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ORIGINAL PAPER

Feather corticosterone and stable isotopes explain fledging and adult breeding success in a burrow-nesting seabird, the Yelkouan shearwater *Puffinus Yelkouan*

Martin Austad[1,2] · Benedetta Catitti[3] · Bettina Almasi[3] · Paco Bustamante[4] · Francesca Visalli[2] · Rita Matos[2] · Nicholas Barbara[2] · Benjamin Metzger[2] · Petra Quillfeldt[1]

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Abstract

Seabirds face a trade-off between offspring provisioning and foraging effort. The hormone corticosterone regulates energy balance, while stable isotopes are proxies for diet composition. Measurements of Mercury (Hg), corticosterone ($CORT_f$) and stable isotope values of C ($\delta^{13}C$) and N ($\delta^{15}N$), integrated during feather growth in Yelkouan shearwater (*Puffinus yelkouan*) nestlings, were used to understand whether chick provisioning explains fledging and adult breeding success. Chicks at colonies and fledglings that failed their first fledging attempt were sampled in three breeding seasons (2020–2022) on Malta (36.01° N, 14.35° E). Failed fledglings were found at sea unable to fly or on urban coasts, presumably attracted by light pollution. Adult shearwaters were GPS-tracked in multiple seasons (2012–2022). Differences in provisioning measures ($\delta^{15}N$, $\delta^{13}C$ and $CORT_f$) between failed fledglings and chicks at colonies, associations between provisioning and adult breeding success, and adult foraging strategies were investigated. Shearwater nestlings showed a response to variations in diet, by which $CORT_f$ was inversely related to $\delta^{15}N$ and $\delta^{13}C$. Hg load was larger at higher trophic position, while there was no evidence for $CORT_f$ suppression by Hg. Failed fledglings had disproportionally higher $CORT_f$, indicating that rearing conditions affect fledging success. Adult breeding success was related to provisioning in nestlings, while adult shearwaters at the colony with higher breeding success made shorter foraging trips. Findings suggest that several chicks experience sub-optimal provisioning, with negative implications on fledging and grounding risk during light pollution attraction. Foraging conditions affect adult breeding success, specifying that seabird conservation at colonies needs complementary marine restoration.

Keywords Foraging ecology · Mercury · Nutritional stress · Light pollution · Conservation physiology

Introduction

Effective conservation of threatened species requires monitorable parameters sensitive to the measures implemented (Wikelski and Cooke 2006; Frederiksen et al. 2014). For example, estimating breeding success can explain whether predator control is having the desired effect in populations where invasive alien species predate nests (Pascal et al. 2008; Oppel et al. 2022), and whether efforts aimed at restoring food webs have increased food availability where this has been restricting offspring provisioning (Sydeman et al. 2021). Disentangling the effects of multiple pressures is especially important for seabirds as they forage at sea but nest on land, thus facing both marine and terrestrial threats (Dias et al. 2019). A major terrestrial threat to

Responsible Editor: V. Paiva.

✉ Martin Austad
martinaustad93@gmail.com;
martin.austad@bio.uni-giessen.de

1 Justus-Liebig University Giessen, Heinrich-Buff-Ring 26, 35392 Giessen, Germany

2 BirdLife Malta, Abate Rigord Street 28, XBX 1120 Ta' Xbiex, Malta

3 Swiss Ornithological Institute, Seerose 1, Sempach 6204, Switzerland

4 Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS-Université de la Rochelle, 2 rue Olympe de Gouges, La Rochelle 17000, France

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seabirds is invasive alien species introduced to islands, but nest and adult predation can be alleviated through predator eradication or control (Phillips et al. 2022). Another threat particularly affecting burrow-nesting species and demanding increasing rescue campaign effort, is the grounding of fledglings attributed to light pollution, by which young seabirds land in urban areas away from water, instead of flying out to sea (Raine et al. 2020; Rodríguez et al. 2022). At sea, food available to seabirds is affected by competition between seabirds and fisheries and the threat still calls for large scale harvest management (Grémillet et al. 2018). The marine prey, trophic position and foraging areas determine pollutant load such as mercury (Hg), which in turn has also been shown to contribute to lower breeding success (Goutte et al. 2014), linked for example to higher egg neglect (Tartu et al. 2015).

Seabird breeding success is reduced in response to low food availability, small prey size and low energetic content (Wanless et al. 2005; Paiva et al. 2013; Fayet et al. 2021). However, the effect of food supply on breeding success is sometimes only registered when prey density falls below critical thresholds (Piatt et al. 2007; Quillfeldt et al. 2007). Predators, particularly generalists, can change to other, less-preferred prey species (Will et al. 2015; Romero et al. 2021), or increase foraging effort (Harding et al. 2007; Bertrand et al. 2012; Paiva et al. 2013). In such cases, behavioural adaptations may entail physiological costs, and measuring levels of corticosterone can give additional insights into the sublethal effects of resource availability (Kitaysky et al. 2001; Quillfeldt and Möstl 2003; Quillfeldt et al. 2010; Will et al. 2015; Lamb et al. 2016).

Corticosterone is the main glucocorticoid hormone in birds, primarily modulating energy balance (MacDougall-Shackleton et al. 2019), while elevated levels are involved in mediating perceived or actual stressors through physiological and behavioural means (Blas 2015; Romero and Fairhurst 2016). In addition to a relationship with feeding ecology (Fairhurst et al. 2014), corticosterone shows a response to social and environmental conditions (Fairhurst et al. 2012a; Catitti et al. 2022), while pollutants such as Hg can disrupt corticosterone secretion (Herring et al. 2012; Provencher et al. 2016). Circulating corticosterone is incorporated into growing feathers ($CORT_f$) (Jenni-Eiermann et al. 2015), as is Hg (Blévin et al. 2013). Likewise, during feather growth the stable isotope ratios of C ($^{13}C/^{12}C$, $\delta^{13}C$) and N ($^{15}N/^{14}N$, $\delta^{15}N$) are determined by the assimilated diet (Bearhop et al. 2002) and physiology (Sears et al. 2009). Specifically, $\delta^{13}C$ indicates foraging habitat (e.g. inshore vs. offshore, pelagic vs. benthic or demersal), while $\delta^{15}N$ indicates trophic position because it is enriched up the food chain and predominantly feeding on prey with higher $\delta^{15}N$ increases $\delta^{15}N$ values in the predator (Hobson et al. 1994). Therefore, $\delta^{15}N$ values are taken as an indication of relative diet quality (Pollet et al. 2014), with for example higher $\delta^{15}N$ indicating a large proportion of fish compared to zooplankton in the diet (Péron et al. 2013). In seabirds, $\delta^{15}N$ values are also affected by provisioning quantity, with lower $\delta^{15}N$ values following smaller meal size (Williams et al. 2007), but these differences are not necessarily detectable in feathers (Sears et al. 2009). Feather keratin is metabolically inert after synthesis, and therefore the $CORT_f$ and stable isotope values give an integrated measure of the physiological response to provisioning and pollutant load on the same time scale (Fairhurst et al. 2014). Feathers that are grown in the nest before fledging give retrospective measures of parental provisioning during the rearing period (Will et al. 2015; Romero and Fairhurst 2016).

Long lived birds are expected to prioritise self-maintenance over the current breeding attempt (Williams 1966), meaning nestlings often experience the most apparent effects of poor foraging conditions (Quillfeldt and Möstl 2003; Séchaud et al. 2022; Whitehead et al. 2022). However, monitoring chicks of cliff nesting seabirds in deep burrows is limited by difficult access and number of nests visible to human observers, leading to small nest sample sizes, few visits and uncertainty on nest outcome (see also Rodríguez et al. 2022). Adult breeding success in several burrow nesting seabirds in the order Procellariiformes, is in practice an estimate of nest success, but not whether chicks successfully leave the colony on their first flight out to sea, which they do in the absence of parental influence following a desertion period (Brooke 1986). Particularly high mortality takes place within days of seabirds fledging from the colony, highlighting the need for understanding this life stage better (Rodríguez et al. 2017a, b; Afán et al. 2019; Weimerskirch et al. 2019). Estimating successful fledging is uncertain when using capture-mark-recapture models because in long lived species individuals might take several years to return to the colonies (Jenouvrier et al. 2008), although such studies can reveal long-term relationships between survival and fledging body mass (Swanson et al. 2023). Tracking fledglings can be expensive and biased towards a small sample of the fittest individuals (Afán et al. 2019; Raine et al. 2020). Establishing retrospective measures of parental provisioning is a potential method to understand causes of fledging failure.

This study investigates chick-rearing provisioning measured with $\delta^{13}C$, $\delta^{15}N$, $CORT_f$ and Hg in feathers of Yelkouan shearwater *Puffinus yelkouan* (henceforth shearwater) chicks, and the effect on their fledging success by comparing chicks sampled at the colonies prior to fledging and those rescued at sea and urban areas (failed fledging). Shearwater fledglings rescued at sea were too weak to fly or their feathers lacked the necessary waterproofing rendering

them waterlogged, while fledglings found on land in urban settings were likely attracted by light pollution, a process that might not be affected by their condition (Rodríguez et al. 2017b; Weimerskirch et al. 2019). The $\delta^{13}C$, $\delta^{15}N$ and $CORT_f$ measures in chicks are then used to test for effect of rearing conditions on adult breeding success at the colony level to disentangle between provisioning effects and external effects (f.eg. nest predation) on nest success. Finally, to investigate possible mechanisms underlying differences between colonies in chick provisioning, adult foraging strategies measured as trip metrics and foraging area overlap are compared between the two main colonies. Four main hypotheses are defined in the study:

1. Nestlings' and fledglings' $CORT_f$ and Hg are related to stable isotope values. An inverse relationship between $CORT_f$ and $\delta^{15}N$ and a positive relationship between Hg and $\delta^{15}N$ are expected since higher $\delta^{15}N$ reflects provisioning at higher trophic positions.
2. Fledging success is dependent on rearing conditions. Since there are potentially different mechanisms causing fledging to fail (Rodríguez et al. 2017b), shearwater fledglings rescued at sea are expected to have proportionally higher $CORT_f$ and lower $\delta^{15}N$ (i.e. poor rearing conditions), but shearwaters rescued from urban areas are not expected to have significantly different values to fledglings at colonies (i.e. light pollution effect is stronger than rearing conditions).
3. Poor rearing conditions are reflected in adult breeding success at the colony level. We expect higher nestling $CORT_f$ and lower $\delta^{15}N$ to be associated with lower breeding success.
4. Differences in foraging strategies are present between colonies with divergent breeding success, with longer foraging trips at the colony with lower breeding success.

Materials and methods

Study species and site

The study species is a burrow-nesting seabird with nocturnal colony attendance and nesting in deep caves and cliffs. It is a generalist marine predator with a wide trophic niche and diversity of marine prey consumed (Péron et al. 2013; Austad et al. 2025). A single egg is incubated for around 50 days and the nest-bound chick is fed by both parents for around 60–80 days. All four colonies monitored in this study (Fig. 1), Rdum tal-Madonna (RM), Ċumnija & Majjistral (MJ), Comino & Cominotto (CM) and St Paul's Islands (SP), are subject to annual seasonal rodent control resulting in improved shearwater breeding success, since 2007 for RM and since 2018 for the other three colonies (Lago et al. 2019). Control at all colonies is aimed at the black rat *Rattus rattus* and carried out using second-generation anticoagulant rodenticide baiting during the shearwater nesting season as described by Lago et al. (2019) and complimented by mechanical auto-resetting GoodNature A24 traps (GoodNature Ltd. Wellington, NZ). Control differs from eradication in that it aims to suppress the population of invasive alien species at sites where eradicating whole populations

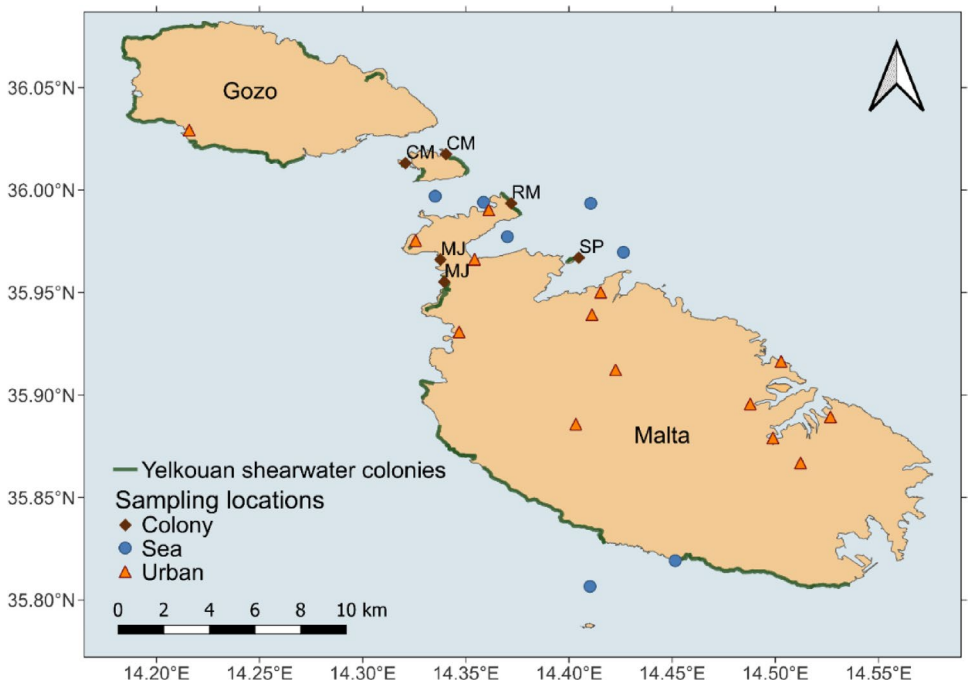

Fig. 1 Map of Yelkouan shearwater colonies in the Maltese Islands (dark green lines). Adult breeding success and feathers from chicks were sampled at four colonies (brown diamond markers; Rdum tal-Madonna – RM; Ċumnija & Majjistral – MJ; Comino & Cominotto – CM and St Paul's Islands – SP). Fledglings were rescued on failed fledging by members of the public across various locations, both at 'sea' (blue circle markers) or grounded in 'urban' light polluted areas (orange triangle markers)

is not practicable, resulting in similar benefits at local scales but requiring repeated efforts while not excluding predation risk entirely (Pascal et al. 2008; Lago et al. 2019). All four colonies are within 10 km of each other on the Maltese Islands (36.01° N, 14.35° E: Fig. 1), of which RM and MJ are the largest in terms of population size (Gatt et al. 2019; Lago et al. 2019).

Feather collection

We plucked entire undertail covert feathers from chicks still in the nest as well as chicks training their wings outside their burrows at four colonies during three breeding seasons (2020 $N=54$ [inside nest = 18, outside burrows = 36]; 2021 $N=43$ [28, 15]; 2022: $N=42$ [24, 18]). We also collected feathers from fledglings found at sea or on land in urban areas away from the nesting sites by members of the public who contacted BirdLife Malta (Figs. 1 and 2020: $N=7$; 2021: $N=15$; 2022: $N=8$). Six of these, and all being birds found at sea, were either dead or died shortly after collection, while all other birds were subsequently released. We weighed birds with a spring balance (±10 g) and measured tarsus and wing length (mm; Fig. S1), but do not use these measurements further in the current study, since we were not able to determine age and time after failed fledging, which is spent fasting (Rodríguez et al. 2017b).

To determine the age at which undertail feathers are grown, we benefited from a nestbox programme to measure nestlings ($N=10$) from hatching to fledging on a regular basis. We determined the undertail covert feather growth to occur between 25 and 72 days of age (mean ± SD = 47 ± 11 days), which corresponds to the period with most rapid wing length growth (Fig. S2).

Adult breeding success estimation

Apparent adult breeding success was estimated during the seasons 2020, 2021 and 2022 on a sample of nests through at least three checks per season, during incubation, early and late chick-rearing, respectively. Success was estimated from the number of nests occupied by incubating adults, as the percentage of nests with a chick reaching at least four weeks of age or finding a nest empty at the expected age of fledging. In the latter case nests were only marked successful if they contained shed down indicating that the nest had been occupied by a nestling that reached fledging age. To reduce bias from unequal visit frequency (Mayfield 1975), we estimated daily survival rates (DSR) at the colony level using the R package 'RMark' (Laake 2013) with colony and year as covariates. We use DSR as an indicator of adult breeding success.

Tracking adult shearwaters during foraging trips

Annual consistency in foraging areas by chick-rearing seabirds tends to be high (Beal et al. 2023) and we use tracking data collected within a decade to test differences in foraging trips by adult shearwaters from RM and MJ colonies. We obtained foraging tracks during the chick-rearing period from GPS-loggers on 21 shearwaters at MJ and 25 at RM in 2012–2014 (unpackaged CatLog Gen2 [Catnip Technologies, Anderson, USA] and i-gotU GT-120 [Mobile Action Technology, New Taipei City, Taiwan], ~14 g) (Gatt et al. 2019), on two shearwaters at RM in 2019 (Nanofix® GEO + RF [Pathtrack Ltd, Otley, UK], 5 g) and on six shearwaters at MJ and 13 at RM in 2021–2022 (Pinpoint-75 [Lotek Wireless Inc., Newmarket, Canada], 4.5 g and AxyTrek [Technosmart Europe srl, Rome, Italy], 8 g). GPS-fix frequencies varied between two to 60 min, and were interpolated to a constant interval of 30 min using the 'redisltraj' function in 'adehabitatLT' R package (Calenge 2006).

Corticosterone measurement in feathers

To measure CORT deposited in the feather during growth and to exclude any CORT circulating in the blood during sampling, the vascularised section of the calamus was cut off (Bortolotti et al. 2008). The remaining length of the feather was measured to the nearest mm, flat against a ruler (mean ± SD = 59.5 ± 6.9 mm). We extracted CORT from single feathers using 1.5 ml methanol, after milling each feather to a fine powder inside 2 ml centrifuge tubes with ~30 grinding metal balls at 30 Hz for 6 min in a mill (RETSCH MM400, Retsch GmbH, Haan, Germany). The feather powder and methanol were incubated for 10 h at 50 °C in a water bath (Bortolotti et al. 2008), after which 1 ml was pipetted to a clean tube and the methanol was evaporated with nitrogen gas at 50 °C (Catitti et al. 2022). The mean ± SD proportion of methanol extracted was 0.66 ± 0.04. Corticosterone was then resuspended in assay buffer and measured in duplicate using in a corticosterone ELISA kit (ADI-901-097, Enzo Life Sciences Inc., New York, USA). The assay cross reactivity for this kit is high with corticosterone (100%) but low with related steroids (e.g. progesterone: 1.7%; cortisol: 0.046%), and we did not use a steroid displacement reagent. A microplate reader measured the resulting colour in each well. When duplicates had a coefficient of variance in net optical density larger than 10%, or when values were on the limit of the standard curve prepared on the same plate, we did not retain the reading for further analysis. We excluded 58 readings for these reasons, but for 32 individuals with sufficient feather material and a failed first reading, we repeated corticosterone extraction. Readings were obtained from 11 plates, where samples from different sites were distributed

across plates (Fig. S3). Two feather pools from shearwater feathers (2020–2021 and 2022 samples) were used as internal controls intra-assay variation was 9.8% ($N=11$) and inter-assay variation was 39% ($N=8$) and 18% ($N=3$) respectively. To report concentration in relation to feather length (pg mm^{-1}) (Jenni-Eiermann et al. 2015), the concentration of CORT per feather was calculated as follows:

$$Concentration/\left(\left(\frac{Feather\ length * proportion\ methanol\ extracted}{assay\ buffer\ volume}\right) * volume\ in\ each\ well\right)$$

where volume in each well was 100 µl.

Bulk stable isotope analysis

To obtain an understanding of provisioning trophic ecology during the rearing period, we analysed bulk stable isotope ratios of N and C. The feathers used for stable isotope and for $CORT_f$ measurements were different but were from the same part of the body and grown simultaneously. We packaged between 0.33 and 0.57 mg of feather vane material in tin-cups. Stable isotope measurements were obtained with a Thermo Scientific Delta V Plus mass spectrometer (Thermo Scientific, Bremen, Germany) coupled to a Thermo Scientific elemental analyser (Thermo Scientific, Milan, Italy) at the LIENSs Stable Isotope Facility. Results are expressed in the δ unit notation as deviations from N_2 in air for $\delta^{15}N$ and Vienna Pee Dee Belemnite for $\delta^{13}C$, following the formula:

$$\delta\,^{15}N\ or\ \delta\,^{13}C = [(R_{sample}/R_{standard}) - 1]\ x\ 10^3$$

where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. Internal laboratory standards USGS-61 (Caffeine) and USGS-63 (Caffeine) were used to check accuracy. The analytical precision was <0.15‰ for both $\delta^{15}N$ or $\delta^{13}C$.

Mercury analysis

Analysis of total Hg (THg) includes both inorganic and organic Hg, the latter being mainly methyl-Hg (MeHg). In feathers, more than 90% of THg is in the form of MeHg (Renedo et al. 2017). THg (hereafter Hg) was used as an indicator of MeHg in the shearwater feathers. Measurements of Hg were made for the feathers collected in 2022 ($N=50$), on aliquots of finely cut feathers ranging from 0.45 to 0.96 mg and analysed in duplicates per sample using an Advanced Mercury Analyzer spectrophotometer (Altec AMA 254, Altec, Prague, Czech Republic). Accuracy was checked using a Certified Reference Material, Tort-3 Lobster Hepatopancreas (NRC, Canada), leading to a recovery rate of 98.9±0.5% ($N=6$). Hg concentrations are presented as the average of the duplicate reads in µg g^{-1} dry weight (dw). The variation between duplicates±SD was 2.03±1.69%. Blanks were analysed at the beginning of each set of samples and the detection limit of the analyser was 0.1 ng.

Statistics

All analyses and graphical representations were performed in R v4.0.5–4.4.2 (R Core Team 2021). Generalised linear mixed models (GLMMs) were fit in 'glmmTMB' package (Brooks et al. 2017), while residual diagnostics were checked with the 'DHARMa' package (Hartig 2022). To improve normality, we log-transformed $CORT_f$ response variable in all models.

We first correlated $\delta^{15}N$ with $\delta^{13}C$ in an GLMM, including year as a random effect. In a second GLMM we tested for the effect of $\delta^{15}N$ and $\delta^{13}C$ on $CORT_f$. Using a GLM, since no random effects were applicable, we tested for the effect of $\delta^{15}N$ and $\delta^{13}C$ on Hg. We then tested for the effect of Hg and stable isotopes on $CORT_f$ using a GLMM. In addition to the models testing the relationship between these measurements, we repeated each model with 'Site' as a predictor variable, where the four colonies (RM, MJ, SP, CM) and the two rescue location types (Sea, Urban) were each factor levels. We conducted pairwise post-hoc comparisons between sites using the package 'emmeans' (Lenth 2025). In all models with $CORT_f$, we included a categorical predictor variable for whether feather growth was complete, because some nestlings (N=33) were sampled before sampled feathers were fully grown and changes in CORT levels might occur with age (Quillfeldt et al. 2010). $CORT_f$ models also include a random effect for PlateID (N=11) to account for inter-assay variation.

To address the question on whether fledging success is dependent on rearing conditions we test for proportionally lower $\delta^{15}N$ and higher $CORT_f$ in failed fledglings compared to chicks outside their nests ready to fledge from the colonies, using GLMMs and post-hoc pairwise tests. While excluding nestlings, we grouped all chicks sampled prior to fledging at the colonies, and kept fledglings found at sea and in urban areas separate (Fig. 1), leading to a three-level factor. In the GLMM with $\delta^{15}N$ as a dependent variable, we additionally included $\delta^{13}C$ as a predictor variable and year as a random effect, and in the GLMM with $CORT_f$ as the dependent variable we included year and plate ID as random effects.

To test for differences in breeding success at the colony level and effect of rearing conditions, we scaled the DSR estimate for improved normality and first tested for colony differences in a GLMM with colony as the predictor variable and year as a random effect. We then separately tested for the effect of mean $CORT_f$, mean $\delta^{15}N$ and mean $\delta^{13}C$

per colony and year as predictor variables, while colony and year were random effects. The latter model had 10 data points because we did not have stable isotope and $CORT_f$ measurements for SP in 2020 and only two measurements from SP in 2022 (Table S1).

Tracking data analysis

Kernel density estimation and trip summaries were analysed for the two colonies with tracking data (RM, MJ), using the R package 'track2KBA' (Beal et al. 2021). First, these analyses were performed for all years together (2012–2022), and then repeated for 2021 alone. 2021 was the only year with feather sampling and tracking data at both MJ and RM concurrently.

Utilisation distribution (UD) was estimated using kernel density estimation in the R package 'track2KBA' at 50% for each individual track to identify core foraging areas (Beal et al. 2021). Prior to UD estimation, we removed points within 10 km of the colonies to eliminate bias towards non-foraging behaviour such as rafting (Richards et al. 2019). To find a suitable smoothing parameter for the kernel density estimation, we used first passage time analysis in the 'findScale' function to identify the scale at which shearwaters perform area-restricted search whilst foraging (Beal et al. 2021). We used the mean of the values obtained for MJ (13) and RM (6) as the smoothing parameter (9.5), to make sure that any differences in foraging areas is not an artifact of different smoothing parameters. To estimate how representative the sample of tracked shearwaters was per colony we used the function 'repAssess', which over multiple iterations measures the overlap between a sub-sample of core areas and tracks of individuals not included in the sub-sample (Beal et al. 2021). The foraging area shared by shearwaters from the two colonies was calculated using the following formula (Ravache et al. 2020):

$$\%\, Shared\ Area = [A0] \div [(AColony1 - A0) + (AColony2 - A0) + A0]$$

Where A0 is the area of 50% UD intersection between colonies, and AColony is the area of the 50% UD per colony, calculated with the R package 'sf' (Pebesma 2018).

Trip summaries only considered complete trips. Difference in trip duration (hr), total distance travelled (km), maximum distance travelled from colony (km) and mean speed (total distance divided by duration) per colony was tested for using separate GLMMs in 'glmmTMB' (Brooks et al. 2017), with individual and year as random effects. All trip metrics were log transformed. Only four tracked adults were parents to sampled nestlings, and we do not carry out direct analysis to link specific foraging areas with measured values in nestlings. Maps were produced using QGIS, in EPSG 4326 WGS 84.

Results

Relationships between stable isotopes, $CORT_f$, Hg and site

The range of $\delta^{15}N$ in shearwater feathers was wider than the range of $\delta^{13}C$ ($\delta^{15}N$: 7.24 to 11.45‰, mean ± SD = 10.373 ± 0.622‰ and $\delta^{13}C$: −19.48 to −16.86‰, mean ± SD = −18.460 ± 0.470‰, N = 145). On removing three data points that were violating the outlier test, we found a strong positive effect of $\delta^{13}C$ on $\delta^{15}N$ (GLMM parameter estimate ± SE = 0.468 ± 0.085, P = < 0.001, residual *d.f.* = 138; Table S2). When including 'Site' as predictor to the model, it was evident that chicks at RM had higher $\delta^{15}N$ than at MJ (Tukey post hoc estimate ± SE = 0.470 ± 0.113, P < 0.001, residual *d.f.* = 133) and higher than grounded fledglings (Tukey post hoc estimate ± SE = 0.373 ± 0.114, P = 0.017, residual *d.f.* = 133, Fig. 2).

We found moderate evidence for higher $CORT_f$ in response to both lower $\delta^{15}N$ (GLMM parameter estimate ± SE = −0.127 ± 0.050, P = 0.012; Fig. 3) and $\delta^{13}C$ (GLMM parameter estimate ± SE = −0.147 ± 0.066, P = 0.026; Fig. 3), with no effect of feather growth completeness (GLMM parameter estimate ± SE = −0.076 ± 0.076, P = 0.322) within the same model (residual *d.f.* = 116; Table S2). In the model including 'Site' as a predictor variable, fledglings found at sea had higher $CORT_f$ than chicks at all other sites (GLMM parameter estimate ± SE = 0.761 ± 0.163, P < 0.001, residual *d.f.* = 111; Fig. 3; Table S2), confirmed with post hoc tests between all respective pairs. The moderate evidence for an inverse relationship between $CORT_f$ and $\delta^{15}N$ was maintained in the 'Site' model (GLMM parameter estimate ± SE = −0.134 ± 0.066, P = 0.043, residual *d.f.* = 111; Table S2).

Mean Hg ± SD was 1.301 ± 0.529 μg g^{-1} and we found strong evidence that Hg increased with higher $\delta^{15}N$ (GLMM parameter estimate ± SE = 0.429 ± 0.133, P = 0.002) and $\delta^{13}C$ (GLMM parameter estimate ± SE = 0.487 ± 0.134, P = 0.001), within the same model (residual *d.f.* = 47; Table S2). None of the pairwise comparisons between sites were significant (residual *d.f.* = 42, Fig. 4). We found no evidence of a relationship between Hg and $CORT_f$ (GLMM parameter estimate ± SE = −0.063 ± 0.117, P = 0.594, residual *d.f.* = 39; Table S2).

Effect of chick provisioning on fledging success

We found weak evidence that fledglings grounded in urban areas had proportionally different $\delta^{15}N$ to chicks

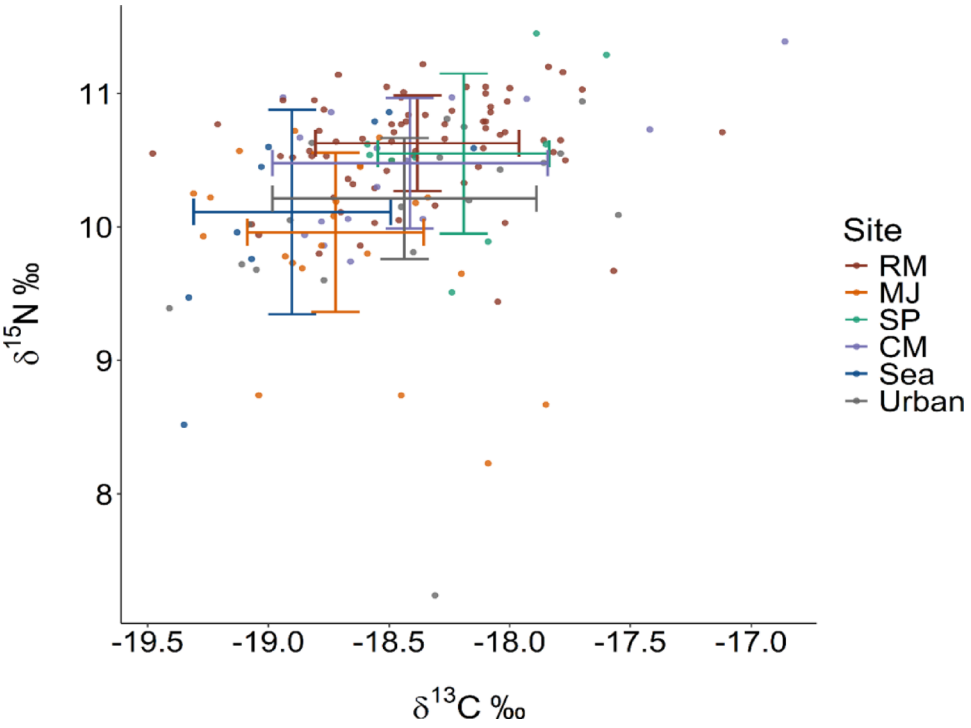

Fig. 2 $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) in Yelkouan shearwater nestling and fledgling feathers sampled in three breeding seasons (2020–2022), and error bars (mean ± standard deviation) per site where RM, CM, SP and MJ are colonies and 'Sea' and 'Urban' are fledglings rescued on failed fledgling either at sea or grounded in urban areas

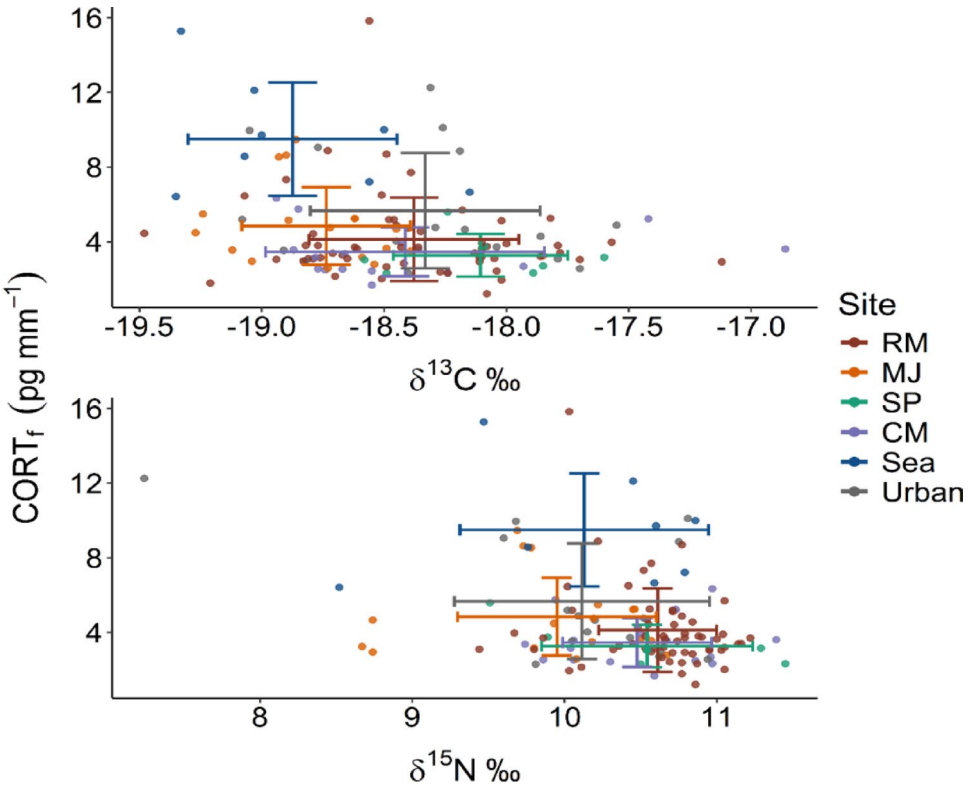

Fig. 3 Feather corticosterone ($CORT_f$ pg mm^{-1}) against $\delta^{13}C$ (‰) $\delta^{15}N$ (‰) in Yelkouan shearwater nestling and fledgling feathers sampled in three breeding seasons (2020–2022). Error bars (mean ± standard deviation) are presented per site where RM, CM, SP and MJ are colonies and 'Sea' and 'Urban' are fledglings rescued on failed fledgling either at sea or grounded in urban areas

in the colonies (Tukey post hoc estimate ± SE for Colony – Urban = 0.262 ± 0.113, $P = 0.059$, residual *d.f.* = 73) and no difference in fledglings rescued at sea (Tukey post hoc estimate ± SE for Colony – Sea = 0.053 ± 0.166, $P = 0.946$, residual *d.f.* = 73; Fig. 5; Table S2). However, we found strong evidence that fledglings rescued at sea had higher $CORT_f$ (Tukey post hoc estimate ± SE for Colony – Sea = −0.905 ± 0.169, $P < 0.001$, residual *d.f.* = 75), as did the ones grounded in urban areas (Tukey post hoc estimate ± SE for

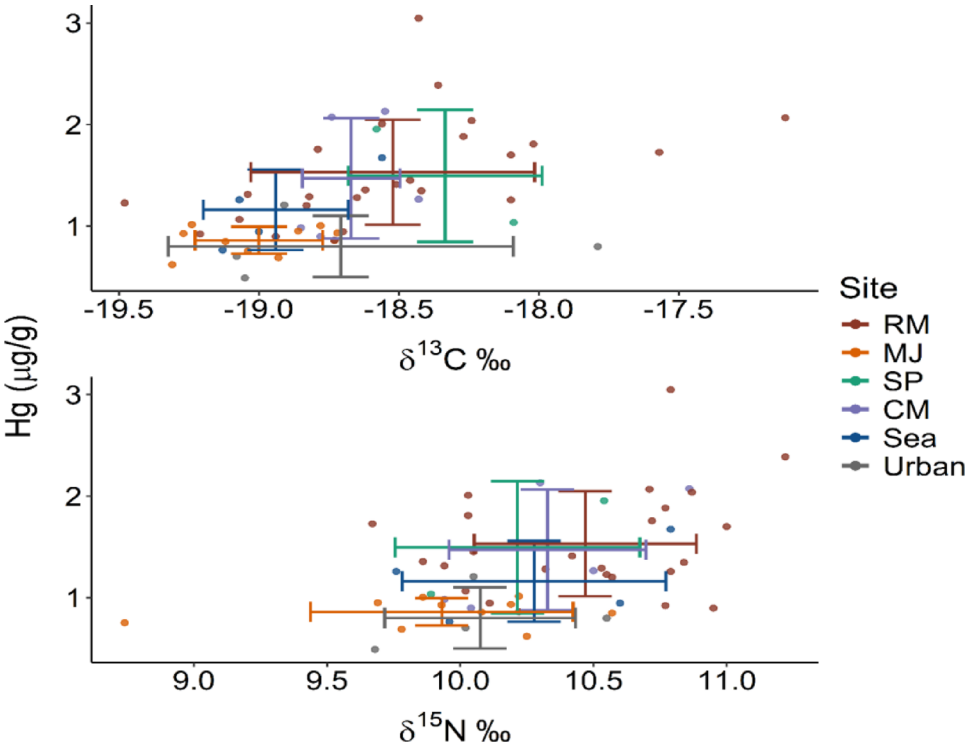

Fig. 4 Hg (µg g^{-1} dry weight) against $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) in Yelkouan shearwater nestling and fledgling feathers collected in one breeding season (2022). Error bars (mean ± standard deviation) are presented per site where RM, CM, SP and MJ are colonies and 'Sea' and 'Urban' are fledglings rescued on failed fledgling either at sea or grounded in urban areas

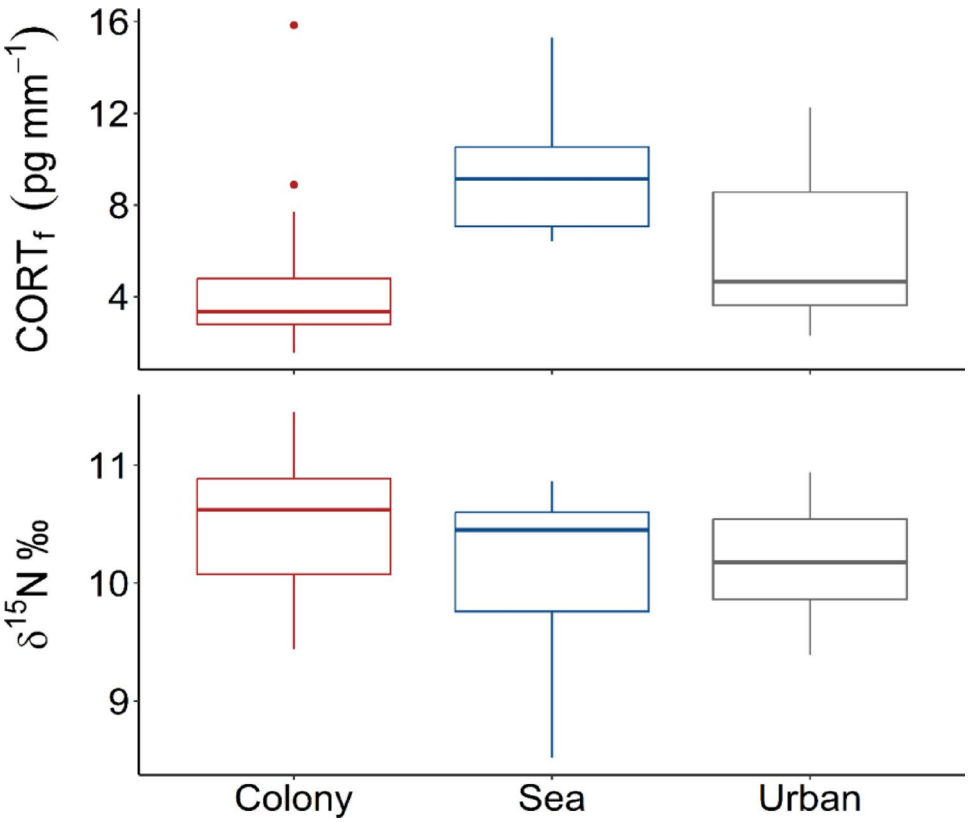

Fig. 5 Feather corticosterone ($CORT_f$ pg mm^{-1}) and stable isotope values of nitrogen ($\delta^{15}N$ ‰) in Yelkouan shearwater chicks ready to fledge from colonies ($N = 53$), compared to fledglings with failed fledging, which were either found at sea unable to fly ($N = 9$) or grounded in urban areas ($N = 19$). $\delta^{15}N$ and $CORT_f$ were measured in three breeding seasons (2020–2022). The central mid-line in each boxplot corresponds to the median, the lower and upper horizontal lines to the first and third quartiles and the vertical whiskers extend to the values at 1.5 of the inter-quartile range

Colony – Urban = −0.351 ± 0.117, P = 0.010, residual *d.f.* = 75; Fig. 5; Table S2), compared to chicks in the colonies.

Adult breeding success at colonies

Apparent adult breeding success ranged from 31% to 87% and varied between colonies and years (Table S3). MJ had lower DSR estimates than all the other colonies (Tukey post hoc estimates ± SE for: RM – MJ = 1.552 ± 0.145, P < 0.001, residual *d.f.* = 6; MJ – SP = −1.628 ± 0.145, P < 0.001, residual *d.f.* = 6; MJ – CM = −0.823 ± 0.145, P = 0.005, residual *d.f.* = 6; Fig. S4), while RM had also higher DSR than CM (Tukey post hoc test estimate ± SE for RM – CM = 0.728 ± 0.145, P = 0.009, residual *d.f.* = 6), but not higher than SP (Tukey post hoc test estimate ± SE for RM – SP = −0.076 ± 0.145, P = 0.951, residual *d.f.* = 6). We found evidence that provisioning conditions affect breeding success at the colony level. Mean $CORT_f$ had an inverse relationship with DSR (GLMM parameter estimate ± SE = −0.319 ± 0.078, P < 0.001, residual *d.f.* = 5, Fig. 6; Table S2), while $\delta^{15}N$ had a positive relationship with DSR (GLMM parameter estimate ± SE = 1.012 ± 0.129, P < 0.001, residual *d.f.* = 5; Fig. 6; Table S2).

Differences in foraging ecology

We obtained 146 trips by 67 individual shearwaters during the chick-rearing periods of 2012–2014, 2019, 2021–2022 (MJ = 42 trips, 27 individuals; RM = 104 trips, 40 individuals). Representativeness of tracked shearwaters per colony was high, calculated at 84.7% for MJ and at 90.4% for RM, showing that with the sample size of tracked individuals, we captured most of the variation in foraging areas used by the population. Overlap in area used by shearwaters from both colonies was estimated at 24.08% (Fig. 7).

After removing trips with missing outward or return portions, 122 trips (MJ = 35, RM = 87) of 53 individuals remained for calculation of trip metrics. Here we present means ± SD per colony, while parameter estimates for GLMMs are presented in Table S4. Shearwaters breeding at MJ made longer trips both in duration (MJ 73.5 ± 62.59 h, RM 50.94 ± 61.32 h) and distance (MJ 694.96 ± 483.03 km, RM 480.75 ± 479.25 km), travelled further away from the colony (MJ 237.93 ± 142.05 km, RM 158.99 ± 128.10 km), but were not faster (MJ 11.23 ± 4.47 km hr^{-1}, RM 11.36 ± 4.49 km hr^{-1}) than shearwaters at RM. Results from 2021 alone show the same differences in colony foraging strategies (Table S5, Fig. S5).

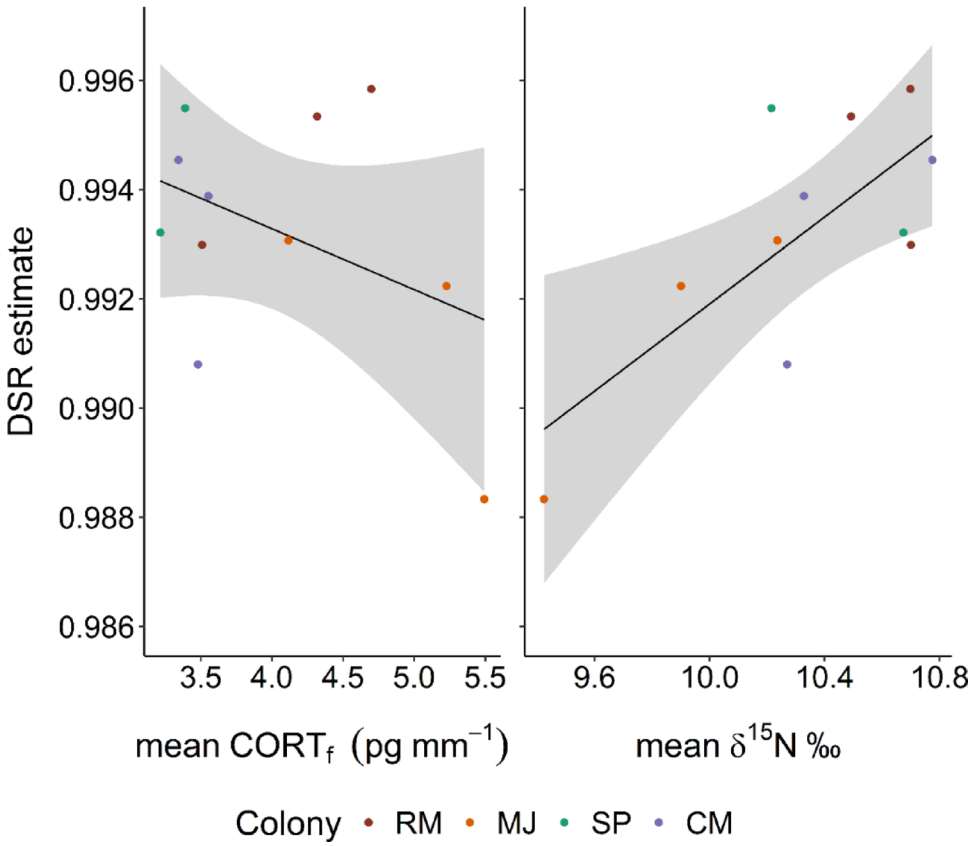

Fig. 6 Yelkouan shearwater daily nest survival rate estimates (DSR) per colony (RM, MJ, SP and CM) and year, as explained by mean feather corticosterone ($CORT_f$) and mean $\delta^{15}N$ in shearwater chicks in the respective colonies

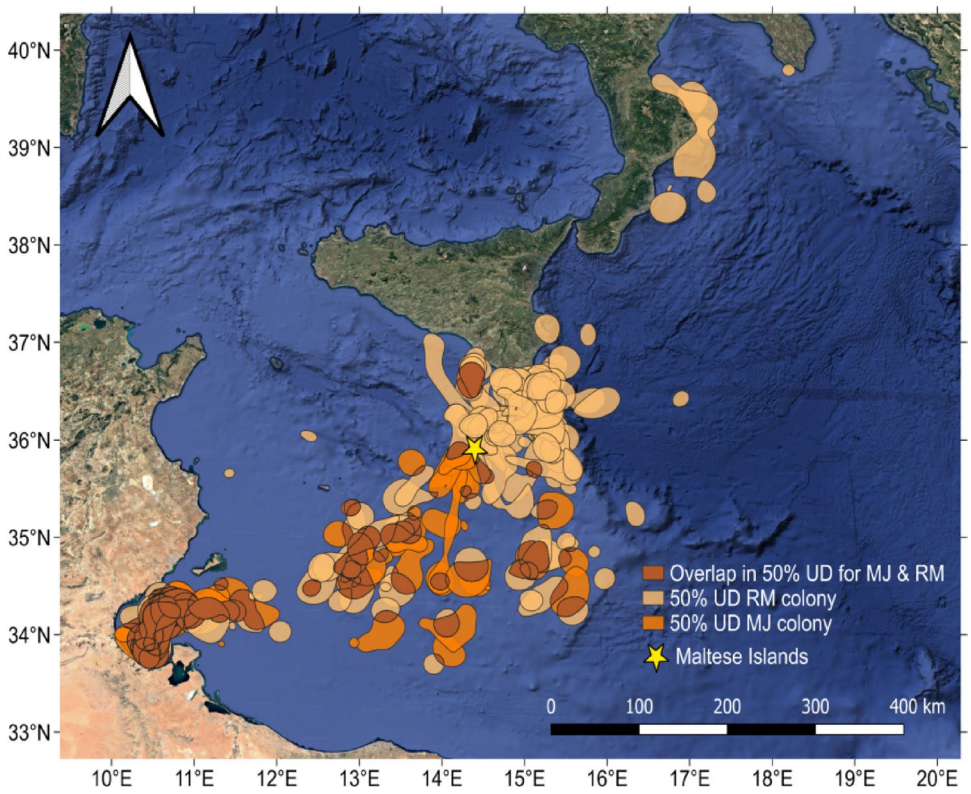

Fig. 7 Overlap in 50% utilisation distributions (UDs) of adult Yelkouan shearwaters from two colonies (RM, MJ) on Malta during the chick-rearing period, based on GPS-tracks from 2012–2014, 2019, 2021–2022. Study site is marked with a yellow star. Base map source: Google.com

Discussion

We retrospectively investigated natal conditions in shearwater nestlings using feathers grown during the nest-bound life stage prior to fledging. Trophic ecology influenced corticosterone levels in young shearwaters in inverse relationships between both $\delta^{15}N$ and $\delta^{13}C$ with $CORT_f$. Since higher $\delta^{15}N$ reflects foraging up the food chain and an indication of higher diet quality (Fairhurst et al. 2014; Pollet et al. 2014), but also larger provisioning quantity (Williams et al. 2007), the inverse relationship between $\delta^{15}N$ and $CORT_f$ indicates a response to sub-optimal provisioning during the chick-rearing period (Hypothesis 1). The inverse relationship also found between $\delta^{13}C$ and $CORT_f$ as well as the strong positive relationship between $\delta^{15}N$ and $\delta^{13}C$ indicates that spatial differences in foraging areas might affect provisioning quality (Hipfner et al. 2007). By combining $CORT_f$ and stable isotope values we show a physiological response, albeit a moderate one, to diet and food provisioning, the inverse relationship being an indication of nutritional stress in several of the shearwater chicks (Fairhurst et al. 2014; Will et al. 2015). We cannot exclude that $CORT_f$ was suppressed in some chicks to prevent detrimental effects of chronic elevated CORT (Kitaysky et al. 2001; Fairhurst et al. 2012b). Suppression processes are species specific and probably occur in phases dependent on severity and duration of food shortages, which require experimentally controlled setups to determine (Kitaysky et al. 2001, 2005). Additional factors might also induce changes in physiological response in seabirds, such as microclimate (Lamb et al. 2016), other pollutants (Tartu et al. 2015), social density (Herring et al. 2012) and ectoparasites (Kitaysky et al. 2001). In this study, we did not find support for Hg exposure affecting $CORT_f$.

As expected, Hg was positively correlated with $\delta^{15}N$ in young shearwaters (Hypothesis 1), due to biomagnification of Hg up trophic webs (Goutte et al. 2014; Binkowski et al. 2021). Concentrations of Hg found in the feathers of Maltese shearwaters were within the range found in studies on seabird chicks in general, but higher than in chicks from most sampled Procellariidae (Blévin et al. 2013). Hg concentrations measured in this study are unlikely to have strong adverse health effects (values within "no risk" and "low risk" categories according to Chastel et al. (2022). However, Hg might still have a negative effect on chick growth rate (Amélineau et al. 2019; Bertram et al. 2025) and breeding success (Goutte et al. 2014; Tartu et al. 2015). More years of Hg measurements, in both chicks and adults but also eggshells (Bertram et al. 2025), are needed to understand the effect of Hg on breeding success of the study species.

Furthermore, rearing conditions affect fledging success by which fledglings which failed the first fledging attempt particularly had higher $CORT_f$ (Hypothesis 2). Following predictions, young shearwaters that were rescued at sea had the highest $CORT_f$, higher than chicks in colonies and those

grounded in urban areas. However, $\delta^{15}N$ was not found to be different, which contradicts our predictions. In our study, we are unable to quantify the food deprivation nestlings experienced. However, protein catabolism likely occurred in chicks with poor or absent lipid reserves, a process which would have been induced by high corticosterone levels (Kitaysky et al. 2001). While lower $\delta^{15}N$ can be expected in chicks with moderate food restriction (Williams et al. 2007), in chronic food restriction resulting in protein catabolism, $\delta^{15}N$ is enriched, obscuring trophic level effects (Cherel et al. 2005; Hatch 2012). Therefore, we suggest that these shearwaters found at sea might have experienced the most extreme nutritional stress.

Contrary to our predictions, grounded fledglings in urban areas were found to have higher $CORT_f$ and lower $\delta^{15}N$ than the other chicks (Hypothesis 2). Disproportionally higher nutritional stress during the rearing period would not be expected in grounded fledglings if all fledglings were equally attracted by light pollution on their first flight and grounded irrespective of their fledging conditions. Therefore, our results indicate that grounding might be affected by other and so far, under-documented processes linked to rearing conditions (Brown et al. 2022). One of them might be the time young shearwaters are able to train their wings before first flight. Training wings outside burrows is thought to be crucial for successful fledging, and heavier and faster growing nestlings spent more time training (Yoda et al. 2017). Moreover, fledglings should reach optimal wing load for a successful first flight, but fledglings in poor condition and elevated CORT might leave before wings are completely grown (Sprague and Breuner 2010). Through tracking rescued fledglings, it has been shown that the probability of re-grounding by light pollution was higher if birds flew slower and in a circling fashion, but also if proportion of down plumage, an indication of pre-mature fledging, was higher (Rodríguez et al. 2022). Therefore, it is possible that poor provisioning leading to higher CORT triggers fledging prior to optimal flight efficiency being reached (Quillfeldt et al. 2010; Sprague and Breuner 2010). Early fledging would make young shearwaters more prone to collision or exhaustion during first flight, especially during light attraction at urban areas.

Some of the shearwaters in colonies had similarly high $CORT_f$ and low $\delta^{15}N$ values to those of fledglings that failed fledging (Fig. 5), and it is likely that a larger proportion of fledglings than those rescued failed their first flight from the colony. In fact, only a small proportion of grounded seabirds are thought to be found and rescued, especially for smaller species and in campaigns dependent on volunteers and public awareness (Rodríguez et al. 2017a; Brown et al. 2022). The higher proportion of fledglings potentially failing at first flight urgently calls on other conservation measures in addition to predator control and grounded shearwater rescue. Moreover, fledgling tracking studies (Raine et al. 2020) should additionally incorporate $CORT_f$ and stable isotope measurements to increase understanding of differences in fledging survival.

The measures of rearing conditions in nestlings also explain nest survival rates and indicate that differences in provisioning conditions contribute to the discrepancy in adult breeding success between colonies. As expected, higher $CORT_f$ and lower $\delta^{15}N$ in nestlings were associated with lower DSR (Hypothesis 3; Fig. 6). We measured provisioning retrospectively in nestlings with grown feathers but were unable to measure provisioning experienced by chicks that died before feather growth. Based on our results, we suggest that the same processes leading to nutritional stress in grown chicks might cause failure in nests at an earlier stage. The differences in breeding success between colonies, particularly the lower rates at MJ, sustained over several years, are likely substantial enough to drive population decline and merit demographic modelling (Tinker et al. 2022). On the other hand, and unlike Lago et al. (2019), we did not find a difference between breeding success at RM and SP, meaning that rodent control has a positive impact, especially in the absence of contrasting provisioning in shearwaters.

Compared to RM, nest survival rates were lower at MJ, where nestlings also had lower $\delta^{15}N$. Following predictions, tracked adults at MJ made longer trips and had low spatial overlap in foraging areas with RM shearwaters (Hypothesis 4). Similar to the comparison in foraging trip length at RM and MJ colonies, other adult seabirds in colonies where foraging trip distance was longer or in areas with poorer conditions, had slightly lower survival (Horswill et al. 2023), lower breeding success (Hipfner et al. 2007; Fayet et al. 2021) and nestlings with higher $CORT_f$ levels (Whitehead et al. 2022). In addition to the longer foraging trips in MJ adult shearwaters, provisioning frequency at the colony is potentially also affected by distinct light pollution events from bunkering ships during which adult shearwaters reduced colony attendance by an hourly mean of $18 \pm 24\%$ (Austad et al. 2023). Further study is needed to differentiate between the effects of provisioning quality, quantity and frequency (Cherel et al. 2005; Williams et al. 2007; Sears et al. 2009) on $\delta^{15}N$ measured in feathers within our study system. Moreover, while $\delta^{15}N$ is an indicative measure of diet quality (Pollet et al. 2014), it could be complimented by other measures such as energetic content (Wanless et al. 2005; Lamb et al. 2016) and essential fatty acids (Santos et al. 2023; Laranjeiro et al. 2025). Future research needs to account for nest microclimate due to effects on chick physiology (Fairhurst et al. 2012a; Lamb et al. 2016; Casagrande and Dell'Omo 2025).

Conclusion

By combining measures of stable isotopes and the hormone corticosterone we demonstrate the presence of nutritional stress in seabird nestlings dependent on parental provisioning. While further research is needed to disentangle between the effects of diet quality and quantity, as well as the roles of pollutants such as mercury, poor provisioning seems to have negative effects on both fledging and adult breeding success. Through the retrospective measures of rearing conditions and novel comparison between failed fledglings and a wider cohort we contribute knowledge to an otherwise poorly studied, but crucial life stage. We support previous findings that fledglings found at sea are in poor condition (Rodríguez et al. 2017b; Swanson et al. 2023), but provide alternative insight on light pollution attraction (Brown et al. 2022) and propose that grounding risk is related to rearing conditions.

Furthermore, we show that one of the possible underlying causes for differences in provisioning and breeding success at colonies, is differing foraging trip length by adult shearwaters. Our results are in line with those of other studies showing that short travel distances to foraging areas are related to increased adult breeding success (Paiva et al. 2013; Fayet et al. 2021). Fishing pressure on small pelagic species which are prevalent in shearwater diet (Austad et al. 2025) is increasing worldwide, including in the Mediterranean Sea (Grémillet et al. 2018). Our study indicates nutritional stress in nestlings with implications on fledgling survival as well as breeding success at colony level. Therefore, it contributes to calls for fish stock management at spatial scales relevant to seabird foraging effort (Bertrand et al. 2012; Sydeman et al. 2021) and for a more extensive marine protected area network that considers climate change impacts (Sarzo et al. 2023). Finally, our results highlight that while terrestrial conservation measures such as predator management at colonies and grounded fledgling rescue are important, they do not necessarily compensate for threats in the marine environment.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04748-8.

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Authors' contributions Martin Austad, Benedetta Catitti and Petra Quillfeldt conceived the study. Martin Austad, Francesca Visalli, Rita Matos, Nicholas Barbara and Benjamin Metzger collected samples and tracking data. Martin Austad, Benedetta Catitti, Bettina Almasi, Paco Bustamante and Petra Quillfeldt carried out or supervised lab analysis. Martin Austad analysed the data and wrote the original draft of the manuscript. All authors contributed critically to earlier versions of the manuscript, read and approved the final version.

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Data Availability All data is deposited to Zenodo Repository https://doi.org/10.5281/zenodo.17219417 (Austad 2025). R scripts written to analyse data are provided in the same repository. Tracking data are available at https://www.seabirdtracking.org/.

Declarations

Conflict of interest The authors declared that they have no conflict of interest.

Ethical approval All handling, sampling and tagging of shearwaters were carried out under permits from the Environment & Resources Authority (ERA) and the Wild Birds Regulation Unit (WBRU), Malta. Fieldwork was carried out with moral responsibility and with the aim to provide knowledge important to the conservation of the study species. No specimens were collected for the study.

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