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Adverse weather reduces the spatial use of an opportunistic gull

Nere Zorrozua [*], **Sergio Delgado**, **Asier Aldalur and Juan Arizaga**
Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11,
E-20014 Donostia, Spain
[*]Corresponding author's e-mail address: nzorrozua@aranzadi.eus

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Abstract
Studying the individual or population response of species to variations in weather is gaining impetus due to increased interest in quantifying the effect of global change on biodiversity. Our goal here was to test the role of meteorological conditions (particularly extreme weather) on the activity budget of a generalist seabird species during its breeding season. To this end we used data from GPS-tracked adult yellow-legged gulls (*Larus michahellis*). Precipitation and wind had a significant impact on spatial use, reducing foraging distances and forcing gulls to spend a longer period within the colony and promoting a change in habitat use. The results suggest that rainfall and wind forced breeding gulls to desist from the area and habitats used under favourable weather, which might affect chicks' food provisioning. In a future with increasing rainfall and a higher number of extreme bad weather events, investigation should be conducted to establish the extent to which reduction in spatial use may negatively impact reproduction and, hence, demography.

Keywords
foraging distances, GPS, habitat use, rainfall, wind.

1. Introduction

Understanding the individual or population response to variations in weather is gaining more and more impetus due to ever increasing interest in quantifying the effect of global change on biodiversity (e.g., Sillett et al., 2000; Sanz, 2002; Haest et al., 2018). When breeding, birds must find food not only for themselves but also for their mate during the incubation period, and/or offspring, once the eggs hatch. Bad weather presents a challenge in such cir-

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cumstances because it not only affects foraging success (Finney et al., 1999; Pistorius et al., 2015; Chard et al., 2018), but also imposes a threshold in relation to nest attendance (Schulz et al., 2014; Öberg et al., 2015).

Rain is considered to be one of the most important weather factors affecting bird behaviour (Elkins, 1983). This may be directly, as rainfall will theoretically force birds to invest more energy in flying, since water adherence can increase the mass of the wings and body and, therefore, increase the cost of staying airborne (Haines & Luers, 1983), as well as through increasing aerodynamic drag and thus affecting the bird's control and manoeuvrability (Voigt et al., 2011). Recent research, however, demonstrates that even small birds like hummingbirds can fly relatively well in heavy precipitation (Ortega-Jimenez & Dudley, 2012). Though, in larger taxa, such as many seabirds, the role of precipitation on flight performance might exhibit a smaller influence (Gaston, 2004). However, rainfall can also have indirect consequences on birds, e.g., due to its effect on prey availability or prey seeking and detection (Sergio, 2003). Indeed, it seems that in many cases, birds spend more time looking for food when it is raining (Finney et al., 1999; Sergio, 2003; Pistorius et al., 2015). During the breeding season, the search for food must also fit in with the need to incubate eggs and rear offspring. Reproductive success may also be affected by precipitation in different ways, e.g., high levels of rainfall decrease nestling survival (Kosicki, 2011; Yannic et al., 2014), while a dry season may hamper the food provisioning of the parents and hence provoke lower breeding success (Thyen & Becker, 2006). Interestingly, under rain conditions Cape gannets (*Morus capensis*) were observed to spend shorter amounts of time on their nests (Pistorius et al., 2015). Few studies have, however, focused on the effect of rain on foraging performance of individually-tracked birds during the breeding season, when they need to attend to their nests/chicks.

In addition to rain, strong wind can also have a significant impact on flight performance (Thorup et al., 2003; Erni et al., 2005; McLaren et al., 2012; Collins et al., 2020; Santos et al., 2020). Strong winds, especially when blowing either against the direction of flight or laterally, force birds to invest more energy in moving, and in fact migrants commonly make a stopover when prevailing wind conditions are not favourable for their migration (Åkesson & Hedenstrom, 2000; Danhardt & Lindström, 2001; Barriocanal et al., 2002; Arizaga et al., 2011). That said, the effect of wind on the spatial use of breeding birds remains a poorly studied area. In birds with large foraging areas, such is the case for many seabirds, it might be stated that prevailing wind conditions will have an impact on their spatial ecology given that these birds must find a balance between investing high amounts of energy in moving and obtaining enough food to feed themselves and their offspring.

Besides the body of studies focused on the consequences of climate change on birds (e.g., Crick, 2004; Cox et al., 2019), relatively little attention has been paid to the behavioural responses of individuals to climatic variation (Buchholz et al., 2019). The capacity to quickly address and adapt to rapid environmental shifts (i.e., behavioural flexibility) is one of the main responses that species have to cope with the current climate warming process (Beever et al., 2017). As such, behavioural flexibility appears before changes in the size and distribution of given populations become obvious (Beever et al., 2017), although it must be highlighted that our knowledge of the limits and constraints of behavioural responses to climate change is still limited. Such studies are crucial to comprehending the resilience of species/populations to climate change and, therefore, to evaluating our capacity to plan actions to mitigate the effects of climate change on birds. Specifically, more research on the effects of extreme and specific weather conditions are needed in order to extend our knowledge of the effects of climate change on birds (Møller et al., 2004).

Using a data set of GPS-tracked adult yellow-legged gulls (*Larus michahellis*), we investigated the role of rain and wind on the activity budgets of this seabird. On the basis of previous research, we hypothesize that (1) gulls will spend more time in their colony during rainy days, because of their duties of attending to the nest/chicks, and (2) foraging trips on rainy days and days with strong winds will involve shorter distances.

2. Material and methods

2.1. Study species

The yellow-legged gull in the Bay of Biscay (north of Spain; for details see also Figure 1) is a resident coastal seabird species that feeds on a very broad range of prey, both marine and terrestrial, including waste taken from landfill sites (Arizaga et al., 2013; Zorrozua et al., 2020a). Foraging trips can, therefore, be purely marine or terrestrial, or mixed (Arizaga et al., 2018).

Our study was carried out using adult individuals caught during the breeding season at two of the main colonies in the south-eastern part of the Bay

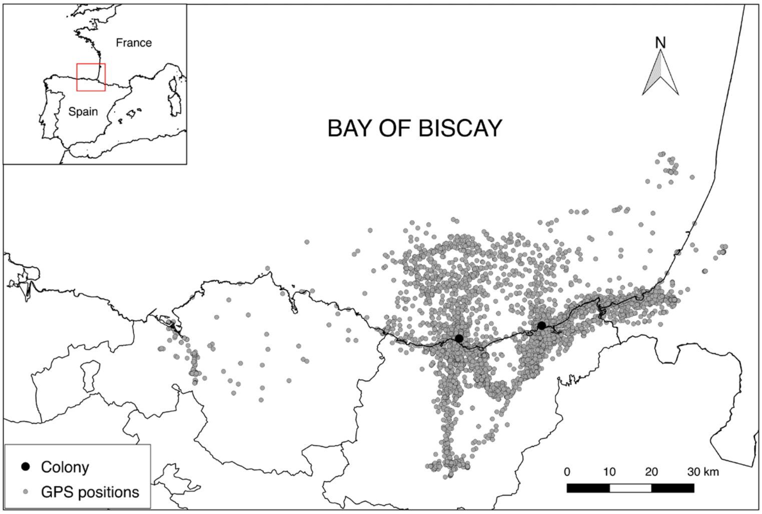

Figure 1. Location of the two colonies in the south-eastern part of the Bay of Biscay studied in this work (black dots) and the GPS positions (grey dots) recorded for breeding yellow-legged gulls.

of Biscay: Ulia (43°20′N, 01°57′W) and Getaria (43°18′N, 02°12′W) (Figure 1). Ulia is by far the largest colony within the region, with ca. 660 breeding pairs, while Getaria hosts ca. 165 breeding pairs (in 2017; Zorrozua et al., 2020b). The breeding season begins in April (eggs are laid during the second half of April and first half of May). Hatchings occur during the second half of May (when the adults in this study were captured), and the majority of chicks fledge before mid-July.

2.2. Sampling protocol, GPS settings and data collection

In May 2019, we captured 17 adult breeding yellow-legged gulls: 9 in Ulia and 8 in Getaria (see Table A1 in the Appendix). Each individual bird was ringed with an official (metal) ring, together with a Darvic ring. In addition, each bird was fitted with a GPS (model Wimbi SF-25, Wimbitek, Gipuzkoa, Spain) mounted on a hand-made Teflon harness which was adjusted to fit each individual. These GPS were equipped with a solar panel to charge the battery and registered positions every 30 minutes. The first inner primary feather (P1) was taken from each gull to sex the birds using DNA analysis at the University of Navarra.

Weather data (rainfall and mean daily wind speed values) were provided by the Igeldo meteorological station (43°18′23″N, 2°2′28″W; source:

AEMET, Ministry of Ecological Transition, Spain). Specifically, in this work we used the total daily amount of rain collected (mm) and the mean wind speed (km/h) between 1 May and 30 June 2019.

2.3. Data processing, statistical analyses

For each bird, all the data (positions) provided by the GPS were grouped into trips, with a trip being defined as the total number of positions of every movement which started and ended in the colony (i.e., first and last position of a trip was the colony). Colony positions were considered to be those within a radius of 1 km from the centre of the colony. As meteorological data were collected on a daily basis, we removed trips that lasted for more than one day (5%). To determine the main habitat type covered on each trip, each GPS location within each trip was classified as either marine or non-marine using Corine Land Cover (CLC, 2012) in QGIS (QGIS Development Team, 2009). Thereafter, each trip was classified as either marine (when all the locations of a trip were situated in the sea) or non-marine, the latter being composed of both terrestrial and mixed trips, including positions in the fishing harbour.

For each bird and trip, we calculated four further variables: the number and duration of trips (NT and DT, respectively), maximum distance travelled (MD), and the accumulated distances of trips (AD). Regarding rain, we considered four variables: (1) *rain*, the amount of rain fallen in one day (in mm); (2) *rain.qual*, a recodification of *rain* in a binary (0/1) variable: rain/no rain (rain $>$ 2 mm); (3) *rain10*, a recodification of *rain* in a binary variable: in this case we segregated the data into days with rain values $\geqslant$10 mm and days with no rain or rain values $<$10 mm.; (4) *rain.semi*, a recodification of *rain* in a semi-quantitative variable with three fixed factors: days with rain values $\geqslant$10 mm, days with rain values from 2 to 10 mm, and days with rain values with $<$2 mm. Precipitation values $<$2 mm were considered to be too low to be taken into account (since they may be due to the condensation of mist within the beaker), hence, as is often recommended, they were categorised as days of no rain (Schaub et al., 2004). With respect to wind, we considered only one single variable, *wind*, which corresponded to daily mean wind speed.

Following data collection and manipulation we built Generalized Linear Mixed Models (GLMM) of NT, DT, MD and AD, with *rain*, *rain.qual*, *rain10*, *rain.semi*, *wind* and sex as explanatory variables. Individual was included as a random factor and the number of locations as an offset. For models of DT, MD and AD we also included trip type (marine/non-marine) as a fixed factor. Distance variables were log-transformed in order to better adjust to normality and reduce over-dispersion within the models. The GLMMs were run with the 'lmerTest' package (Kuznetsova et al., 2017) for R (R Core Team, 2014). We also looked for any association between rain and wind values using a Pearson correlation test.

Second, we also calculated the size of the home range area used on days of either rain or no rain. To this end, we estimated Utilization Distribution (UD) using 95% fixed Kernel polygons (KDE), separating the positions according to the different values of the qualitative parameters defined for rain (*rain.qual*, *rain10* or *rain.semi*), for which we used the 'adehabitatHR' package (Calenge, 2006) for R with the 'href' reference bandwidth. Once again, GLMMs were conducted with the log-transformed Kernel 95% as an object variable, and with the remaining independent, random factor and offset variables being the same as described earlier.

Finally, we also compared the extent to which the proportion of marine trips varied between rainy or non-rainy days, for which we built binomial models with the type of trip as a response variable (marine/non-marine). The factors sex, wind and rain, the latter codified as explained above, were added as fixed factors/covariates. The number of positions per day was added as an offset variable, and the individual as a random factor.

3. Results

From 1 May to 30 June 2019, rainfall was 278.1 mm. It rained on 27 days (44%), of which 9 had precipitations >10 mm, accounting for 229 mm of accumulated rain (i.e., 82% of the rain that fell over the two months) (Fig. 2). Rainfall on 18 and 19 May and 5 June was especially heavy, with total accumulated daily values on those three days being above 30 mm. For the same 2-month period, mean (±SD) wind speed was 26.2 ± 9.6 km/h, ranging between 13 and 49 km/h. Rain and wind were positively correlated ($r = 0.42$, $p < 0.001$, 95% CI: 0.38–0.47).

Overall, we obtained 1221 valid trips (65 being excluded because they lasted more than a day). Of these, 35% were made on rainy days (>2 mm). Mean (±SD) trip duration was 4.0 ± 3.6 h, with a maximum distance travelled of 12.4 ± 11.2 km. The mean home range area was 515 km^2 (95% CI = 232–1147 km^2).

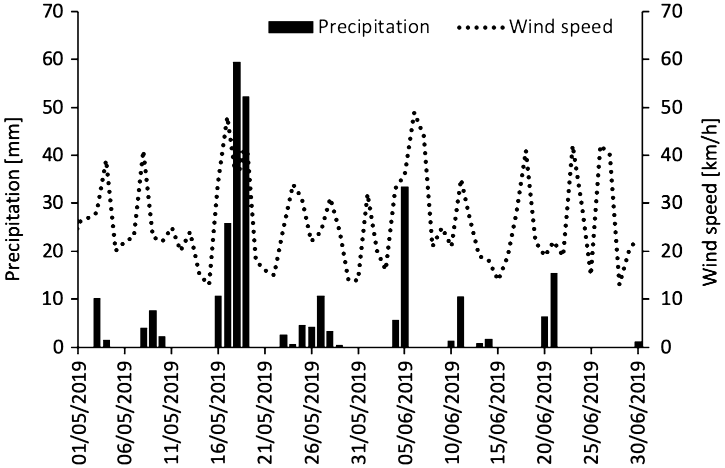

Figure 2. Amount of rainfall and daily mean wind speed in Gipuzkoa (source: Igeldo station, AEMET) from the start of May to the end of June in 2019.

On rainy days, compared to days with no rain, the GPS-tracked gulls tended to have fewer trips, of lower duration, and also involved shorter distances (Table 1). This effect was found even with low rain levels (<10 mm) on certain parameters (Table 1). Maximum distance also tended to be less on days with higher wind speed (Table 1). Sex was not found to have a significant effect on duration, distance or number of trips (Table 1). Regarding wind, gulls tended to move less as wind speed increased. Home ranges were also significantly reduced on rainy days, even under only modest rainfall (Table 1).

The probability of the birds making a marine or a non-marine trip was not affected by rain, but was impacted by the parameter wind (Table 1). On days with higher wind speed, gulls tended to travel out to sea less, and thus exhibiting more terrestrial behaviour. We also detected that males tended to make proportionally more marine trips than females.

4. Discussion

This is one of the first studies dealing with the effect of meteorological parameters on the spatial use of breeding gulls, and also one of the few dealing with this issue in birds in general (Sergio et al., 2003; Chard et al., 2017). The findings will contribute to a better understanding of the foraging be-

Table 1.
The *beta*-parameter estimates (±SE and the associated p-value) and the adjusted R^2 (in parentheses) of models conducted to determine the effect of rain and wind on foraging performance of adult yellow-legged gulls during the incubation and chick-rearing period in the south-eastern part of the Bay of Biscay.

	NT		DT		MD		AD		log(K95)		MT	
	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p
Rain	($R^2 = 0.275$)		($R^2 = 0.278$)		($R^2 = 0.282$)		($R^2 = 0.282$)				($R^2 = 0.186$)	
Rain	−0.04 ± 0.02	0.093	−0.04 ± 0.01	0.006	−0.04 ± 0.01	0.004	−0.04 ± 0.01	0.003			−0.01 ± 0.01	0.132
Wind	−0.04 ± 0.03	0.216	−0.05 ± 0.02	0.009	−0.05 ± 0.02	0.009	−0.05 ± 0.02	0.009			−0.03 ± 0.01	< 0.001
Sex(M)	1.01 ± 2.07	0.632	0.53 ± 1.77	0.769	0.69 ± 1.77	0.704	0.66 ± 1.77	0.715			0.67 ± 0.39	0.082
Trip(Mar)			0.12 ± 0.58	0.840	0.09 ± 0.57	0.874	0.05 ± 0.57	0.931				
Sex(M)×Trip(Mar)			−0.52 ± 0.80	0.518	−0.53 ± 0.80	0.506	−0.52 ± 0.80	0.518				
Rain.qual	($R^2 = 0.282$)		($R^2 = 0.282$)		($R^2 = 0.284$)		($R^2 = 0.285$)		($R^2 = 0.306$)		($R^2 = 0.182$)	
Rain	−1.75 ± 0.62	0.005	−1.73 ± 0.37	< 0.001	−1.69 ± 0.37	< 0.001	−1.70 ± 0.37	< 0.001	−2.18 ± 0.63	0.001	0.03 ± 0.16	0.839
Wind	−0.03 ± 0.03	0.288	−0.04 ± 0.02	0.015	−0.04 ± 0.02	0.012	−0.05 ± 0.02	0.011	−0.03 ± 0.03	0.290	−0.04 ± 0.01	< 0.001
Sex(M)	1.03 ± 2.07	0.626	0.60 ± 1.75	0.739	0.75 ± 1.75	0.676	0.72 ± 1.75	0.686	0.81 ± 2.24	0.722	0.67 ± 0.39	0.084
Trip(Mar)			0.14 ± 0.58	0.806	0.12 ± 0.57	0.837	0.08 ± 0.57	0.894				
Sex(M)×Trip(Mar)			−0.47 ± 0.80	0.553	−0.48 ± 0.79	0.544	−0.47 ± 0.79	0.557				
Rain10	($R^2 = 0.275$)		($R^2 = 0.273$)		($R^2 = 0.276$)		($R^2 = 0.277$)		($R^2 = 0.296$)		($R^2 = 0.183$)	
Rain	−1.37 ± 0.78	0.080	−1.00 ± 0.47	0.035	−1.09 ± 0.47	0.021	−1.09 ± 0.47	0.021	−1.73 ± 0.80	0.032	−0.21 ± 0.21	0.327
Wind	−0.04 ± 0.03	0.198	−0.06 ± 0.02	0.002	−0.06 ± 0.02	0.002	−0.06 ± 0.02	0.002	−0.04 ± 0.03	0.172	−0.03 ± 0.01	< 0.001
Sex(M)	1.01 ± 2.07	0.633	0.51 ± 1.76	0.775	0.66 ± 1.75	0.710	0.64 ± 1.75	0.721	0.76 ± 2.23	0.740	0.67 ± 0.39	0.082
Trip(Mar)			0.10 ± 0.58	0.860	0.07 ± 0.57	0.897	0.03 ± 0.57	0.954				
Sex(M)×Trip(Mar)			−0.44 ± 0.81	0.581	−0.45 ± 0.80	0.573	−0.43 ± 0.80	0.586				

Table 1.
(Continued.)

	NT		DT		MD		AD		log(K95)		MT	
	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p	$\beta \pm$ SE	p
Rain.semi	($R^2 = 0.282$)		($R^2 = 0.282$)		($R^2 = 0.284$)		($R^2 = 0.285$)		($R^2 = 0.306$)		($R^2 = 0.184$)	
Rain(2–10)	−1.74 ± 0.78	0.026	−1.92 ± 0.46	< 0.001	−1.80 ± 0.45	< 0.001	−1.81 ± 0.45	< 0.001	−2.18 ± 0.80	0.007	0.16 ± 0.19	0.381
Rain(>10)	−1.76 ± 0.80	0.028	−1.51 ± 0.49	0.002	−1.56 ± 0.48	0.001	−1.57 ± 0.48	0.001	−2.21 ± 0.82	0.007	−0.16 ± 0.22	0.470
Wind	−0.03 ± 0.03	0.303	−0.05 ± 0.02	0.011	−0.05 ± 0.02	0.011	−0.05 ± 0.02	0.011	−0.03 ± 0.03	0.287	−0.03 ± 0.01	< 0.001
Sex(M)	1.03 ± 2.07	0.626	0.60 ± 1.75	0.735	0.75 ± 1.74	0.674	0.72 ± 1.75	0.684	0.78 ± 2.24	0.731	0.66 ± 0.39	0.085
Trip(Mar)			0.16 ± 0.58	0.784	0.13 ± 0.57	0.824	0.09 ± 0.57	0.880				
Sex(M)×Trip(Mar)			−0.49 ± 0.80	0.543	−0.49 ± 0.79	0.538	−0.47 ± 0.79	0.551				

Abbreviations: NT: Number of trips per day; DT: duration (minutes) of trips; MD: maximum distance (km) travelled in one day; AD: accumulated distance (km) of trips in one day; K95: Kernel 95% area; MT: Marine trip (Yes/No).

Reference values (*beta* = 0): *Rain.qual*: no rain (rain = 0); *Rain10*: rain < 10 mm; *Rain.semi*: no rain (rain < 2 mm); *Sex*: Female; *Trip*: non-marine.

haviour of breeding seabirds and help to predict potential effects, especially in response to climate change.

Rainfall and wind influenced the spatial use of our breeding gull population, promoting a reduction in both the duration and the distance of foraging trips, as well as fewer trips and the adaptation of smaller home range areas under rainy conditions. All these findings would indicate that in rainy and windy conditions gulls have to invest more time in tending their nests to protect eggs or chicks. In a study of gannets, these birds were found to make longer trips under moderately rainy conditions (Pistorius et al., 2015), while, in contrast, we found that rain prevented breeding yellow-legged gulls from moving to more distant areas. Rain and wind, therefore, seem to be limiting factors in terms of the capacity of breeding gulls to exploit all the feeding resources potentially at their disposal if there were no rain or wind. Additionally, gulls made proportionally less marine trips on very windy days, suggesting that wind might limit the use of the marine habitat. Rainfall and wind were positively correlated, since very rainy days within the region are commonly associated with cyclonic conditions linked to strong north-westerly winds (Puillat et al., 2006). An increase in the number and strength of these north-westerly storms within the region might, therefore, have an impact on the use of one of the foraging habitats available to the species. Models predict, respectively, an increase and a decrease in precipitation for the northern and southern Atlantic regions in Europe (Meaurio et al., 2017). The Bay of Biscay, however, is situated in a transition zone between the two regions, thus climate predictions for the area are far more uncertain (Meaurio et al., 2017). Nonetheless, if heavier rains become more common, we might expect a decrease in the home range area used in spring, something that should be investigated in relation to the potential reproductive costs that could be experienced by this species. Flexibility in foraging patterns in order to cope with adverse weather could be crucial in better adapting to the consequences of climate change (Gilmour et al., 2018).

The fewer marine trips made on windy days could be attributed to the greater difficulty of searching for food in the sea or to the differential availability of prey depending on the meteorological conditions (Sergio, 2003). With respect to the distances travelled, the reason for the shorter distances on rainy or windy days remains unknown for the time being. In principle, rainfall would not have great influence on the flight performance of large birds (Gaston, 2004). We cannot assess whether our results, which show a change in spatial use under rainy or windy conditions, are due to the impact of rain or wind on flight performance, or on other aspects which may also have an effect on spatial use, such as prey avalilability, prey catchability or nest attendance.

The effect of meteorological parameters on foraging activity would allow us to infer the potential effects of weather on the food provisioning of chicks. Potentially, either the quantity or the type of prey provided to chicks could differ between days with rain/wind or those with no rain/wind, or between springs that are rainy (or windy) or drier. In particular, our results indicate the reduced consumption of prey of marine origin under worse meteorological conditions. Fish prey have been reported to offer a higher energy reward than other types of prey such as waste in landfills (Annett & Pierotti, 1999). Rain and wind, therefore, may shape the diet during the breeding season and could, potentially, have an impact on the physical condition of chicks, which may result in, hitherto unstudied, consequences on their fitness and survival. From a methodological standpoint, this potential weather-related effect on the diet might suggest that when carrying out trophic ecology studies, more than one single sampling year should be considered in order to reduce possible year-associated bias.

In conclusion, rainfall and wind affect the foraging behaviour of breeding yellow-legged gulls by reducing their spatial use. Under a scenario of climate change, with, presumably, increased precipitation in spring in the Bay of Biscay, the population can be expected to exploit a smaller home range area, although the potential cost of this behaviour (in terms of reproduction) remains still unknown.

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Appendix

Table A1.
Information on different individuals tagged with a GPS: Individual, Colony, Sex, Date when GPS device was attached (Attach date), Last data, Number of locations, Number of trips, % of Marine trips, % of Terrestrial trips and % of Mixed trips.

Individual (colour ring)	Colony	Sex	Attach date	Last date with data	No. of locations	No. tracks	Marine	Terrestrial	Mixed
1900501	Ulia	F	09/05/2019	30/06/2019	952	43	13.95%	34.88%	51.16%
1900502	Getaria	F	23/05/2019	30/06/2019	1597	48	29.17%	39.58%	31.25%
1900503	Ulia	M	09/05/2019	30/06/2019	1748	66	22.73%	54.55%	22.73%
1900504	Ulia	M	13/05/2019	30/06/2019	2287	78	28.21%	42.31%	29.49%
1900505	Ulia	M	14/05/2019	30/06/2019	1624	87	20.69%	62.07%	17.24%
1900506	Ulia	F	13/05/2019	31/05/2019	849	49	20.41%	69.39%	10.20%
1900507	Ulia	F	13/05/2019	30/06/2019	2244	71	2.82%	59.15%	38.03%
1900508	Ulia	F	14/05/2019	30/06/2019	2259	77	24.68%	51.95%	23.38%
1900509	Ulia	M	15/05/2019	30/06/2019	2147	105	15.24%	71.43%	13.33%
1900510	Ulia	F	14/05/2019	30/06/2019	2262	65	12.31%	72.31%	15.38%
1900511	Getaria	F	15/05/2019	30/06/2019	2150	79	11.39%	46.84%	41.77%
1900512	Getaria	M	16/05/2019	30/06/2019	2043	105	57.14%	25.71%	17.14%
1900513	Getaria	M	15/05/2019	30/06/2019	2178	120	47.50%	26.67%	25.83%
1900514	Getaria	F	15/05/2019	30/06/2019	2152	102	46.08%	40.20%	13.73%
1900515	Getaria	F	21/05/2019	30/06/2019	1798	103	15.53%	64.08%	20.39%
PG1900501	Getaria	M	22/05/2019	30/05/2019	371	18	33.33%	38.89%	27.78%
PG1900502	Getaria	F	22/05/2019	30/06/2019	1874	70	24.29%	35.71%	40.00%