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ORIGINAL ARTICLE

Quantifying nutrient inputs by gulls to a fluctuating lake, aided by movement ecology methods

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Abstract

1. Eutrophication of aquatic ecosystems is a global problem with major ecological and economic impacts. In many lakes and reservoirs, guano-trophication occurs when roosting waterbirds import nutrients (nitrogen and phosphorus) from surrounding terrestrial habitats. To date, nutrient loading by waterbirds has been estimated based on censuses in the absence of detailed information on their movements. We quantified nutrient importation by the lesser black-backed gull (*Larus fuscus*) to Fuente de Piedra (1,350 ha) in Andalusia (south-west Spain), where an average of 36,288 individuals are counted in January.
2. During seven winters from 2010 to 2017, we used movement data from 20 individual gulls tagged with Global Positioning System trackers that foraged in four landfills. Together with monthly bird counts and measurements of total N and P content in faeces and pellet samples, movement data were used to quantify the total external loading effect for different winters. Movement data allowed us to quantify the proportion of time spent in the lake and the time spent at different foraging sites and enabled correction of censuses.
3. According to tracking data, on average 69% of the birds had already left the lake to head for feeding sites when waterbird counts were carried out. Nutrient inputs to the lake depend partly on the proportion of the day that gulls spend there, which was higher in late winters and was reduced when lake depth went below or above 20–35 cm. An estimated average of 10.17 kg N ha⁻¹ year⁻¹ and 2.07 kg P ha⁻¹ year⁻¹ were imported to this closed-basin lake by gulls each winter, with highest values recorded in winter 2016–2017.
4. Gull guano is the most important winter source of nutrients to the lake. Regurgitated pellets have been ignored as a source of nutrients in other guano-trophy studies, but we found them to be a more important source of P than faeces. A movement ecology approach complements traditional censuses and facilitates the study of guano-trophication in multiple ways, including identification of sources of nutrients, correction of censuses, and measuring time spent at roost sites.

KEYWORDS

Global Positioning System, guano-trophication, landfills, *Larus fuscus*, waterbirds

1 | INTRODUCTION

Eutrophication of aquatic ecosystems is a serious environmental problem worldwide (Carpenter, 2005; Harper, 1992) and is one facet of the global water crisis (Mateo-Sagasta, Zadeh, Turrall, & Burke, 2017). In the European Union, nearly 40% of water bodies are affected by eutrophication due to agricultural pollution (WWAP, 2015), and many others are affected by inputs of urban wastewaters (de-los-Ríos-Mérida et al., 2017; Vymazal, 2010). The need to reduce eutrophication has led to a number of EU Directives (van Buuren, 2014; Knockaert, 2014a,b). Eutrophication can lead to excessive plant productivity, harmful algal blooms, proliferation of floating plants, anoxic events, and fish mortality, with major impacts on diversity and food web structure (Bauer & Hoyer, 2014; Vizzini, Signa, & Mazzola, 2016). The impact of eutrophication is expected to increase in coming years due to the increase in human population, land use conversion, soil erosion, and fertilisation (Millennium Ecosystem Assessment, 2005) and the consequences of climate change (Green et al., 2017; Hanjra & Qureshi, 2010).

While most studies have focused on human-mediated eutrophication (i.e. cultural eutrophication), guanotrophication (i.e. animal-derived fertilization) can also be important. This typically occurs when large numbers of birds feed elsewhere, but roost or nest in lakes or reservoirs and is particularly problematic in closed-basin lakes (i.e. those with no outflow). Birds can be key biovectors of nutrients and have important effects on ecosystem functioning (Dessborn, Hessel, & Elmberg, 2016; Green & Elmberg, 2014). Waterbirds produce

faeces that are rich in phosphorus (P) and nitrogen (N), and omnivorous birds such as gulls (*Laridae*) have higher protein content in their diets than herbivorous birds such as geese, leading to higher P loading into roost sites. This in turn promotes harmful algal blooms and the loss of submerged plants (Marion, Clergeau, Brient, & Bertru, 1994). Guanotrophication by gulls that use landfills for foraging then roost in lakes or reservoirs is a widespread problem, causing damage to ecosystem services estimated at \$100 million in North America alone (Winton & River, 2017).

Guanotrophy studies rely partly on estimates of body mass functions and daily food intake to model the nutrient loading to wetlands (Hahn, Bauer, & Klaassen, 2007, 2008). These models also rely on waterbird counts at wetland roosts and assumptions about the proportion of time that birds spend in the wetland, which has a direct influence on the proportion of daily faecal output egested there (Hahn et al., 2008; Winton & River, 2017). However, tracking daily movements of individuals allows the quantification of time use and movements between feeding and roosting sites that can then complement censuses and help to quantify nutrient loading. Global Positioning System (GPS) tracking also allows identification of specific feeding sites (e.g. landfills), which act as a source of the nutrients imported to wetlands, as well as of contaminants (e.g. heavy metals) or pathogens (Bauer & Hoyer, 2014).

In Andalusia, the lesser black-backed gull (LBBG) *Larus fuscus* has become an important wintering waterbird on inland waterbodies, due to a major increase of the European breeding population since the middle of the twentieth century (Hagemeijer

FIGURE 1 (a) Location of Fuente de Piedra shallow lake in the Iberian Peninsula. (b) Four landfills used as foraging sites by gulls making daily movements from Fuente de Piedra. The size of the circle is proportional to the total cumulative time gulls spent in each site between 2010 and 2017. Matagrande landfill was opened in 2006, Antequera in 1993, Montalbán in 1992 and Córdoba in 1986. (c) Dots show the location of the main roosting sites of gulls within Fuente de Piedra [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 (a) Plot of corrected counts (mean $\pm$ SE) in Fuente de Piedra (FP) between 2010 and 2017, based on six monthly counts per winter. The mean ($\pm$ SE) water level per winter is shown in red, based on daily measures. (b) Monthly seasonal variation in corrected counts (mean $\pm$ SE) in FP between 2010 and 2017. Significant differences ($p < 0.05$) between months in the number of gulls in FP lake are represented by different letters below error bars, based on a Tukey post hoc test. The mean ($\pm$ SE) water level per winter is shown in red [Colour figure can be viewed at wileyonlinelibrary.com]

& Blair, 1997; Wetlands International, 2019). The LBBG has also undergone a roughly 10-fold increase in numbers since the 1970s in Andalusia (Rendón, Green, Aguilera, & Almaraz, 2008), and is now the second most numerous wintering waterbird, after the northern shoveler *Anas clypeata* (census data from the Junta de Andalucía). This increase is probably related to the expansion of anthropogenic habitats such as rice fields (which have doubled in surface area since the 1960s, Ramo, Aguilera, Figuerola, Manez, & Green., 2013) and landfills (Figure 1, and Arizaga et al.,

2018) that increase resource availability. Communal roosting by LBBG at wetlands is common, thereby reducing thermoregulatory costs and predation risk (Galván, Marchamalo, Bakken, & Traverso, 2003). This behaviour, along with its abundance and the availability of GPS-tracking data, makes the LBBG an ideal study model to apply movement data to evaluate avian inputs of nutrients into wetlands. Here, we use the most important mid-wintering site for LBBG in Andalusia as a case study. Fuente de Piedra (FP) is a shallow, hypersaline (average salinity 41.2 g/L, Rodríguez-Rodríguez, Moral, Benavente, & Beltrán, 2010), closed-basin lake and a protected wetland famous for its waterbirds.

We test the following hypotheses: (1) movement data allow us to quantify the proportion of the day birds spend at FP, and hence the proportion of daily excreta likely to be deposited there; (2) changing water levels in the lake lead to variation in gull numbers and the proportion of time spent each day at the lake, within and between winters. Low water levels would expose gulls to predators such as foxes, whereas very high water levels would inundate islands in the lake where gulls roost (Figure 1c and Bijleveld, Egas, van Gils, & Piersma, 2010). Therefore, we expect higher gull numbers and longer roosting time at intermediate water levels; (3) movement data allow us to identify different open landfills used as feeding sites by the gulls roosting at FP, and allow us to quantify their relative importance for nutrient loading; (4) regurgitated pellets represent an important fraction of the contribution of LBBGs to the nutrient budget of FP. Pellets are produced regularly by LBBG at roost sites (Lovas-Kiss et al., 2018), yet have been overlooked in previous guanotrophy studies (Winton & River, 2017).

2 | METHODS

2.1 | Study area

This study was performed in FP, a shallow lake located in Malaga province (south-west Spain; 37°6'N, 4°44'W), which is protected at regional (Natural Reserve), European (Special Protection Area) and international (Ramsar site) levels (Figure 1). It is the most important breeding site for greater flamingos (*Phoenicopterus ruber*) in the Iberian Peninsula, with around 10,500 breeding pairs (Bechet et al., 2012). LBBGs are now abundant at FP in winter, but January counts did not exceed 40 individuals prior to 1988 (M. Rendón, personal communication). Fuente de Piedra is the largest natural lake in Andalusia, covering an area of 1,350 ha (6.8 km long and 2.5 km wide) and is situated in a closed basin of karstic origin (Batanero et al., 2017) at 400 m above sea level (García, García-Ruiz, Rendón, Niell, & Lucena, 1997). Inputs of water come from rainfall, ground water, and two intermittent streams, whereas output is mainly due to evaporation (Rodríguez-Rodríguez, Benavente, & Moral, 2005). Fuente de Piedra fluctuates in water level, salinity, and nutrient concentrations, tending to increase in depth during the course of the winter (Figure 2b) but drying out in summer in most years, although it retains water throughout wet years (Rodríguez-Rodríguez

et al., 2005). It is a hypersaline lake of the Cl-(SO₄)-Na-(Mg)-(Ca)-type, and concentrations of dissolved solids vary between 18 and 200 g/L (Kohfahl et al., 2008). Salinity varies seasonally, ranging from 10 g/L to a maximum in summer of 400 g/L (Benavente, Rodríguez-Rodríguez, & Almécija, 2003). In wet and dry years, total nitrogen (TN) ranged on average from 0.22 to 0.59 mmol N/L; total dissolved nitrogen from 0.18 to 0.28 mmol N/L; total phosphorus (TP) from 4.85 to 12.61 µmol P/L and soluble reactive phosphorus from 0.45 to 0.74 µmol P/L (Batanero et al., 2017). Daily water level measurements were provided by the Junta de Andalucía (regional government) and taken using a limnigraph that registers water level variations through movements of a floating sensor located in an open shallow well in the lake.

2.2 | Global Positioning System tracking

We used GPS tracking data collected as part of long-term studies of several breeding populations using UvA-BiTS (Baert et al., 2018; Shamoun-Baranes, Burant, van Loon, Bouten, & Camphuysen, 2017; Thaxter et al., 2015) (<http://www.uva-bits.nl>; Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013). We first selected all data points from a centralised database that fall spatially within the boundaries of FP from September through February (i.e. the wintering period) in 2010–2017 (i.e. seven winters). We applied a buffer zone of 50 m to account for individuals roosting around the lake edge. The resulting dataset included tracking data from 20 individuals. Eight individuals originated from the Zeebrugge colony (Belgium), five from Texel (the Netherlands), three from Walney (U.K.), three from Skokholm (U.K.) and one from Orford Ness (U.K.). In winter, the trackers recorded GPS movements at intervals of 10–30 min. Each individual was recorded at FP for 1–6 different winters and, in total, we had data from 29 bird-winters (Figure 3).

For our study, we only considered daily trips in which the tagged individuals departed from FP and came back to roost the same day. Each GPS point was assigned a duration (min) based on the backward and forward intervals between consecutive GPS points providing a *centred duration*. We removed gaps in the data that had a centred duration of more than 60 min. The number of GPS fixes per day varied between individuals and during the course of the winter, so we calculated the percentage of daily time spent at FP on a given day as the accumulated minutes for the fixes whilst residing at FP, divided by the total accumulated minutes for all fixes that day. Days in which the position of individuals was known for less than 1,000 min/day (e.g. because of missing data) were discarded. After data visualisation, we identified four landfills as foraging destinations (Figure 1). The accumulated time spent (in minutes) of the fixes that fell spatially within the boundaries (determined from Google Earth Satellite images) of each landfill was calculated for each day when a gull roosted at FP.

2.3 | Census estimation and analysis

Monthly censuses (from September to February) during seven winters from September 2010 to February 2017 were carried out at FP by the Junta de Andalucía, but no counts were made at foraging sites. Bird

FIGURE 3 Proportion of daily time spent ratio (mean + SE) in Fuente de Piedra (FP) per winter for tagged gulls over seven different winters, in relation to the number of days spent at the lake the same winter. When considering data for all years combined and the proportion of daily time as dependent variable, there was a significant relationship with the number of days that individuals spent at FP ($F_{1,28} = 12.96$, $p = 0.001$). When controlling for years with a factor, the year effect is not significant whereas the relationship with number of days remains significant ($F_{1,22} = 11.69$, $p = 0.002$) [Colour figure can be viewed at wileyonlinelibrary.com]

counts were performed between 08:00 and 12:00 hr local time, but the precise time on each occasion was not recorded (M. Rendón, personal communication.). Missing counts (five out of 42 months; 11%) were imputed based on the type III Poisson regression trend by using the *RTRIM* package in R (Van Strien, Pannekoek, Hagemeijer, & Verstraal, 2004). Using GPS movement data, we determined the departure times (converted from UTC to local time) of all gull-trips ($n = 374$) from FP after nocturnal roosting for all available data during the 7 years of study. For each interval of 5 min between 08:00 and 12:00 hr, we calculated the proportion of individuals that roosted during the previous night, which still remained at FP. In this way, we estimated the proportion of gull-trips that had not yet started, enabling correction of counts at the lake.

2.4 | Variation in time spent at the lake

We tested if the proportion of time spent at the lake on a given day was related to the number of days spent there. We performed a linear model with *number of days* and *winter* as response variables and *daily proportion of time spent* (logit transformed) as dependent variable. Next, to evaluate the effect of a specific winter, water level, and date within the winter season on the *daily proportion of time spent* at the lake, we performed a generalised linear mixed-effect model with binomial error distribution and logit link function. *Day of the year* and *water level* were included in the generalised linear mixed-effect

model as a second-order polynomial, in order to allow for non-linear relationships through the wintering season. To reduce collinearity between *day* and *day squared* (Legendre & Legendre, 1998), the first of January was set as day 0 and the days from September to December were given negative values. For the same reason, water level was first transformed by deducting the mean from all values and then added as a second order polynomial. The complete model included *winter* as a fixed factor with seven levels, and *water level*, *water level squared*, *day*, and *day squared* as continuous predictor variables. The *daily proportion of time spent* roosting at FP was the dependent variable. We first included *individual* as random factor, but it only explained 0.0001% of the variation of the data (because different winters generally featured different individuals), so it was finally removed from the model. Akaike information criterion (AIC) model selection was used through the *drop1* function in R in order to gradually drop variables from the complete model (AIC = 741.20) until a minimum adequate model was reached. The final model (AIC = 737.91) had *winter*, *water level*, and *water level squared* as predictor variables. The fit of the final model was assessed by the ratio between the residual deviance and the number of degrees of freedom (the ideal ratio being one; Crawley, 1993). Main effects were tested by comparing the final model with an alternative model without the variable to be tested. Post hoc tests for the differences between winters were performed with multiple comparisons of means (Tukey contrast with Holm adjustment). The non-linear relationship between water level and the proportion of time spent at the lake was fitted via a Loess smooth regression.

2.5 | Variation in time spent at foraging sites

To test for differences in the *daily time spent* per visit at each of the landfills used as foraging sites (daily accumulated time, log transformed to normalise residuals), we performed a linear mixed model with a normal error distribution and Gaussian link function, including *site* and *winter* as fixed factors, and *individual-ID* as a random factor. Post hoc tests for differences between foraging sites were performed as above.

2.6 | Variation in numbers of gulls at the lake

To determine if gull imputed counts varied between different months or in response to changing water level, we performed a general linear model with quassi-Poisson error distribution and log link function. We selected *winter* and *month* as factors with seven levels and six levels, respectively, and *water level* and *water level squared* as continuous variables.

All analyses were performed in R (v.3.4.1) using packages *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017), *lme4* (Bates, Maechler, Bolker, & Walker, 2014), *multcomp* (Hothorn et al., 2016) and *blme* (Korner-Nievergelt et al., 2015).

2.7 | Nitrogen and P content in gull excreta

Ten fresh gull faecal samples and 10 fresh pellets were collected in FP in February 2017 and placed in ice in the field, then frozen at -20°C within

3 hr to prevent ammonium volatilisation. Samples were taken from three different roosting sites separated by up to 2 km (see Figure 1), and within each site were collected from spots separated by at least 1 m to ensure that they were from different individuals. Samples were later dried at 60°C during 24 hr to obtain dry weight. Pellets were triturated into dust in a mixer mill (Retsch MM 400) during 3 min at 230 Hz. We then diluted 0.5 g in 500 ml of Milli-Q water and stored it at -20°C until analysis in April 2017 (for faeces) and October 2018 (for pellets). We analysed TN by digestion with potassium persulfate (Nydahl, 1978). Total phosphorus concentration was measured using the molybdenum blue method (Murphy & Riley, 1962). The coefficient of variation ($\text{CV} = (\sigma/\mu) \times 100$) was calculated for each sample type and nutrient type.

2.8 | Nutrient quantification

Total nutrient loads (NL) of LBBG per winter were estimated as follows (the same equation can be used for either N or P):

$$\text{NL} = \text{NL}_{\text{faeces}} + \text{NL}_{\text{pellets}} \quad (1)$$

$$\text{NL}_{\text{faeces}} = \text{TS} * \text{ER}_{\text{faeces}} * \text{ND} * \text{MW} * \text{NC}_{\text{faeces}} \quad (2)$$

$$\text{NL}_{\text{pellets}} = \text{ER}_{\text{pellets}} * \text{PW} * \text{ND} * \text{MW} * \text{NC}_{\text{pellets}} \quad (3)$$

where TS = time spent; ER = excretion rate; PW = pellet weight; MW = mean winter counts; and NC = total nutrient (either N or P) content.

TS = average daily proportion of time spent at the lake per individual per winter.

$\text{ER}_{\text{faeces}}$ = excretion rate per individual per day (g/day), considered as a fixed parameter (21.06 g/day), calculated using Equation of the Hahn et al. (2007) model for nutrient transport by carnivorous birds. For these calculations, we assumed that LBBGs have a mean body mass of 792 g (Hahn et al., 2007) and a daily energy requirement of 968.66 kJ (Nagy, Girard, & Brown, 1999). We adopted values of food energy content of 23.9 kJ/g based on landfill diet (Winton & River, 2017), a metabolisable energy coefficient of 0.76 (Karasov, 1990), and an intake: excretion ratio of 0.395 (Dobrowolski, Kozakiewicz, & Leżnicka, 1993; Nixon & Oviatt, 1973).

$\text{ER}_{\text{pellets}}$ = egestion rate of pellets per day. One pellet is assumed to be produced per day (Lovas-Kiss et al., 2018), and deposited within the roosting site.

PW = mean pellet weight. Based on the average dry weight of pellet samples collected ($3.74 \text{ g pellet}^{-1} \pm 1.18 \text{ SD}$).

ND = number of days per winter (180 days, for a wintering period from September to February inclusive).

MW = mean winter count of LBBG after we corrected the counts for gulls that were missing (i.e. those that had already set off for feeding sites by the time the lake was counted).

$\text{NC}_{\text{faeces}}$ = average total nutrient (either N or P) in g/g of faeces.

$\text{NC}_{\text{pellets}}$ = average total nutrient (either N or P) in g/g of pellet.

We also compared our results to those predicted from previous literature that does not include movement data. Following Hahn et al.

(2007), we took TS as a fixed value of 0.6 and calculated MW directly from counts without correcting for birds that had already left the lake.

3 | RESULTS

Gulls predominantly used the lake for nocturnal roosting. In a small minority of gull-days (30 of 786 gull-days [3.8%] during winters from 2010 to 2017), tagged gulls remained at FP all day without leaving to feed elsewhere.

3.1 | Evaluating errors in censuses

Using the departure times of GPS-tagged gulls from FP, we estimated that on average only 31% of the gulls were present at the lake when counts were made (decreasing from 59% at 08:00 hr to 26% at 12:00 hr in intervals of 5 min, Figure 4). Using this proportion (0.31) we estimated the number of gulls that were present at FP from 2010 to 2017 (Figure 2a), as well as the fluctuations in their abundance across months (Figure 2b). A general linear model of corrected count data showed that gull numbers varied significantly among months (model comparison: $F = 22.312$, $df = 5$, $p < 0.0001$). Gull numbers were significantly higher at FP in January than other months (Figure 2b).

3.2 | Time spent by gulls in FP

Within a single winter, individual gulls varied in the proportion of the day spent at the lake (Figure 3). Furthermore, data were available for a smaller number of tagged gulls during the first four winters than in the last three winters (range one to eight individuals, Figure 3). In addition, individuals that spent more days at FP also tended to spend a greater proportion of the day there (Figure 3).

For the proportion of daily time spent at the lake, the final model with parameters *winter*, *water level*, and *water level squared* provided a good fit to the data (ratio of 0.92; deviance = 717.9, $df = 776$). Model comparison showed that the *winter* factor had a significant effect on time spent by gulls in the lake ($\chi^2 = 12.84$, $p = 0.046$). Comparison between winters showed that gulls spent most time per day in the lake during winter 2016–2017, followed by 2015–2016 and 2014–2015, respectively (Figure 5). Water level did not significantly influence the time gulls spent in FP when combined with winter ($\chi^2 = 2.97$, $df = 2$, $p = 0.228$), but it did when analysed on its own and in a non-linear manner ($Z = -3.958$, $df = 783$; $p < 0.0001$) with most time spent when water levels were close to 30 cm (Figure S1).

3.3 | Location of foraging sites and time spent there

Based on the GPS tracks, the feeding sites used by LBBG when roosting at FP were the landfills at Antequera (17.8 km from FP), Matagrande (26.7 km), Montalbán (44.7 km) and Córdoba (78.3 km, Figure 1). Matagrande landfill was the site where gulls spent most accumulated time, followed by Montalbán and

FIGURE 4 The proportion of tagged gulls (based on 374 gull-trips) that remained in Fuente de Piedra lake (FP) during the time range when gull counts were conducted, in intervals of 5 min. Those gulls not present at the lake had already left for the foraging sites [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Proportion of daily time spent at the roost (Fuente de Piedra) in winters from 2010 to 2017. Median values with quartiles are presented, with the arithmetic mean shown by grey squares. No shared letters above bars indicate a significant difference ($p < 0.05$) between years, based on a Tukey post hoc test

Antequera landfills (Figure 1). According to a linear mixed model, *site* had a significant effect on the time spent at the foraging site per visit ($F_{3,914.71} = 33.94$, $p < 0.0001$), whereas *winter* did not ($F_{6,159.70} = 2.1$; $p = 0.055$). Gulls spent significantly less time per

daily visit at Antequera landfill, which was the closest foraging site and the one visited most often (Figure 6).

3.4 | Nutrient loading quantification

Mean TP in faecal samples was 1.82 (± 0.86 SD; CV = 47.6%) mg P/g dry mass, whereas mean TN was 18.86 (± 6.55 SD; CV = 34.7%) mg N/g dry mass (Figure 7). Therefore, the N:P ratio in faeces was approximately 8:1. Mean TP in the pellet samples was 5.68 (± 4.86 SD; CV = 85.5%) mg P/g pellet whereas mean TN was 10.90 (± 3.39 SD; CV = 31.1%) mg N/g pellet (Figure 7), so the N:P ratio in pellets was approximately 1.9:1. Based on means for nutrient content, % time spent in the lake per winter (September–February 2010–2017) and corrected censuses (together with fixed parameters such as excretion rate and number of days per winter), we determined the TN and TP loading by LBBG into FP for both faeces and pellets (Figure 8). Average annual total N and P loads of gulls into FP amounted to 10.17 kg N ha⁻¹ year⁻¹ and 2.07 kg P ha⁻¹ year⁻¹ respectively but varied between years (Figure 8). Although faeces were more important than pellets as a source of imported N, pellets were more important than faeces as a source of P (Figure 7).

Our estimates of nutrient inputs based on GPS movement data were compared with those based on the models of Hahn et al. (2007). Although there was strong variation between winters, on average our

estimates of nutrient imports were 47% higher than those based on Hahn et al. (2007), partly because gull counts underestimate the number of birds present, and partly because the true proportion of the day spent at the lake was on average higher than the 60% estimated by Hahn et al. (2007) (although in some winters it was lower, Figure 5).

4 | DISCUSSION

As far as we know, this is the first study to take advantage of detailed information from GPS data on time use and behaviour of waterbirds to complement waterbird counts and so estimate nutrient inputs by waterbirds with more confidence. All four of our initial hypotheses were accepted. We recorded substantial inputs of N and P by wintering gulls into a Mediterranean shallow lake and found that these inputs increased in recent winters and are dependent on lake water levels.

By using GPS tracking data, we also identified the relative importance of different landfills which are the sources of nutrients imported to the lake, and which ultimately may have fuelled the increase in the gull population and in guano inputs over time. The landfills used by LBBGs roosting at FP were created between 1986 and 2006, a period that coincides with the increase in the numbers of LBBG wintering in Andalusia. Similar effects have been observed in North America, where the creation of landfills has resulted in increased gull populations and guanotrophic effects (Winton & River, 2017).

Previous studies that estimate nutrient contribution by waterbirds lack detailed behavioural information, and use fixed parameters to estimate the time spent at the roosting site without accounting for variation within or between winters (Dessborn

FIGURE 6 Time spent (in min) per daily visit in the foraging sites by gulls roosting at Fuente de Piedra from 2010 to 2017. Sites are in order of increasing distance to Fuente de Piedra from left to right. Median values with quartiles are presented, with the arithmetic mean shown by grey squares. A Tukey post hoc test from a linear mixed model revealed a significant difference between Antequera and all other sites ($p < 0.05$). N = numbers of visits per foraging site. Note the difference with Figure 1, which shows the total time spent at each site when summing all visits together

FIGURE 7 Total N and total P content of *Larus fuscus* droppings in grey ($n = 10$) and pellets in white ($n = 10$) from Fuente de Piedra lake

FIGURE 8 Estimated loading (kg/ha) for (a) nitrogen and (b) phosphorus in Fuente de Piedra by *Larus fuscus* from faeces (light grey) and pellets (black) for each winter from 2010 to 2017

et al., 2016; Hahn et al., 2007, 2008) or correcting censuses for birds that were away from the roost site. When comparing nutrient loading estimations with and without use of movement data, we found an average increase of 47% when GPS data were used. This is mainly due to the effect of underestimating bird numbers when counting and suggests that gull impacts may have been underestimated in previous guanotrophy studies (e.g. Winton & River, 2017).

4.1 | Numbers of gull present

By using GPS movement data, we showed that approximately 69% of the birds were not present in FP during the times of day when counting was conducted. Unfortunately, we have no way of knowing if the error in counts varied seasonally or between years, but we cannot rule out this possibility (e.g. if the delay between sunrise and counting changed during the course of the winter), which in turn would influence our estimates of nutrient inputs. This underlines the importance of recording the timing of waterbird counts with precision.

The highest number of LBBGs was recorded in January. During the first half of the winter when numbers were relatively low at FP, LBBG concentrate in rice fields in the Doñana area 150 km to the west, to feed on alien crayfish, waste grain and other food during the harvest (Lovas-Kiss et al., 2018; Rendón et al., 2008). From November onwards, individuals disperse around Andalusia, using FP mainly during the second half of the winter. In January, FP holds 27% of the total number of LBBG counted in Andalusia (Junta de Andalucía data).

4.2 | Gull activity in FP

Gull tracking revealed that time spent at the roost site is not a fixed parameter but is instead subject to considerable variation in behaviour between individuals. More research is required to investigate why some birds stay at the lake longer than others, and how this relates to variation in the quality of roost sites. Clearly, increasing the number of tagged individuals is desirable, so that average values for time spent at FP are more reliable, and to throw further light on how and why different individuals contribute unequally to guanotrophication.

According to movement data, gulls also increased the number of hours a day they spent at FP in more recent winters, with the greatest proportion of time spent during the winter of 2016-2017. This trend may be partially driven by changes in the water level since levels were lower in recent winters. The time spent at the roost site was highest when water levels within the lake were around 30 cm.

4.3 | Gull activity at foraging sites

Our study reveals a massive translocation of nutrients from landfills to a natural, protected lake by roosting gulls (see Winton & River, 2017 for similar examples in North America). Gulls spent most time at the Matagrande and Montalbán landfills (both in terms of total time and time per visit) at an intermediate distance. Despite the much greater distance from FP to the Córdoba landfill, the time spent there per visit was as high as at the Matagrande and Montalbán landfills, although the total number of visits was lower. In contrast, gulls visited the closest landfill at Antequera more frequently but spent less time there per visit. Hence, distance seems to play a role in determining the number of visits to each foraging site, and LBBG compensates for travel costs to a more distant foraging site by spending more time there (see also Arizaga et al., 2010). Movement data also

show that individual LBBG frequently switched between the four foraging sites within and between winters (results not shown), probably in relation to changes in the quantity of food available (Arizaga et al., 2014).

Variation in management procedures and protocols may determine the quantity and quality of food at each landfill, but new national directives concerning refuse management may change gull behaviour in the future. A new National Framework Waste Management Plan (Boletín Oficial del Estado, 2015), based on the Landfill Management Directive, was approved in 2015 for the period from 2016 to 2022. This directive requires the gradual reduction of biodegradable waste to 35% in 2016, with a further reduction of 35% in 2020, as well as measures to improve waste separation and recycling. Those initiatives are likely to reduce resources available to gulls. In combination with measures to deter gulls from foraging in key landfills (Castege, Milon, Lalanne, & d'Elbee, 2016), such measures could potentially reduce the number of gulls wintering at FP, and hence their guanotrophication effects.

4.4 | Quantification of nutrient loading

We found an increase of external nutrient loading by gulls in FP in more recent winters, related to an increase in both the proportion of time spent at the lake and the number of gulls wintering at the lake. Although our estimations are aided by precise information on gull movements, they also depend on other parameters that we did not directly measure. For example, our calculations assume a fixed defecation rate, while this may vary with diet (Dessborn et al., 2016). We used our own measures of the nutrient content of excreta, but our results were highly variable between samples. There were also high levels of variation within and between previous studies of N and P concentrations of excreta (Winton & River, 2017), and overall results are highly sensitive to the nutrient concentrations used in loading calculations. Previous gull studies reported average concentrations of 68.6 mg/g of N and 4.3 mg/g of P in faeces (i.e. 4.8 and 2.3 times higher than our mean value respectively; Winton & River, 2017). Hence our calculations may underestimate the true loading rates by gulls at FP. By contrast, pellet concentrations showed high P levels with much individual variation, and we included pellets in our loading calculations, unlike previous authors (Hahn et al., 2007; Winton & River, 2017). It is also noteworthy that studies of guanotrophy have not taken into account additional nutrient inputs from feathers (Williams & Berruti, 1971), which may be important (Figure S2).

4.5 | Relative importance of gull nutrient inputs compared to other nutrient sources

Expressed in hectares, the average nutrient inputs by the gulls in FP amount to 10.17 kg N ha⁻¹ year⁻¹ and 2.07 kg P ha⁻¹ year⁻¹ (Figure S3). Total nutrient load by flamingos at FP was estimated as 16.7 kg N ha⁻¹ year⁻¹ and 1.24 kg P ha⁻¹ year⁻¹, but these inputs are concentrated during the summer months when flamingos breed

(Batanero et al., 2017). Atmospheric inputs were estimated as 5.89 kg N ha⁻¹ year⁻¹ and 0.18 kg P ha⁻¹ year⁻¹ for the study region (Morales-Baquero, Pulido-Villena, & Reche, 2013). A stream associated with the water treatment plant in the nearby town reportedly discharges 1.05 kg N ha⁻¹ year⁻¹ and 0.28 kg P ha⁻¹ year⁻¹ (de-los-Ríos-Mérida et al., 2017). Flamingo inputs thus seem to be the main source of N in FP (Figure S3), but these estimates were made in the absence of movement data and inflated by an unrealistic assumption that flamingos deposit 100% of their excreta at the lake (Batanero et al., 2017). By contrast, according to our estimates, gull excreta is the most important external P source to FP (Figure S3).

Flamingos prefer deeper water and their numbers decline faster than gull numbers when water levels drop at the lake (Batanero et al., 2017). Gull guanotrophy effects are thus particularly likely at FP when winter water levels are low (e.g. winters 2014–2015, 2015–2016 and 2016–2017), since gull numbers remain high and nutrients further concentrate in the water column. We are not aware of estimates of N and P inputs to the lake from runoff from the relatively small watershed and from the aquifer, so the overall relative contribution of gulls to the nutrient budget remains unclear, but it is likely to be a major fraction of the overall budget.

4.6 | Ecosystem effects of guanotrophy

Gull populations have previously been shown to cause guanotrophication at roost sites, including drastic changes in ecosystem state such as a shift from clear water and high diversity into a turbid, low diversity state (Moss, 1994; Signa, Mazzola, Costa, & Vizzini, 2015). Since P input from excreta is more rapidly bioavailable than P from runoff, which is mainly bound to the sediment, it is more likely to trigger rapid effects on algal growth and chlorophyll content (Winton & River, 2017).

Transportation of external nutrients into FP is a concern for managers as it affects the biodiversity of the lake (de-los-Ríos-Mérida et al., 2017). Eutrophication is considered responsible for a loss of diversity of aquatic plants at FP since the 1990s (Junta de Andalucía, 2005). The recent proliferation of the filamentous alga *Ulva flexuosa* in the lake is one indication of eutrophication (Conde-Álvarez, Bañares-España, Nieto-Caldera, Flores-Moya, & Figueroa, 2012). Guanotrophication by gulls is likely to be one cause of these changes.

The biogeochemical effects of gull guano are probably strongly conditioned by the high salinity of the lake, which is likely to reduce methane production but increase phosphate release from the sediment (Camacho et al., 2017; Clavero, Fernandez, & Niell, 1990). The water column in FP holds higher concentrations of N than of P, but nutrient dynamics are highly dependent on hydrology (Batanero et al., 2017; García et al., 1997). Batanero et al. (2017) reported a TN:TP ratio of 49:1 (range 25–85) in the dry year 2011–2012 and 52:1 (range 30–93) in the wet year 2010–2011. Therefore, P appears to limit in the system based on the Redfield ratio 16:1 at which primary production is expected to switch from N-limitation to P-limitation (Redfield, 1958). On the other hand, P-rich guano from gulls and other waterbirds may contribute to microbial activity in the lake

(Batanero et al., 2017). Moreover, P and uric acid (N) in excreta tend to accumulate in the sediment, partly delaying eutrophication effects until those nutrients are released again due to disturbance or changes in water conditions (Dessborn et al., 2016).

Furthermore, reductions in water level in dry years and due to human activities (Rodríguez-Rodríguez et al., 2005) increase nutrient concentrations in the FP water column by three-fold (Batanero et al., 2017). Ongoing climate change in Andalusia acts in synergy with nutrient loading and water extraction to further enhance their impacts (Espinar, Díaz-Delgado, Bravo-Utrera, & Vila, 2015), and reductions in nutrient loading are required to ensure that Mediterranean wetlands such as FP maintain their resilience to climate change (Green et al., 2017).

4.7 | Future studies

For studies such as ours based on movement and count data, acquiring more data on spatial and temporal variation in nutrient concentrations in excreta and on defecation rates is likely to be the best way to further improve estimates of nutrient inputs. Future work should also consider the implications of carbon inputs by gulls to lakes and reservoirs, which may reduce methane emissions from landfills by substituting anaerobic decomposition for aerobic respiration (Winton & River, 2017). Further distinction between behaviours within trips, for example using accelerometry, would be useful to understand in more detail how birds are using different foraging habitats within their home range. Finally, integrating movement analysis also allows the identification of source areas for contaminants, plastics, pathogens, or alien species likely to be imported to lakes such as FP (Figure S4). Gulls using landfills may transport harmful bacteria such as *Salmonella* or *E. coli* including strains resistant to antibiotics (Ahlstrom et al., 2018; Dolejska, Bierošová, Kohoutova, Literak, & Čížek, 2009), as well as a range of contaminants (Belant, 1997).

5 | CONCLUSIONS

Population increases of opportunistic, omnivorous birds such as gulls can pose threats to freshwater ecosystems. Fuente de Piedra is a good example of how, even when strictly protected, inland lakes can be impacted by inputs of nutrients and other matter imported by birds from outside the watershed. Ultimately, this is a consequence of the dramatic changes in land use during the anthropocene, which are particularly well represented by landfills. Efforts are required to reduce nutrient inputs to freshwater ecosystems from gulls feeding at landfills, in line with the recommendations under the landfill directive (e.g. refuse reduction, and improved waste separation and recycling).

Interest in guanotrophication processes in inland waters is longstanding, but ongoing developments in tracking technology allow guanotrophy to be studied with greater precision. Advances in tracking methods and reductions in costs make it increasingly feasible to integrate studies of waterbird movements into studies of nutrient loading, and into management of freshwater habitats.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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