Science of the Total Environment 1003 (2025) 180672

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Experimental anthropogenic food restrictions drive short-term foraging and immuno-haematological changes in sympatric breeding gulls

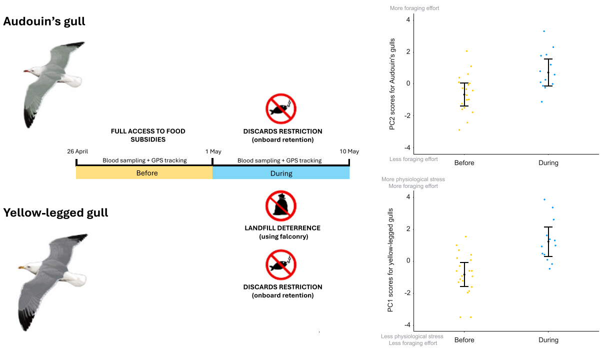
Jorge M. Pereira [a,*], Jaime A. Ramos [a], Adriana Domingues [a], Ana Almeida [b], Ana Marçalo [c], Catarina Cascão [a], Carlos Silva [b], Daniel Rey [d], Filipe R. Ceia [a], Flávia Carvalho [b,c], Ivo dos Santos [a,e], Jorge M.S. Gonçalves [c], Lara R. Cerveira [a], Magda Frade [c], Maria I. Laranjeiro [a,f,g], Nuno Oliveira [b], Tânia Nascimento [b], Vítor H. Paiva [h,1], Ana C. Norte [a,1]

[a] *University of Coimbra, MARE - Marine and Environmental Sciences Centre / ARNET - Aquatic Research Network, Department of Life Sciences, Calçada Martim de Freitas, 3000-456, Coimbra, Portugal*
[b] *Sociedade Portuguesa para o Estudo das Aves (SPEA), Av. Almirante Gago Coutinho, 46 A, 1700-031, Lisboa, Portugal*
[c] *Centre of Marine Sciences, CCMAR, University of the Algarve, Campus de Gambelas, FCT Ed7, 8005-139, Faro, Portugal*
[d] *SEO/BirdLife – Marine Programme, 08026, Barcelona, Spain*
[e] *Littoral Environnement et Sociétés (LIENSs), UMR 7266, CNRS-La Rochelle Université, 2 rue Olympe de Gouges, 17000, La Rochelle, France*
[f] *MARE – Marine and Environmental Sciences Centre & ARNET – Aquatic Research Network, ESTM, Politécnico de Leiria, 2520-641, Peniche, Portugal*
[g] *Institut de Ciències del Mar (ICM), CSIC, Passeig Marítim de la Barceloneta 37-49, Barcelona, 08003, Spain*
[h] *University of Coimbra, CFE - Centre for Functional Ecology - Science for People & the Planet, Associate Laboratory TERRA, Department of Life Sciences, Calçada Martim de Freitas, 3000-456, Coimbra, Portugal*

HIGHLIGHTS

- Combined GPS and blood analysis showed gull responses to food access restrictions.
- Gulls increased foraging effort when food access was restricted.
- Yellow-legged gulls showed stress-linked shifts in leucocyte profiles.
- Audouin's gulls showed milder physiological stress responses.
- Reliance on PAFS may constitute ecological traps for breeding seabirds.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Audouin's gull
Foraging effort
Physiological condition

ABSTRACT

Fishery discards and landfills provide major subsidies to scavenging seabirds, shaping their foraging behaviour and population dynamics. However, few studies have compared the behaviour and health of individuals with and without access to such predictable anthropogenic food subsidies (PAFS). We assessed the foraging behaviour and immuno-haematological condition of incubating Audouin's (*Ichthyaetus audouinii*) and yellow-legged gulls (*Larus michahellis*) in response to an experimental restriction of access to fisheries and landfill food subsidies in southern

---

[*] Corresponding author.
E-mail address: jorge.pereira@uc.pt (J.M. Pereira).
[1] Senior authorship with equal contribution.

https://doi.org/10.1016/j.scitotenv.2025.180672
Received 30 May 2025; Received in revised form 1 October 2025; Accepted 1 October 2025
Available online 9 October 2025

Predictable anthropogenic food subsidies
Yellow-legged gull

Portugal. In response to food restrictions, gulls from both species increased their foraging distance from the colony, likely relying on alternative prey, and/or foraging in association with other fishing fleets in Portuguese or nearby Spanish waters. This was supported by a decrease in the number of yellow-legged gulls observed at both the landfill and the Culatra fishing harbour during the food restriction trials. These changes were followed by alterations in the leucocyte profiles of yellow-legged gulls, characterised by a predominance of heterophils over lymphocytes, i.e. an indicator of physiological stress. Our findings show that limited access to PAFS can influence gulls' foraging behaviour and physiological condition, highlighting their reliance/dependence on these predictable subsidies. These short-term responses suggest that PAFS may function as ecological traps for opportunistic seabirds during the breeding period. Understanding such responses is critical to predict long-term ecological consequences and to develop waste and fisheries management policies aligned with EU strategies.

1. Introduction

Human activities have negatively impacted global biodiversity (Newbold et al., 2015; O'Hara et al., 2021), but can also create ecological opportunities by providing predictable anthropogenic food subsidies (PAFS) (Oro et al., 2013). Anthropogenic food subsidies, such as landfills and fishery discards, are increasingly used by wildlife, contributing to the growth of specific wildlife populations (Bicknell et al., 2013; Plaza and Lambertucci, 2017). For instance, urban red foxes (*Vulpes vulpes*), urban coyotes (*Canis latrans*) or urban yellow-legged gulls (*Larus michahellis*) consume predominantly human-related food compared to their rural or natural counterparts (Contesse et al., 2004; Murray et al., 2015; Pais De Faria et al., 2021).

Fishery discards significantly influence seabird diet by providing new prey items such as bathypelagic and demersal species, which would otherwise not be available to surface-feeders (Alonso et al., 2015; Mariano-Jelicich et al., 2014). This suggests a strong association between gulls' foraging distribution and fishery activities, a global pattern observed in many gull populations and species (Arcos and Oro, 2002; Calado et al., 2021; Marinao et al., 2018). Dietary analyses indicate that the most consumed fish species by yellow-legged gulls across four breeding colonies in the western Iberian Peninsula are similar to the most landed fish species by local fisheries (Calado et al., 2021).

The predictable and consistent availability of anthropogenic food from landfills and fishery discards can contribute to reduce starvation risk (Bartumeus et al., 2010; Oro et al., 2013). Moreover, the reduced foraging effort may lower energy expenditure (Fuirst et al., 2018), allowing animals to allocate more energy towards other energetically demanding processes like growth and reproduction. Although, foraging on anthropogenic food subsidies may also have negative effects, as these are often poor in certain nutrients (Grémillet et al., 2008), and may contain higher levels of contaminant loads (Sorais et al., 2020) and pathogens (Martín-Vélez et al., 2025), potentially jeopardising the health condition of consumers. However, there are virtually no population-level studies simultaneously comparing the foraging behaviour and health of animals with and without easy access to anthropogenic food subsidies.

In this context, understanding the foraging behaviour and immuno-haematological consequences of restricted access to anthropogenic food subsidies is particularly relevant for Audouin's (*Ichthyaetus audouinii*) and the yellow-legged gulls, which breed in sympatry at Ria Formosa, southern Portugal. Previous studies have shown that Audouin's gulls breeding in Ria Formosa forage exclusively at-sea, relying mainly on small pelagic and demersal fish species obtained from fishery discards (Calado et al., 2021; Matos et al., 2018). According to individual tracking information, Audouin's gulls from Ria Formosa are not known to forage on land, unlike some other Mediterranean populations which regularly use terrestrial habitats such as rice fields or other agricultural areas (Bécares et al., 2015). Despite the strong population increase over the past decade in the Ria Formosa region (SPEA, unpublished data), Audouin's gull remains listed as Vulnerable by the IUCN. In contrast, yellow-legged gulls breeding in Ria Formosa forage mainly in association with local fisheries (Pereira et al., 2025), but they also make regular use of fishing harbours and terrestrial landfills (Matos et al., 2018; Mendes et al., 2018). This behavioural flexibility has contributed to the strong population increase across Europe, including in mainland Portugal (Oliveira et al., 2023), with the species being currently classified as Least Concern by the IUCN. As part of the LIFE Ilhas Barreira project https://www.lifeilhasbarreira.pt/en/, in 2023, falconry was used for one month in May to prevent gulls from accessing the largest landfill in the region during the breeding period. Contemporaneously, both species experienced a restriction in fishery discards availability during this period, as the local fishing fleet from the main harbours in the gulls' colony surroundings (Olhão and Culatra) was provided with containers and encouraged, through awareness campaigns, to retain offal and discards, releasing them exclusively while navigating to the ports, i.e. a period of low gull attendance to fishing vessels (Frade et al., 2025). As a result, yellow-legged gulls were prevented from accessing two important food resources (landfills and fishery discards), whereas Audouin's gulls were only prevented from accessing fishery discards.

In response to restricted access to anthropogenic food subsidies from both landfills and fisheries, we hypothesise that breeding Audouin's and yellow-legged gulls will increase their foraging effort and face greater physiological stress. Based on this hypothesis, we predict that gulls of both species will travel longer distances and expand their foraging ranges (Langley et al., 2021; Matos et al., 2018). We also predict that immuno-haematological parameters of both gull species will be negatively affected, with a stronger effect on yellow-legged gulls (Oro et al., 2013). This study is particularly relevant for informing waste management strategies, as many European countries are progressively closing landfill sites in compliance with the EU Directive 2018/850. This restriction in access to waste is expected to significantly decrease food sources for landfill-foraging species, such as yellow-legged gulls, potentially leading to ecological consequences that remain poorly understood (Oro et al., 2013). Moreover, this study is still relevant to the reform of the Common Fisheries Policy of the European Union, which includes the discard ban policy that leads to an obligation to land the unwanted part of the catch (EU 1380/2013, Article 15). Although aimed at improving the sustainability of the fishing industry, this policy may also negatively affect vulnerable species such as Audouin's gulls, highlighting the importance of assessing how changes in anthropogenic food subsidies influence wildlife body condition and health from a conservation perspective (Bicknell et al., 2013).

2. Materials and methods

2.1. Experimental design and monitoring

Experimental food restriction trials were conducted from 1 to 31 May 2023, during the breeding period of Audouin's and yellow-legged gulls, at the Sotavento (also known as the leeward region or eastern Algarve) landfill and at the fishing harbours of Olhão and Culatra (Fig. 1). The Sotavento landfill is the largest in the region, with an annual solid waste capacity of approximately 130,000 t (https://www.algar.com.pt/pt/algar/historia/). The fishing harbour of Culatra holds a small artisanal fishing fleet, whereas Olhão, located just 4 km away, is one of the most important harbours in the region. In 2023, the fishing harbour of Olhão accounted for approximately 58 % (3865 t) of the fish landed by polyvalent fisheries in the Algarve region (Instituto Nacional de Estatística, 2023).

At the Sotavento landfill, falconry was used to deter gulls and limit their feeding. Falcons were deployed daily from 6:30 a.m. to 2:30 p.m., matching the peak gull activity period identified in previous years through systematic observations at the landfill (SPEA, unpublished data). At the fishing harbours of Olhão and Culatra, awareness campaigns encouraged fishermen to avoid feeding gulls after fishing, particularly while cleaning and mending their nets. Moreover, informational panels were installed, and fishermen were provided with secure 25 L containers. They were encouraged to retain offal, and fishery discards in the containers during fishing and release them in controlled batches while returning to the fishing harbour. A recent study found that this practice significantly reduced interactions with scavenging seabirds (i.e. gulls and gannets) during fishing operations in the artisanal bottom-set net fleet in our study area (Frade et al., 2025).

To monitor gulls at the landfill and fishing harbours, bird counts were conducted on two days in April (one weekday and one weekend day) before the experimental food restriction trials, and followed the same schedule twice per week in May during the trials. At the landfill, observations were made from vantage points, with one count per hour and a minimum of eight counts per day exclusively between 6:30 a.m. and 2:30 p.m. This matched falconry activity in May (during the trials) and no observations were made outside this time-window. At the fishing harbours, counts were carried out along a transect covering the entire harbour area, with a minimum of three daily counts spaced at one-hour intervals. Data were used for statistical analysis as the sum of gulls observed per hour. While the observed gulls likely included individuals from more than one colony, most are expected to originate from Deserta Island, which holds the largest breeding population of Audouin's gulls in the Ria Formosa, with 3821 breeding pairs, and 612 breeding pairs of yellow-legged gulls in 2025 (SPEA, unpublished data). A smaller colony is located on Culatra Island, approximately 8 km northeast of Deserta Island, with 1300 breeding pairs of Audouin's gulls and 250 breeding pairs of yellow-legged gulls also in 2025 (SPEA, unpublished data).

2.2. Fieldwork and data collection

The foraging and physiological responses of incubating Audouin's and yellow-legged gulls to experimental food restriction trials were studied at Deserta Island (36°57′40″N, 7°53′20″W). Deserta Island (Fig. 1) is a sandy island located in the Ria Formosa Natural Park, in the Algarve region of southern Portugal. It lies approximately 35 km from the Sotavento landfill, 9 km from the Olhão fishing harbour, and 6 km from the fishing harbour of Culatra. Before the experimental food restriction trials, on April 26–27, we captured incubating gulls with full clutches using nest traps. All captured individuals were breeding adults of unknown age. Each bird was ringed, weighed (to the nearest 5 g) with a Pesola® spring balance, and equipped with a GPS device. We collected approximately 150 μL of blood from the tarsal vein using two heparinised capillary tubes and immediately stored the samples in a cool box. Whole blood was used for sex identification and total haemoglobin quantification. Additionally, blood smears were prepared from fresh samples and fixed in absolute methanol after air-drying. We recaptured the gulls to retrieve GPS loggers and collect additional blood samples and smears from 7 to 13 days (mean ± SD: 9.7 ± 1.5 days) after the start of the experimental food restriction trials (from May 5 to 10).

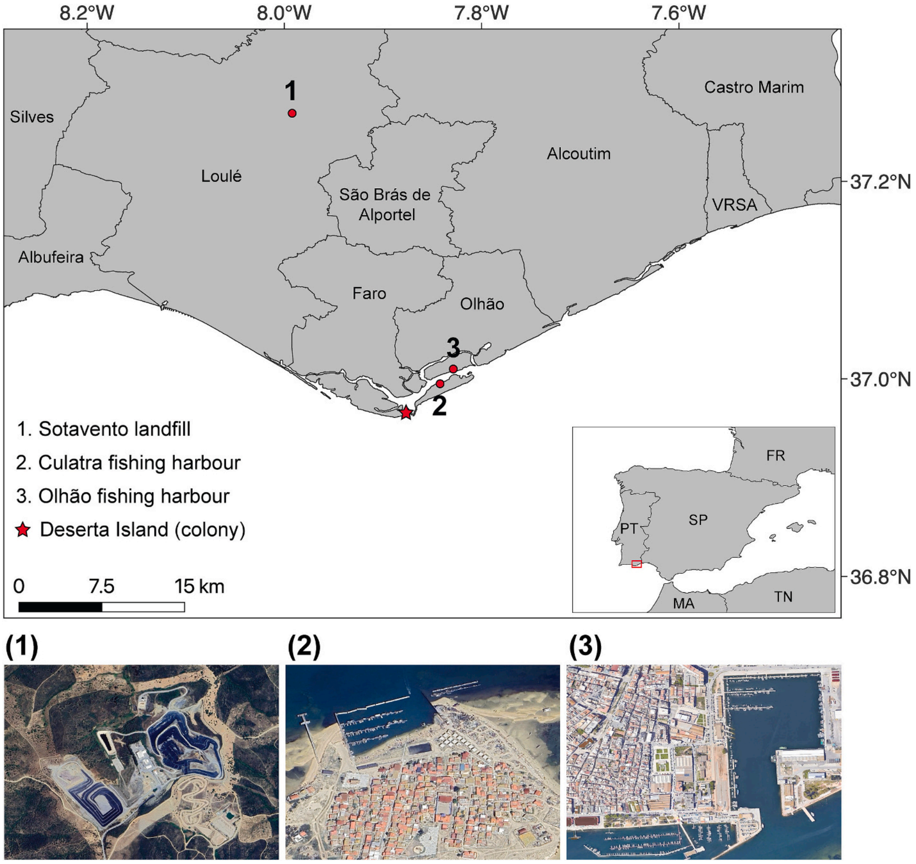


Fig. 1. Map of the study area showing the locations of the food restriction trials: (1) Sotavento landfill, (2) Culatra fishing harbour, and (3) Olhão fishing harbour. A red star marks the breeding colony at Deserta Island, where Audouin's and yellow-legged gulls were GPS-tracked and sampled for physiological parameters during incubation.

2.3. GPS-tagging and analysis

GPS loggers (CatLog2, Perthold Engineering) were also attached to Audouin's and yellow-legged gulls during incubation (April 26–27). GPS devices were attached to the gulls' four central tail feathers using TESA® tape, programmed to record positions every 5 min, and retrieved approximately 10 days after deployment. These devices weighed approximately 15 g for Audouin's gulls (2.9 % of the body mass of the lightest tagged bird), and 17 g for yellow-legged gulls (2.5 % of the body mass of the lightest tagged bird). We found no significant differences in the number of days tracked between Audouin's and yellow-legged gulls (9.8 ± 1.9 days vs. 9.5 ± 1.1 days, respectively; $t_{24} = 0.387$, $p = 0.70$). Similarly, there was no significant change in body mass between capture and recapture in tagged Audouin's gulls (644.8 ± 54.7 g vs. 614.2 ± 77.9 g, respectively; $t_{30} = 1.31$, $p = 0.20$) and yellow-legged gulls (1024.0 ± 166.2 g vs. 1046.2 ± 163.1 g, respectively; $t_{31} = 0.38$, $p = 0.71$).

Tracking data were first filtered to remove positions within a 200 m radius of the nest to reduce the influence of the colony. Next, we identified individual foraging trips and calculated the maximum distance from the colony (linear distance between the furthest location of the trip and the breeding colony, in km). To characterise birds' foraging behaviour during each trip, we used the '*Expectation-Maximisation binary Clustering*' algorithm from package '*EmbC*' (Garriga et al., 2016) to classify each GPS position in either (1) travelling (high velocity, low tortuosity), (2) extensive search (high velocity, high tortuosity), (3) intensive search (low velocity, high tortuosity) or (4) resting (low velocity, low tortuosity). Intensive and extensive search behaviours were grouped as foraging positions, and the percentage of time individuals spent foraging was then calculated.

Kernel density estimates were generated for the foraging positions only (i.e. intensive and extensive search) using the '*adehabitatHR*' R package (Calenge, 2006). We further calculated the area (in km^2) of 50 % kernel Utilization Distributions (UDs) in the foraging trips of each individual, before (26–30 April) and during (1–10 May) the experimental food restriction trials. The most appropriate smoothing parameter (h) was calculated using the R package '*track2KBA*' (Beal et al., 2021), as the average value of area-restricted search (ARS) behaviour for each species (8 km for Audouin's gulls and 3 km for yellow-legged gulls).

2.4. Immuno-haematological analysis

To examine the blood smears, we initially stained them with Giemsa. Subsequently, each blood smear was observed through a microscope using the 1000× objective lens. Twenty-three distinct fields were selected randomly, ensuring no overlap or gaps in the distribution of red blood cells (RBCs), representing an average of 10,000 RBCs per smear. Data were recorded on the number and type of white blood cells (WBCs), from which the ratio of heterophils:lymphocytes was calculated (H/L, in 100 WBCs), the number and type of abnormalities in RBCs' nucleus and the number of polychromatic RBCs (immature cells). If the WBC count did not reach at least 100 cells at the end of the 23 fields, additional random fields were observed until this threshold was met to ensure a proper calculation of the H/L ratio.

To assess blood haemoglobin concentration (g/dL), we diluted 10 μL of whole blood (ensuring no presence of clots) in 1 mL of Spinreact working reagent, following the instructions of the kit (Spinreact haemoglobin quantification kit, Girona, Spain). Samples were read in duplicate at 540 nm in a total of 200 μL reaction volume per well. Haemoglobin concentration was calculated using the formula (absorbance sample - absorbance blank)/ (absorbance standard - absorbance blank)*15 by comparison with a known standard of 15 g/dL (haemoglobin from bovine blood, Sigma-Aldrich, Saint Louis, USA).

2.5. Statistical analysis

We used Wilcoxon rank-sum tests to evaluate whether the abundance of gulls at the Sotavento landfill and the fishing harbours of Olhão and Culatra varied during the experimental food restriction trials. The tests were conducted separately for each site, with the period of the trials (before vs. during) as a fixed effect and the total abundance of gulls at each site as the response variable in each model. Although gull counts were conducted twice per week throughout May, for the statistical analyses we only included counts from the first two weeks of May to match the period of GPS tracking and blood sampling of the individuals from Deserta Island. Counts from the last two weeks of May, as well as the raw dataset used, are reported in Supplementary Material Tables S1 (Sotavento landfill) and S2 (Olhão and Culatra fishing harbours). Due to difficulties in accurately distinguishing immature lesser black-backed gulls (*Larus fuscus*) and yellow-legged gulls in large mixed flocks, both species were merged into a single group. However, during this period, lesser black-backed gulls are very low in abundance in the region, representing less than 5 % of all identified gulls at the species level.

To explore patterns in foraging behaviour and physiological condition in the experimental food restriction trials, a principal component analysis (PCA) was applied to normalised tracking variables (maximum distance from the colony, proportion of time spent foraging, and area of 50 % kernel UDs) and immuno-haematological parameters (count of WBCs, heterophils, lymphocytes, erythrocyte nuclear abnormalities, immature erythrocytes, and total blood haemoglobin). PCA computation and visualisation were performed using the *'FactoMineR'* R package (Lê et al., 2008). We then used generalised linear models (GLMs) to test whether the experimental food restriction trials influenced gulls' foraging behaviour and physiological condition. Separate models were fitted for each species, using the scores of the first two principal components (PC1 and PC2) as response variables in each model. In each model, we included the period in the experimental food restriction trials (before vs. during) and sex (females vs. males) as fixed effects. We chose PCA to reduce the potentially correlated foraging and physiological variables, rather than conducting univariate tests for each variable, to minimise the risk of Type I and Type II errors associated with multiple testing. Lastly, we checked the models for normality and homogeneity by visual inspection of residual plots using the *'performance'* R package (Lüdecke et al., 2021).

All statistical analyses were carried out in R v. 4.1 (R Core Team, 2024). All data are presented as mean ± SD (standard deviation) unless otherwise stated. Differences were considered statistically significant at $p < 0.05$.

3. Results

3.1. Abundance of gulls at the landfill and fishing harbours

The average number of yellow-legged gulls at the Sotavento landfill decreased by 80.6 % during the first two weeks of the experimental food restriction trials (152.0 ± 131.5 birds/day before vs. 29.5 ± 46.3 birds/day during this period; $W = 93.5$, $p = 0.006$), with most counts recording fewer than 50 gulls (Supplementary Material Table S1). At the fishing harbours, the average number of yellow-legged gulls remained unchanged at the Olhão harbour (93.5 ± 35.9 birds/day before vs. 114.5 ± 81.9 birds/day during the first two weeks of trials; $W = 33$, $p = 0.62$, respectively; Supplementary Material Table S2). At Culatra fishing harbour, the average number of yellow-legged gulls decreased by 25.6 % during the first two weeks of the experimental food restriction trials (211.6 ± 33.9 birds/day before vs. 157.5 ± 34.5 birds/day during this period; $W = 50.5$, $p = 0.04$), although the number of gulls remained relatively high during the entire month of May (Supplementary Material Table S2). Audouin's gulls were rarely observed at the landfill or at the fishing harbours, either before or during the experimental food restriction trials (Supplementary Material Tables S1 and S2).

3.2. Changes in foraging behaviour and physiological condition

A total of 19 incubating Audouin's gulls (9 females, 10 males) and 20 yellow-legged gulls (9 females, 11 males) were GPS-tracked and sampled for physiological parameters both before and during the experimental food restriction trials. Sample sizes and summary statistics for tracking variables and immuno-haematological parameters are provided in Table 1.

For Audouin's gulls, PC1 and PC2 explained 46.1 % of the total variance in the PCA (Table 2). PC1 scores ranged from −2.91 to 3.05, with higher values indicating a greater number of heterophils and lower values corresponding to higher number of lymphocytes (Table 2 and Fig. 2). PC2 scores ranged from −2.87 to 3.30, with higher values indicating a larger 50 % kernel UD area and greater maximum distance from the colony, while lower values reflected more time spent foraging (Table 2 and Fig. 2). Audouin's gulls increased foraging effort during the food restriction trials (PC2 scores: $F_{2,29} = 9.76$; $\beta \pm$ SE: 1.38 ± 0.44, $t = 3.12$, $p = 0.004$; Figs. 3 and 4a). Their physiological condition showed no significant change, though the result was marginal (PC1 scores: $F_{2,29} = 4.10$; $\beta \pm$ SE: 1.04 ± 0.51, $t = 2.02$, $p = 0.05$). We found no evidence for sex-differences in PC1 ($F_{2,29} = 1.56$; $\beta \pm$ SE: -0.69 ± 0.50, $t = 1.38$, $p = 0.18$) and PC2 ($F_{2,29} = 0.46$; $\beta \pm$ SE: 0.21 ± 0.43, $t = 0.48 \pm 0.51$, $p = 0.64$).

For yellow-legged gulls, PC1 and PC2 explained 51.4 % of the total variance in the PCA (Table 2). PC1 scores ranged from −3.45 to 3.85, with higher values indicating greater maximum distance from the colony and a higher number of heterophils, while lower values were associated with higher number of lymphocytes (Table 2 and Fig. 2). PC2 scores ranged from −2.69 to 3.34, with lower values reflecting more time spent foraging and higher values indicating a larger 50 % kernel UD area (Table 2 and Fig. 2). Yellow-legged gulls increased foraging effort and showed a decline in physiological condition during the food restriction trials (PC1 scores: $F_{2,30} = 18.51$; $\beta \pm$ SE: 2.06 ± 0.48, $t = 4.30$, $p < 0.001$; Figs. 3 and 4b). There were no changes in PC2 before and during the experimental food restriction trials (PC2 scores: $F_{2,30} = 1.94$; $\beta \pm$ SE: -0.69 ± 0.49, $t = 1.39$, $p = 0.17$). Moreover, we found no evidence for sex-differences in PC1 ($F_{2,30} = 0.24$; $\beta \pm$ SE: 0.06 ± 0.47, $t = 0.12$, $p = 0.91$) or PC2 ($F_{2,30} = 0.67$; $\beta \pm$ SE: 0.45 ± 0.48, $t = 0.94$, $p = 0.36$).

4. Discussion

In this study, we evaluated the consequences of experimental food restriction trials on the foraging behaviour and physiology of two sympatric gull species during incubation. When access to the landfill site, a frequent foraging site for yellow-legged gulls in southern Portugal (Matos et al., 2018; Mendes et al., 2018), and to fishery discards from local fishing boats were restricted simultaneously, breeders of both gull species increased their foraging distance from the colony. This behavioural shift was further supported by a sharp decline in the number of yellow-legged gulls observed both at the Sotavento landfill and at the Culatra fishing harbour during the food restriction trials. In contrast, Audouin's gulls at Ria Formosa are known to rely heavily on at-sea discards from local fisheries during the breeding period (Calado et al., 2021). Their response to the experimental restriction in food availability

Table 2

Variable loadings from principal component analysis (PCA) of normalised tracking variables, i.e. maximum distance from the colony (MDC), proportion of time spent foraging (TSF) and area of 50 % kernel UDs (UD50); and immuno-haematological parameters, i.e. counts of white blood cells (WBC), heterophils (HET), lymphocytes (LYM), erythrocyte nuclear abnormalities (ENA), immature erythrocytes (IE), and haemoglobin (HB) collected from incubating Audouin's and yellow-legged gulls before (26–30 April) and during (1–10 May) the experimental food restriction trials. Variables are listed in ascending order based on the variable loadings of PC1 per gull species.

Variables	Audouin's gull	
	PC1	PC2
Lymphocytes (LYM)	−0.64	0.06
White blood cells (WBC)	−0.39	−0.09
Area of 50 % kernel UDs (UD50)	−0.03	0.67
Haemoglobin (HB)	0.00	0.13
Immature erythrocytes (IE)	0.03	−0.12
Proportion of time spent foraging (TSF)	0.06	−0.44
Maximum distance from colony (MDC)	0.10	0.47
Erythrocyte nuclear abnormalities (ENA)	0.10	0.31
Heterophils (HET)	0.64	−0.05
Proportion of variance explained	25.1	21.0

Variables	Yellow-legged gull	
	PC1	PC2
Lymphocytes (LYM)	−0.44	0.39
Erythrocyte nuclear abnormalities (ENA)	−0.32	0.27
Immature erythrocytes (IE)	−0.17	−0.07
Haemoglobin (HB)	−0.15	−0.33
Proportion of time spent foraging (STF)	−0.11	−0.51
White blood cells (WBC)	−0.11	0.21
Area of 50 % kernel UDs (UD50)	0.41	0.43
Heterophils (HET)	0.46	−0.32
Maximum distance from colony (MDC)	0.51	0.26
Proportion of variance explained	29.8	21.6

Table 1

Comparison between tracking variables (i.e. foraging behaviour) and immuno-haematological parameters (i.e. physiological condition) of incubating Audouin's and yellow-legged gulls before (26–30 April) and during (1–10 May) the experimental food restriction trials. Values are mean ± SD. Sample size refers to the total number of individuals sampled.

	Audouin's gull		Yellow-legged gull	
	Before ($N = 19$)	During ($N = 13$)	Before ($N = 20$)	During (N = 13)
Tracking variables				
Maximum distance from colony (km)	77.6 ± 30.4	95.4 ± 36.1	18.9 ± 14.0	32.7 ± 17.8
Proportion of time spent foraging (%)	45.2 ± 12.4	40.5 ± 4.4	54.9 ± 13.8	50.5 ± 14.4
Area of 50 % kernel UDs (km^2)	870.9 ± 406.5	1293.6 ± 563.8	387.2 ± 134.4	449.7 ± 178.2
Immuno-haematological parameters				
White blood cells (counts)	66.2 ± 27.1	60.7 ± 25.1	26.8 ± 19.4	24.5 ± 11.7
Heterophils (counts)	40.6 ± 14.8	51.2 ± 17.6	49.8 ± 12.9	75.2 ± 8.7
Lymphocytes (counts)	55.9 ± 15.0	46.5 ± 17.5	43.4 ± 14.2	20.4 ± 7.5
Heterophils/ Lymphocytes ratio	0.9 ± 0.6	1.5 ± 1.2	1.4 ± 1.2	4.4 ± 1.9
Erythrocyte nuclear abnormalities (counts)	36.8 ± 12.3	58.8 ± 15.1	5.0 ± 5.8	2.8 ± 2.7
Immature erythrocytes (counts)	49.1 ± 11.7	47.9 ± 10.7	6.9 ± 2.7	7.2 ± 2.3
Haemoglobin (g/dL)	16.7 ± 3.2	17.5 ± 4.9	17.6 ± 5.5	18.2 ± 3.7

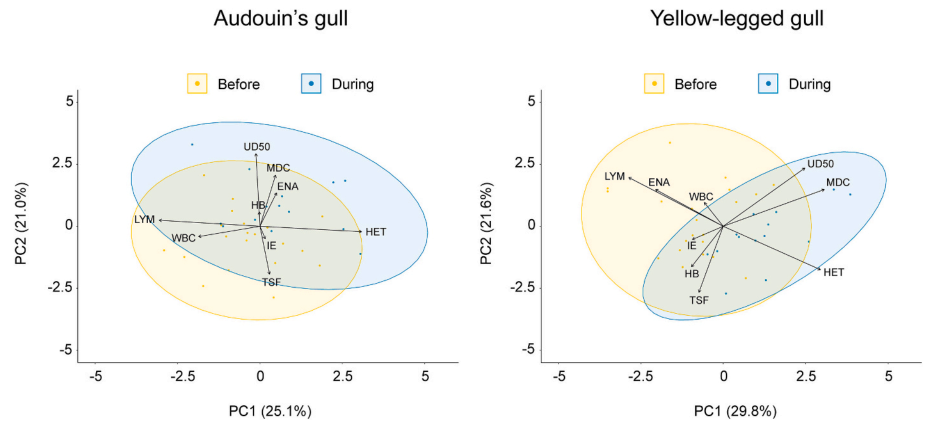


Fig. 2. Biplot of scores extracted by principal component analysis (PCA) on the two main components (PC1 and PC2) applied to normalised tracking variables, i.e. maximum distance from the colony (MDC), proportion of time spent foraging (TSF) and area of 50 % kernel UDs (UD50); and immuno-haematological parameters, i.e. counts of white blood cells (WBC), heterophils (HET), lymphocytes (LYM), erythrocyte nuclear abnormalities (ENA), immature erythrocytes (IE), and haemoglobin (HB) - collected from incubating Audouin's and yellow-legged gulls before (26–30 April) and during (1–10 May) the experimental food restriction trials. Ellipses include 95 % of the data points.

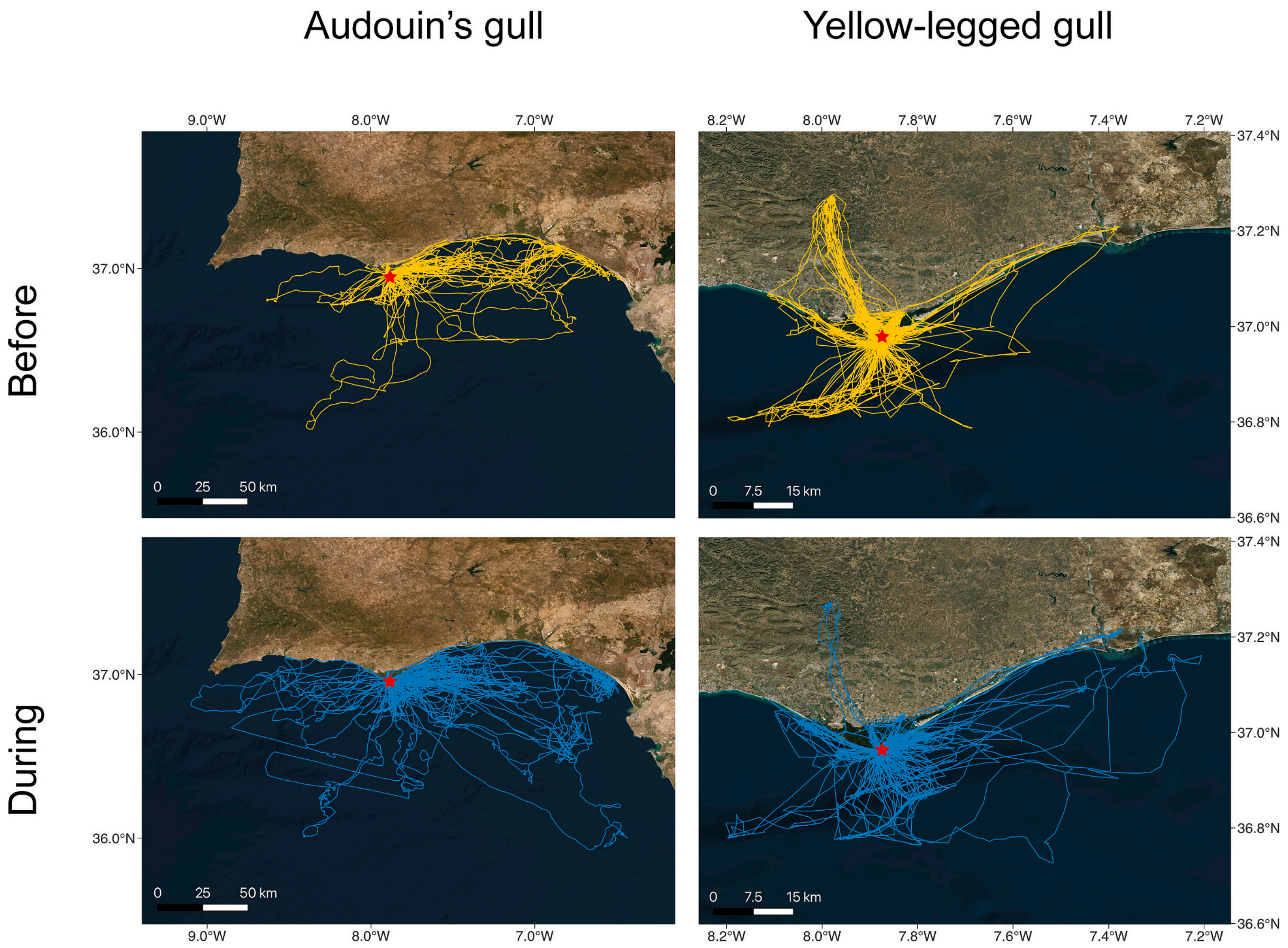


Fig. 3. Overall foraging trips made by incubating Audouin's (N = 19) and yellow-legged gulls (N = 20) before (26–30 April) and during (1–10 May) the experimental food restriction trials. The location of the breeding colony (Deserta Island) is marked with a red star.

likely reflects limited access to discards from local fisheries. While we acknowledged that discard management reduced seabird interactions with local fisheries during the food restriction trials (Frade et al., 2025), we cannot exclude the possibility that discards from other segments of the fleet, including industrial fisheries and boats from other fishing harbours, remained available to gulls, though in limited quantities. Our results suggest that gulls from both species increased their foraging effort during the food restriction trials, likely relying on alternative prey

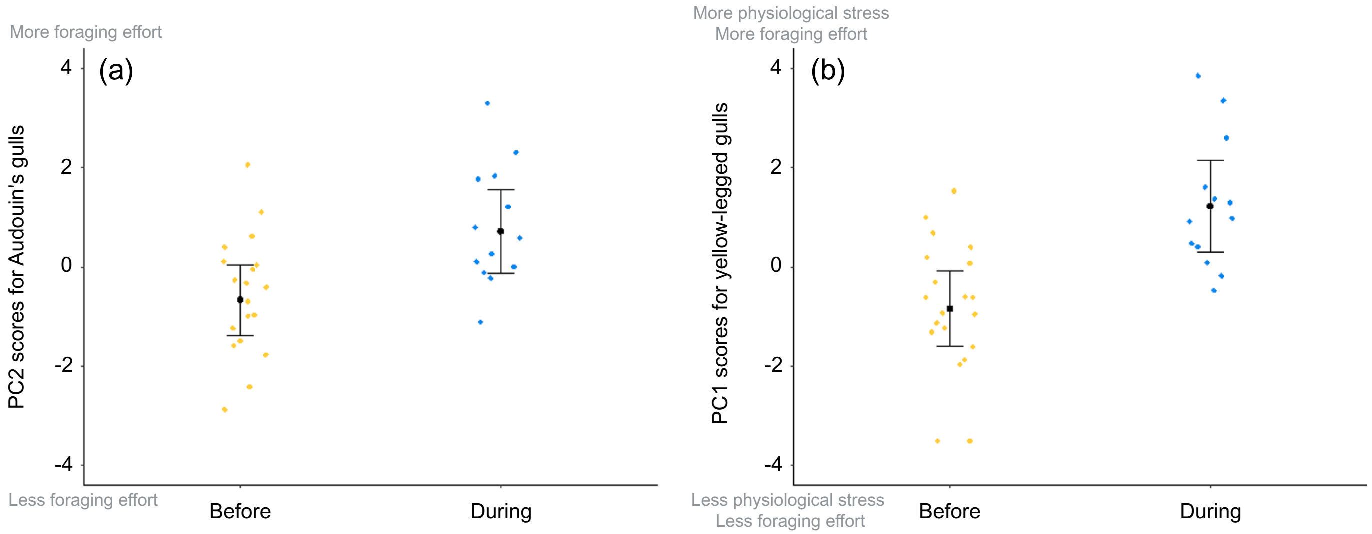


Fig. 4. Model estimates and standard errors (SEs) from models explaining variation in PC2 for incubating (a) Audouin's gulls and in PC1 for (b) yellow-legged gulls, based on tracking variables and immuno-haematological parameters collected before (26–30 April) and during (1–10 May) the experimental food restriction trials.

and/or associating with other fishing fleets operating in the Portuguese Exclusive Economic Zone or adjacent Spanish waters. Future studies combining habitat classification with diet (e.g. pellets, stable isotopes, or fatty acids) would help confirming these potential habitat and dietary shifts. Moreover, long-term GPS tracking would allow a more detailed assessment of habitat use patterns throughout the breeding period.

Yellow-legged gulls, which were deprived of two important PAFS, exhibited significant changes in their physiology, particularly in their leucocyte profile, and showed a clear predominance of heterophils over lymphocytes (resulting in an increased H/L ratio) during the food restriction periods. The increased circulation of heterophils in the bloodstream is a secondary response to stress mediated by the activation of the hypothalamus-pituitary- adrenal (HPA) axis (Maxwell et al., 1992). As a result, the H/L ratio is widely used as a general indicator of stress exposure. Similar patterns have been observed in other seabird species under food-related stress. For instance, Antarctic shags (*Leucocarbo bransfieldensis*) breeding in an area with intense commercial fishing, and likely reduced food availability, showed higher H/L ratio than shags breeding in an area without commercial fishing (Beltran et al., 2024). In addition to responding to variations in food availability, physiological stress responses and immunological parameters change as the breeding season of seabirds progresses (Fitzgerald et al., 2022; Kitaysky et al., 1999), although the magnitude and direction of these changes may differ between sexes (Wojczulanis-Jakubas et al., 2018). In our study, all sampled gulls were in the incubation period, reducing potential variation in stress responses due to breeding stage. Moreover, we found no sex-differences in physiological or foraging effort patterns in either species, suggesting that the observed stress responses may have been driven by the experimental food restrictions rather than natural variation.

GPS data indicated that yellow-legged gulls increased their at-sea foraging effort during the food restriction trials, yet their elevated physiological stress suggests that this additional effort was insufficient to overcome their nutritional needs. It is possible that yellow-legged gulls shifted to alternative, lower-quality resources, including refuse from urban areas or fishing harbours, and terrestrial prey from agricultural fields, which further contributed to the decline of their health condition. Comparable behavioural responses have been observed in other gull species associated with urban environments and landfills. For instance, after a landfill closure, (Langley et al., 2021) showed that breeding lesser black-backed gulls increased foraging effort and shifted foraging habitats, with gulls from one colony increasing their use of agricultural areas, while at another colony they relied more on urban habitats. Despite these behavioural changes, adult body condition remained unaffected, suggesting that the impacts of PAFS restriction may be subtle and primarily manifest at the physiological-level during incubation (this study), or that adults may transfer the costs to offspring through reduced breeding success and juvenile survival (Delgado et al., 2021; Oro et al., 1995).

Audouin's gulls, deprived only of fisheries discards near the breeding colony, displayed a weaker shift in leucocyte profile, with the trend only nearly significant. Because this species also increased its foraging effort, as yellow-legged gulls did during the food restriction trials, the differential physiological responses between the two species suggest that restricted food availability (or increased unpredictability), rather than foraging effort itself, was likely the primary stressor affecting gulls (Beltran et al., 2024; Fokidis et al., 2012; Kitaysky et al., 1999). Unlike yellow-legged gulls, these results suggest that Audouin's gulls were able to cope with this change by foraging farther away, likely accessing prey of similar quality to that available before the experimental restriction. Our results are in line with previous research showing that Kelp gulls (*Larus dominicanus*) feeding at a landfill in northern Patagonia exhibited lower levels of biochemical parameters related to nutrition and immunocompetence, including triglycerides, total proteins, plasmatic enzyme activity, body condition index, and leucocyte count than those foraging at a natural site (Adami et al., 2024). Together, these findings indicate that the differential physiological responses of the two gull species during the food restriction trials were likely driven by the availability and quality of alternative prey. Audouin's gulls were able to maintain physiological balance, while yellow-legged gulls experienced elevated stress when alternative resources were insufficient or of lower quality.

Several studies including seminal experiments on the H/L ratio variation in relation to food restriction in poultry (Maxwell et al., 1992), and manipulative and correlative studies in wild birds have implicated an increase of H/L ratio as a sensitive response to lower food availability (Beltran et al., 2024; Hoi-Leitner et al., 2001; Johnstone et al., 2012). For instance, supplemental feeding improved individual health in several passerine forest bird species, leading to reduced stress (i.e. low H/L ratio), increased antioxidant levels, and even improved body condition index and innate immune defence (in some species), compared to a control area (Wilcoxen et al., 2015). These differences disappeared when feeders were removed. However, when evaluating responses to food unpredictability, there is a higher potential for discrepant results in stress-related physiological responses among studies and species (Acquarone et al., 2002; Fokidis et al., 2012). This is due to differences in body reserve regulation strategies, which arise from different risk-sensitive optimal foraging approaches across bird species (Krebs et al., 1993). In this study, yellow-legged gulls showed lower numbers of erythrocytic nuclear abnormalities during food restriction, reflecting lower oxidative damage to DNA. The number of circulating erythrocytes with abnormalities (other than micronucleus) depends on the erythropoietic rate (positively associated) and clearance in the liver (erythrocytic catabolism - negatively associated) (Pacheco and Santos, 2002). Since erythropoiesis is an energetically demanding function, its reduction in resource-deprived yellow-legged gulls could have lowered the circulation of erythrocytes with nuclear abnormalities in the bloodstream. However, we did not detect a decrease in polychromasia or haemoglobin concentration during the experiment to support this hypothesis (Lebigre et al., 2012).

The observed physiological changes in our study likely reflect short-term effects of an experimentally induced restriction in access to PAFS in gulls, and long-term effects should be further evaluated through monitoring of physiological and reproductive parameters, such as breeding success, chick growth, and adult survival (Delgado et al., 2021). Despite the short data collection period, we detected immediate physiological responses likely driven by restricted access to PAFS during the breeding season. The activation of the HPA-axis constitutes an adaptive response to cope with an acute stressor, but if exposure to stress persists, chronic stress and a sustained inflammatory state may have fitness consequences such as reduced breeding success and survival (Maness et al., 2023; Minias et al., 2018). Unfortunately, we do not have data on the breeding output of the sampled gulls, which would further contribute to linking stress-induced physiological changes to fitness, although this remains extremely challenging in field studies due to behavioural adaptation (Lebigre et al., 2012). Still, this study provides important knowledge on how PAFS may lead to ecological traps due to the reliance/dependence of wild species on these resources, which are often of low nutritional quality. In the case of yellow-legged gulls, limiting access to PAFS may support population management efforts if future studies confirm associated fitness costs such as reduced breeding success or survival (Delgado et al., 2021).

CRediT authorship contribution statement

Jorge M. Pereira: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jaime A. Ramos:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Adriana Domingues:** Methodology, Investigation. **Ana Almeida:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Ana Marçalo:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Catarina Cascão:** Methodology, Investigation. **Carlos Silva:** Methodology, Investigation. **Daniel Rey:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Filipe R. Ceia:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Flávia Carvalho:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Ivo dos Santos:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Jorge M.S. Gonçalves:** Resources, Project administration, Funding acquisition. **Lara R. Cerveira:** Methodology, Investigation. **Magda Frade:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Maria I. Laranjeiro:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Nuno Oliveira:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Tânia Nascimento:** Writing – review & editing, Visualization, Validation, Project administration, Methodology, Investigation, Conceptualization. **Vítor H. Paiva:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Ana C. Norte:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding

This study received financial and logistic support from the project LIFE18 NAT/PT/000927 - LIFE Ilhas Barreira “Conserving the Barrier Islands in Algarve to protect priority species and habitats”, coordinated by Sociedade Portuguesa para o Estudo das Aves (SPEA) and funded by the LIFE EU programme, and co-funded by the Portuguese Government through “Fundo Ambiental". This study also benefitted from funding provided by Foundation for Science and Technology, I.P. (FCT) to MARE under the projects UIDB/04292/2020 (doi:10.544 99/UIDB/04292/2020), UIDP/04292/2020 (doi:10.54499/UIDP/04292/2020), and LA/P/0069/2020 (doi:10.54499/LA/P/0069/2020) granted to the Associate Laboratory ARNET, and through projects UIDB/04326/2020 (doi:10.54499/UIDB/04326/2020), UIDP/04326/2020 (doi:10.54499/UIDP/04326/2020), and LA/P/0101/2020 (doi:10.54499/LA/P/0101/2020) to CCMAR. JMP and VHP were funded by the contracts 2022.07032.CEECIND/CP1714/CT0009 and 2021.01812. CEECIND/CP1656/CT0014, respectively. ACN was supported by the transitory norm contract (DL57/2016/CP1370/CT89). IDS, LRC and MIL were supported by FCT predoctoral fellowships (doi:10.54499/2020.05827.BD, doi:10.54499/2020.07495.BD, and doi:10.54499/UI/BD/150956/2021, respectively). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

We are grateful to Bruno Almeida, Ema Videira, Inês Casinhas, Irene Melero, Javier Rodriguez, Miguel Tapadas, and Patricia Navarro for their participation in gull counts at the landfill and fishing harbours during April and May 2023. To Dr. Carlos Juncal from Algar, S.A., and to Dr. Alcina Souza and Dr. Maria Vicente from the Algarve Ports and Fish Markets Department of DOCAPESCA, for allowing us to carry out these tests at the Sotavento landfill and the fishing ports of Olhão and Culatra. We extend our gratitude to all the skippers and crews of the fishing ports of Olhão and Culatra Island that collaborated with the discard restriction for this study. We would also like to thank the Editor and three anonymous reviewers for their valuable comments that significantly improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.180672.

Data availability

Data will be made available on request.

References

Acquarone, C., Cucco, M., Cauli, S.L., Malacarne, G., 2002. Effects of food abundance and predictability on body condition and health parameters: Experimental tests with the hooded crow. Ibis 144, E155–E163. https://doi.org/10.1046/j.1474-919X.2002.t01-2-00094_1.x.

Adami, M.A., Bertellotti, M., Agüero, M.L., Frixione, M.G., D'Amico, V.L., 2024. Assessing the impact of urban landfills as feeding sites on physiological parameters of a generalist seabird species. Mar. Pollut. Bull. 202, 116327. https://doi.org/10.1016/j.marpolbul.2024.116327.

Alonso, H., Almeida, A., Granadeiro, J.P., Catry, P., 2015. Temporal and age-related dietary variations in a large population of yellow-legged gulls Larus michahellis: implications for management and conservation. Eur. J. Wildl. Res. 61, 819–829. https://doi.org/10.1007/s10344-015-0958-9.

Arcos, J.M., Oro, D., 2002. Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). Mar. Biol. 141, 277–286. https://doi.org/10.1007/s00227-002-0828-3.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., Levin, S.A., 2010. Fishery Discards Impact on Seabird Movement Patterns at Regional Scales. Curr. Biol. 20, 215–222. https://doi.org/10.1016/j.cub.2009.11.073.

Beal, M., Oppel, S., Handley, J., Pearmain, E.J., Morera-Pujol, V., Carneiro, A.P.B., Davies, T.E., Phillips, R.A., Taylor, P.R., Miller, M.G.R., Franco, A.M.A., Catry, I., Patrício, A.R., Regalla, A., Staniland, I., Boyd, C., Catry, P., Dias, M.P., 2021. track2KBA: An R package for identifying important sites for biodiversity from tracking data. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.13713.

Bécares, J., García-Tarrasón, M., Villero, D., Bateman, S., Jover, L., García-Matarranz, V., Sanpera, C., Arcos, J.M., 2015. Modelling Terrestrial and Marine Foraging Habitats in Breeding Audouin's Gulls Larus audouinii: Timing Matters. PLoS One 10, e0120799. https://doi.org/10.1371/journal.pone.0120799.

Beltran, M., D'Amico, V., Bertellotti, M., 2024. Hematologic and plasma biochemistry values of an Antarctic seabird at two sites with different histories of commercial fish exploitation. Mar. Biol. 171, 223. https://doi.org/10.1007/s00227-024-04528-w.

Bicknell, A.W.J., Oro, D., Camphuysen, K.C.J., Votier, S.C., 2013. Potential consequences of discard reform for seabird communities. J. Appl. Ecol. 50, 649–658. https://doi.org/10.1111/1365-2664.12072.

Calado, J.G., Veríssimo, S.N., Paiva, V.H., Ramos, R., Vaz, P.T., Matos, D., Pereira, J., Lopes, C., Oliveira, N., Quaresma, A., Ceia, F.R., Velando, A., Ramos, J.A., 2021. Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast. Mar. Ecol. Prog. Ser. 661, 187–201. https://doi.org/10.3354/meps13601.

Calenge, C., 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F., Deplazes, P., 2004. The diet of urban foxes (Vulpes vulpes) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mamm. Biol. 69, 81–95. https://doi.org/10.1078/1616-5047-00123.

Delgado, S., Herrero, A., Galarza, A., Aldalur, A., Zorrozua, N., Arizaga, J., 2021. Demographic impact of landfill closure on a resident opportunistic gull. Popul. Ecol. 63, 238–246. https://doi.org/10.1002/1438-390X.12083.

Fitzgerald, M., Lynch, S.A., Jessopp, M., 2022. Breeding stage impacts on chronic stress and physiological condition in northern gannets (Morus bassanus). Comp. Biochem. Physiol. A Mol. Integr. Physiol. 274, 111305. https://doi.org/10.1016/j.cbpa.2022.111305.

Fokidis, H.B., Des Roziers, M.B., Sparr, R., Rogowski, C., Sweazea, K., Deviche, P., 2012. Unpredictable food availability induces metabolic and hormonal changes independent of food intake in a sedentary songbird. J. Exp. Biol. 215, 2920–2930. https://doi.org/10.1242/jeb.071043.

Frade, M., Carvalho, F., Samel, V., Oliveira, N., Almeida, A., Andrade, J., Gonçalves, J. Ms., Marçalo, A., 2025. Mitigation measures to reduce seabird's interactions with bottom-set nets in southern Iberia. Ocean Coast. Manag. 268, 107767. https://doi.org/10.1016/j.ocecoaman.2025.107767.

Fuirst, M., Veit, R.R., Hahn, M., Dheilly, N., Thorne, L.H., 2018. Effects of urbanization on the foraging ecology and microbiota of the generalist seabird Larus argentatus. PLoS One 13, e0209200. https://doi.org/10.1371/journal.pone.0209200.

Garriga, J., Palmer, J.R.B., Oltra, A., Bartumeus, F., 2016. Expectation-maximization binary clustering for behavioural annotation. PLoS One 11, e0151984. https://doi.org/10.1371/journal.pone.0151984.

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A.G., Wilkinson, S., Crawford, R.J.M., Ryan, P.G., 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proc. R. Soc. B Biol. Sci. 275, 1149–1156. https://doi.org/10.1098/rspb.2007.1763.

Hoi-Leitner, M., Romero-Pujante, M., Hoi, H., Pavlova, A., 2001. Food availability and immune capacity in serin (Serinus serinus) nestlings. Behav. Ecol. Sociobiol. 49, 333–339. https://doi.org/10.1007/s002650000310.

Instituto Nacional de Estatística, 2023. Estatísticas da Pesca: 2022 [WWW Document]. https://www.ine.pt/xportal/xmain?xpid=INE&xpgid=ine_publicacoes&PUBLICACOESpub_boui=66322600&PUBLICACOESmodo=2. (Accessed 29 August 2024).

Johnstone, C.P., Reina, R.D., Lill, A., 2012. Interpreting indices of physiological stress in free-living vertebrates. J. Comp. Physiol. B 182, 861–879. https://doi.org/10.1007/s00360-012-0656-9.

Kitaysky, A.S., Wingfield, J.C., Piatt, J.F., 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. Funct. Ecol. 13, 577–584. https://doi.org/10.1046/j.1365-2435.1999.00352.x.

Krebs, J.R., Davies, N.B., Parr, J., 1993. An introduction to behavioural ecology. Blackwell Science, Oxford.

Langley, L.P., Bearhop, S., Burton, N.H.K., Banks, A.N., Frayling, T., Thaxter, C.B., Clewley, G.D., Scragg, E., Votier, S.C., 2021. GPS tracking reveals landfill closures induce higher foraging effort and habitat switching in gulls. Mov. Ecol. 9, 56. https://doi.org/10.1186/s40462-021-00278-2.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: An R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Lebigre, C., Alatalo, R.V., Kilpimaa, J., Staszewski, V., Siitari, H., 2012. Leucocyte counts variation and measures of male fitness in the lekking Black Grouse. J. Ornithol. 153, 95–102. https://doi.org/10.1007/s10336-011-0701-6.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139.

Maness, T.J., Grace, J.K., Hirchak, M.R., Tompkins, E.M., Anderson, D.J., 2023. Circulating corticosterone predicts near-term, while H/L ratio predicts long-term, survival in a long-lived seabird. Front. Ecol. Evol. 11. https://doi.org/10.3389/fevo.2023.1172904.

Mariano-Jelicich, R., Copello, S., Seco Pon, J.P., Favero, M., 2014. Contribution of fishery discards to the diet of the Black-browed albatross (Thalassarche melanophris) during the non-breeding season: an assessment through stable isotope analysis. Mar. Biol. 161, 119–129. https://doi.org/10.1007/s00227-013-2320-7.

Marinao, C., Kasinsky, T., Suárez, N., Yorio, P., 2018. Contribution of recreational fisheries to the diet of the opportunistic Kelp Gull. Austral Ecol. 43, 861–875. https://doi.org/10.1111/aec.12627.

Martín-Vélez, V., Montalvo, T., Ramirez, F., Figuerola, J., Morral-Puigmal, C., Planell, R., Sabate, S., Bota, G., Navarro, J., 2025. Opportunistic Gulls Infected by Antibiotic-Resistant Bacteria Show Contrasting Movement Behaviour. Ecol. Evol. 15. https://doi.org/10.1002/ece3.71257.

Matos, D.M., Ramos, J.A., Calado, J.G., Ceia, F.R., Hey, J., Paiva, V.H., 2018. How fishing intensity affects the spatial and trophic ecology of two gull species breeding in sympatry. ICES J. Mar. Sci. 75, 1949–1964. https://doi.org/10.1093/icesjms/fsy096.

Maxwell, M.H., Hocking, P.M., Robertson, G.W., 1992. Differential leucocyte responses to various degrees of food restriction in broilers, turkeys and ducks. Br. Poult. Sci. 33, 177–187. https://doi.org/10.1080/00071669208417455.

Mendes, R.F., Ramos, J.A., Paiva, V.H., Calado, J.G., Matos, D.M., Ceia, F.R., 2018. Foraging strategies of a generalist seabird species, the yellow-legged gull, from GPS tracking and stable isotope analyses. Mar. Biol. 165, 168. https://doi.org/10.1007/s00227-018-3421-0.

Minias, P., Włodarczyk, R., Meissner, W., 2018. Leukocyte profiles are associated with longevity and survival, but not migratory effort: A comparative analysis of shorebirds. Funct. Ecol. 32, 369–378. https://doi.org/10.1111/1365-2435.12991.

Murray, M., Cembrowski, A., Latham, A.D.M., Lukasik, V.M., Pruss, S., St Clair, C.C., 2015. Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. Ecography 38, 1235–1242. https://doi.org/10.1111/ecog.01128.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L. P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.

O'Hara, C.C., Frazier, M., Halpern, B.S., 2021. At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. Science 372, 84–87. https://doi.org/10.1126/science.abe6731.

Oliveira, N., Alonso, H., Encarnação, V., Menezes, D., Magalhães, M., Carreira, G., Heber, S., Pimentel, R., Medeiros, V., Bairos, J., Raposo, P., Coelho, R., Rufino, R., Neves, R., Nascimento, T., Silva, E., Andrade, J., 2023. Changes in numbers and distribution of Yellow-legged Gull Larus michahellis nesting in Portugal during the last two decades. Airo 31, 20–37.

Oro, D., Bosch, M., Ruiz, X., 1995. Effects of a trawling moratorium on the breeding success of the Yellow-legged Gull Larus cachinnans. Ibis 137, 547–549. https://doi.org/10.1111/j.1474-919X.1995.tb03265.x.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514. https://doi.org/10.1111/ele.12187.

Pacheco, M., Santos, M.A., 2002. Biotransformation, genotoxic, and histopathological effects of environmental contaminants in European eel (Anguilla anguilla L.). Ecotoxicol. Environ. Saf. 53, 331–347. https://doi.org/10.1016/S0147-6513(02)00017-9.

Pais De Faria, J., Vaz, P.T., Lopes, C.S., Calado, J.G., Pereira, J.M., Veríssimo, S.N., Paiva, V.H., Gonçalves, A.M.M., Ramos, J.A., 2021. The importance of marine resources in the diet of urban gulls. Mar. Ecol. Prog. Ser. 660, 189–201. https://doi.org/10.3354/meps13599.

Pereira, J.M., Ramos, J.A., Almeida, A., Marçalo, A., Carvalho, F., Fagundes, I., Gonçalves, J.M.S., Frade, M., Oliveira, N., Nascimento, T., Paiva, V.H., 2025. Seasonal variation in seabird abundance and bycatch at artisanal bottom-set net fisheries in the southern Iberian Atlantic coast. Ocean Coast. Manag. 267, 107660. https://doi.org/10.1016/j.ocecoaman.2025.107660.

Plaza, P.I., Lambertucci, S.A., 2017. How are garbage dumps impacting vertebrate demography, health, and conservation? Global Ecol. Conserv. 12, 9–20. https://doi.org/10.1016/j.gecco.2017.08.002.

R Core Team, 2024. R: A Language and Environment for Statistical Computing.

Sorais, M., Mazerolle, M.J., Giroux, J.F., Verreault, J., 2020. Landfills represent significant atmospheric sources of exposure to halogenated flame retardants for urban-adapted gulls. Environ. Int. 135, 105387. https://doi.org/10.1016/j.envint.2019.105387.

Wilcoxen, T.E., Horn, D.J., Hogan, B.M., Hubble, C.N., Huber, S.J., Flamm, J., Knott, M., Lundstrom, L., Salik, F., Wassenhove, S.J., Wrobel, E.R., 2015. Effects of bird-feeding activities on the health of wild birds. Conserv. Physiol. 3, cov058. https://doi.org/10.1093/conphys/cov058.

Wojczulanis-Jakubas, K., Jakubas, D., Kulpińska-Chamera, M., Chastel, O., 2018. Sex- and breeding stage-specific hormonal stress response of seabird parents. Horm. Behav. 103, 71–79. https://doi.org/10.1016/j.yhbeh.2018.06.005.