ran a model on fuel deposition rate (object variable) with the following independent variables: apparent stopover duration, initial body mass and wing length. In both GLMs we used a linear link function with a normal error distribution. In such models, those birds recaptured one-day after first capture were removed to reduce possible handling effects (Schaub *et al*., 2008).

Finally, we analysed whether Willow Warbler capture rates on Izaro were correlated with meteorological conditions: rain/no rain and the daily mean value of the tailwind component. With that goal, the number of captures of Willow Warblers per day were log-transformed and then tested for the Pearson correlation with these two meteorological data sets, considering both the same and the previous date, because bird numbers on a given day might be affected by meteorological conditions the day before, as warblers are nocturnal migrants.

Statistics were calculated using R (R Core Team, 2020). All means are presented ± 95% confidence intervals.

Results

Considering only those days with complete sampling (dawn to dusk), the mean number of captures per day did not vary significantly among years ($F_{3,110} = 1.006$, $P = 0.393$, for details see Supplementary Electronic Material, Appendix 1). Across the four seasons, we captured 4,636 individuals, with 4,531 of them (98%) being long-distance, trans-Saharan migrants. No deaths in the nets were reported.

We captured 28 species overall (Table 1). The assemblage was dominated by the Willow Warbler, which accumulated 84% of the abundance (range: 81.2% in 2021 to 87.2% in 2018). The next top-ranked species, each comprising >1% of the abundance, were: Pied Flycatcher *Ficedula hypoleuca*, Northern Wheatear *Oenanthe oenanthe*, Greater Whitethroat *Sylvia communis*, Black Redstart *Phoenicurus ochruros* and Melodious Warbler *Hippolais polyglotta* (Figure 1). Clustering analyses revealed that the mix was rather homogeneous across the four study years (with similarities of >0.7), except in 2020, which showed a similarity index of <0.6 in relation to the other three years (Figure 2). A detailed analysis per year revealed that this difference was mostly due to the fact that in 2020 we captured a proportionally higher number of two out of those top-ranked species, which had relative abundances of >1%: the Northern Wheatear and the Pied Flycatcher (Table 2).

Overall, most birds probably remained on the island for less than 24 hours, just 3.2%

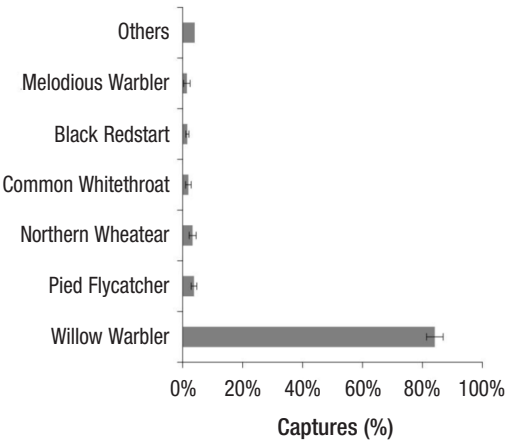

Fig. 2.—Mean percentage (±95% confidence interval) of captures (each bird considered only once per year) of most frequently caught species on Izaro island during autumn migration (2018-2021). *[Porcentaje medio (± intervalo de confianza al 95%) de capturas (cada ejemplar solo se ha considerado una vez por año) de las especies más abundantes capturadas para anillamiento en la isla de Izaro en paso posnupcial (2018-2021).]*

and 1.5% being recaptured once or more within a single season, respectively. Of 28 species, 16 had no recaptures (Table 1). Among species with a sample size of at least ten birds, those with the most recaptures (>50% in each case) were the Blackbird and the Black Redstart, which are among the few resident passerines breeding on Izaro. There was also a small group of passerines with percentage recaptures ranging from almost 10% (3 species) to 36% (Common Nightingale). In this latter group, the three species with the highest capture numbers: Pied Flycatcher, Northern Wheatear and Willow Warbler, showed low recapture percentages (all <5%). Among species with no recaptures only three had sample sizes of ten or more individuals (Table 1).

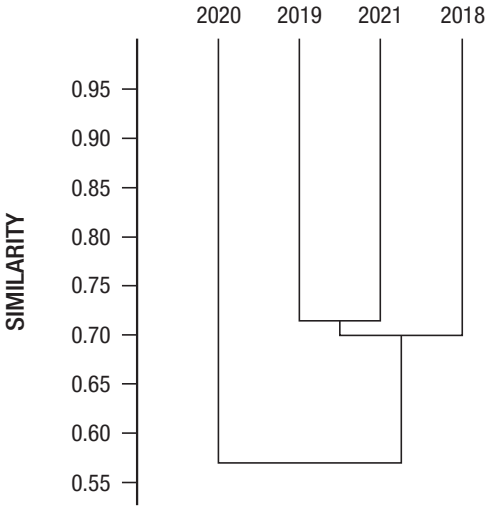

FIG. 3.—Cluster diagram illustrating the similarity between years of the assemblage of passerines and allies captured on Izaro island during autumn migration (2018-2021).
[Diagrama de grupos aplicado para ilustrar la similitud interanual del ensamblado de paseriformes y especies afines capturadas en la isla de Izaro en paso posnupcial (2018-2021).]

Willow Warbler stopover ecology

The first-capture-event body mass of Willow warblers captured only once (8.0g,

TABLE 2

Percentage captures during each autumn season on Izaro island of species that accounted for over 1% of the abundance in at least one of the four study years (2018-2021).
[Porcentaje de capturas (sobre el total de aves capturadas en cada temporada) en Izaro durante el periodo de paso posnupcial (años 2018-2021), de las especies que acumularon más de un 1% de la abundancia.]

	2018	2019	2020	2021
Willow Warbler *Phylloscopus trochilus*	87.2%	85.8%	82.3%	81.2%
Greater Whitethroat *Curruca communis*	1.1%	2.4%	1.0%	2.9%
Pied Flycatcher *Ficedula hypoleuca*	3.4%	3.7%	5.2%	2.9%
Melodious Warbler *Hippolais polyglotta*	0.4%	0.9%	1.4%	2.9%
Spotted Flycatcher *Muscicapa striata*	0.7%	0.6%	0.9%	1.7%
Northern Wheatear *Oenanthe oenanthe*	3.8%	1.7%	4.5%	3.3%
Black Redstart *Phoenicurus ochruros*	0.9%	2.1%	1.8%	1.5%

CI95% 7.8-8.4g, n = 3,672) did not differ from the initial body mass of those captured twice or more times within a season (8.0g, CI95% 7.0-9.0g, n = 64; Table 3). Willow Warblers tended to increase their body mass during the day (with a mean gain of more than 2g from dawn to dusk, as judged by the beta parameter estimates from Table 3). Adults were on average *c*. 2.2g lighter than juveniles (Table 3).

Analysis of fuel deposition rates was only possible for juvenile Willow Warblers due to sample size constraints. Those stopping over on Izaro had a mean fuel deposition rate of –0.2g/day (SE = 0.1g/day), a value that differed significantly from zero (one-sample t-test: t = 3.0292, P = 0.005, n = 30). The fuel deposition rate was not determined by apparent stopover duration, initial body mass or wing length (Table 4). However, when the apparent stopover duration was classified as a binary factor of one (i.e. recaptured the day after being ringed) *vs*. more stopover days (i.e., recaptured more than one day after being ringed), then the fuel deposition rate of Willow Warblers with an apparent stopover duration of one day (–0.36g/d, 95%CI: –0.58, –0.14g/day, n = 11) was significantly lower when compared with those staying longer periods (–0.05g/day, 95%CI: –0.16, +0.05g/day, n = 19; t test for two unpaired samples: t = 3.08, P = 0.005).

The (log-transformed) number of Willow Warblers captures was not significantly correlated with the mean tailwind component of the day of capture (r = 0.18, P = 0.054), but was significantly and positively correlated

TABLE 3

Beta-parameter estimates of a general linear model on body mass (g) with recapture status (yes/no), hour (codified from 0 = 0:00 to 1 = 23:59) and age (as a factor: juvenile, adult or unknown) as predictive variables of Willow Warblers stopping over on Izaro island during autumn migration (2018-2021).
[Beta-parámetros estimados obtenidos de un modelo lineal general con la masa corporal (g) como variable objeto, con la recaptura (si el ave fue recapturada o no), hora (codificada de 0 = 0:00 a 1 = 23:59) y edad (como factor, aves jóvenes, adultas o de edad desconocida) como predictores, llevado a cabo para los mosquiteros musicales sedimentados en la isla de Izaro durante el periodo de paso posnupcial (2018-2021).]

Covariate or factor	Beta (±SE)	*P*-value
Recaptured: yes[1]	−0.03 ± 0.46	0.954
Age: young[1]	+1.22 ± 0.16	<0.001
Age: adult[1]	−1.06 ± 0.17	<0.001
Hour	+2.31 ± 0.30	<0.001

[1] Reference values (Beta = 0): Recaptured: no; Age: unknown.

TABLE 4

Beta-parameter estimates of a general linear model on fuel deposition rates (g/day) with apparent stopover duration, initial body mass (g) and wing length (mm) as predictive variables for Willow Warblers stopping over on Izaro island during autumn migration (2018-2021).
[Beta-parámetros estimados obtenidos de un modelo lineal general con la tasa de ganancia de reservas (g/d) como variable objeto, con el tiempo de estancia aparente, masa corporal inicial (g) y longitud alar (mm) como predictores, llevado a cabo para los mosquiteros musicales sedimentados en la isla de Izaro durante el periodo de paso posnupcial (2018-2021).]

Covariate or factor	Beta (±SE)	*P*-value
Stopover duration	+0.02 ± 0.01	0.096
Initial body mass	−0.10 ± 0.06	0.186
Wing length	+0.00 ± 0.00	0.952

with the mean tailwind component measured one day before capture ($r = 0.30$, $P = 0.001$) (Figure 4), indicating that, to some extent ($r^2 = 0.092$), prevailing wind conditions on a given day predicted the number of Willow Warblers stopping over on Izaro the next day. Regarding precipitation, the mean (log-transformed) number of Willow Warbler captures of on days with rain did not differ significantly from that on days with no rain ($t = 1.70$, $P = 0.092$). Likewise, the mean number of Willow Warbler captures of did not differ significantly relative to presence/absence of rain one day before capture ($t = 0.94$, $P = 0.355$).

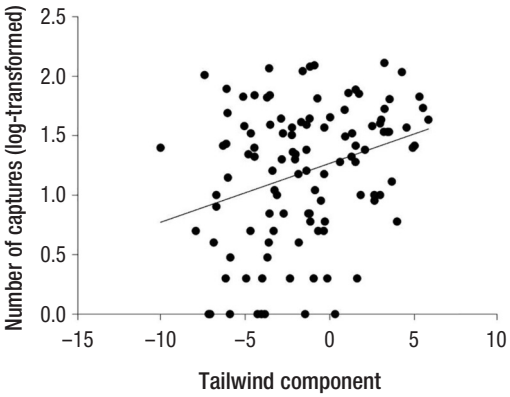

FIG. 4.—Linear relationship between the log-transformed number of Willow Warblers captures per day (all years pooled) as a function of the daily mean value of the tailwind component on the day before each capture date. High positive tailwind component values indicate a strong tailwind and high negative values indicate a strong headwind.
[Relación lineal existente entre el número de capturas por día de mosquiteros musicales (log-transformado) el valor medio del componente de viento de cola medido el día previo. Un valor positivo indica fuerte viento de cola, mientras que valores negativos indican viento de cara.]

DISCUSSION

General use of the island by small migratory birds

This is the first study investigating the stopover ecology of small passerine birds and allies on a small islet in the southern part of the Bay of Biscay during the autumn migration period, i.e., after crossing the Bay of Biscay. Because the sampling was carried out mostly in August, it focuses on long-distance European-Afrotropical migrants that primarily spend the non-breeding season in tropical Africa (Franks *et al*., 2022). In fact, 98% of birds we captured were long-distance European-Afrotropical migrants.

We did not detect particular years with significantly higher or lower number of captures. This result is in part due to the high variance in the number of birds stopping over on Izaro on a daily basis, a consequence of successive migratory waves that filled (arrivals) or emptied (departures) the island.

The structure of the assemblage did not vary substantially among years, showing a clear predominance (80% and occasionally nearly 90%) of Willow Warblers. Even though the Willow Warbler is an open woodland species, it is well-known for regularly using small offshore islands that lack the habitats (green wooded areas) with which it is usually associated (Gargallo *et al*., 2011).

Not surprisingly, the two species: the Blackbird and Black Redstart, most often recaptured (>50% in each case) were those with a small resident population on the island. This result reinforces evidence indicating that the use of Izaro as a long stopover site by migratory birds is marginal.

Willow Warbler stopover ecology

Most Willow Warblers remained on Izaro apparently just a few hours after landing, since only 2% of them were recaptured one

or more days after their first capture. These birds (with those recaptured one-day after first capture excluded due to avoid any possible handling effect; Schaub *et al*., 2008) showed a statistically null mean fuel deposition rate, suggesting that longer-staying individuals are apparently unable to gain fuel reserves, and perhaps only remain on the island to rest and/or to wait for optimal weather. They may even try to store fuel after experiencing a hazardous sea-crossing, albeit unsuccessfully. This stopover site is, therefore, very different from a nearby reed bed area, which has been shown to be used opportunistically, possibly linked to episodes of local super-abundance of reed bed aphids (Rogalla & Arizaga, 2018), and where the Willow Warblers are able to achieve positive fuel deposition rates.

According to a recent review, evaluation of the use of a stopover site by migrants should be focused on the causes underlying landing decisions rather than on those explaining the decision to depart (Schmaljohann *et al*., 2022). In this context, both for the Willow Warblers and other migratory birds, Izaro apparently most often serves primarily as an emergency stopover site (i.e., 'rescue boat') in autumn, where exhausted birds land after hazardous sea-crossings. From a conservation standpoint, and compared with other stopover sites with this 'emergency' nature (Overdijk & Navedo, 2012), Izaro probably has small ecological value for these small birds, for two main reasons. Firstly, this island is just 3km from the mainland so most birds that land on it could probably continue to the Spanish coast, unless exhausted by, for example, strong headwinds. Secondly, due to the size of Izaro, the number of migrants stopping over is relatively small and hence the site may have marginal importance from a population-level perspective.

It is interesting that Willow Warblers tended to be more numerous on days following strong tailwinds, rather than headwinds, suggesting that arrivals on Izaro were more likely to happen after sea crossings favoured by the prevailing winds. This result contradicts local perception that landings along the coast or on small off-coast islets like Izaro mostly happen under strong southerly winds (i.e., headwinds during autumn migration). Future research on other islands in the Bay of Biscay could be key to determine the generality of findings obtained on Izaro. Because Izaro is also located very close to the coast, it would be also important to undertake simultaneous ringing campaigns on the island and mainland to evaluate the behaviour of migrants in both situations.

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Appendix 1. Number of captures of passerines and allies on Izaro island during the autumn migration period (mostly, August) during 2018-2021. September data are excluded here since not all years had samples in this month.

[Número de capturas de paseriformes y especies afines en la isla de Izaro, en paso posnupcial (agosto), durante el periodo en que la campaña de anillamiento estuvo activa (años 2018-2021). Los muestreos de septiembre no se muestran aquí porque la campaña en algunos años se cerró en agosto.]

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