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1 **Running head:** Overabundant species population control

2 **Title:** Population control of an overabundant species achieved through consecutive  
3 anthropogenic perturbations

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14 *Abstract.* The control of overabundant vertebrates is often problematic. Much work has  
15 focused on population-level responses and overabundance due to anthropogenic subsidies.  
16 However, far less work has been directed at investigating responses following the removal of  
17 subsidies. We investigate the consequences of two consecutive perturbations—closure of a  
18 landfill and an inadvertent poisoning event—on the trophic ecology ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$ ),  
19 survival, and population size of an overabundant generalist seabird species, the yellow-legged  
20 gull. We expected that the landfill closure would cause a strong dietary shift and the  
21 inadvertent poisoning a decrease in gull population size. As a long-lived species, we also  
22 anticipated adult survival to be buffered against the decrease in food availability but not  
23 against the inadvertent poisoning event. Stable isotope analysis confirmed the dietary shift

24 towards marine resources after the disappearance of the landfill. Although the survival model  
25 was inconclusive, it did suggest that the perturbations had a negative effect on survival, which  
26 was followed by a recovery back to average values. Food limitation likely triggered dispersal  
27 to other populations, while poisoning may have increased mortality; these two processes were  
28 likely responsible for the large fall in population size that occurred after the two consecutive  
29 perturbations. Life-history theory suggests that perturbations may encourage species to halt  
30 existing breeding investment in order to ensure future survival. However, under strong  
31 perturbation pulses the resilience threshold might be surpassed and changes in population  
32 density can arise. Consecutive perturbations may effectively manage overabundant species.

33 *Key words:* *Food availability, predictable anthropogenic food subsidies, seabird, population*  
34 *size, adult survival, pest, stable isotope analysis, anthropogenic perturbation.*

35

## 36 INTRODUCTION

37

38 Human alterations of natural systems have triggered profound changes in ecosystem  
39 functioning and species communities (Vitousek et al. 1997). For instance, predictable  
40 anthropogenic food subsidies, such as landfill organic waste, have caused ecological and  
41 evolutionary changes at individual, population, community and ecosystem levels (Oro et al.  
42 2013 and references therein). Exploitation of subsidies alters not only dietary preferences but  
43 may increase body mass, body size, breeding performance or survival on a wide range of  
44 species (Newsome et al. 2015). Subsidies are considered responsible for much of the  
45 demographic explosion of a wide range of so-called ‘overabundant’ species such as foxes,  
46 gulls and rats (Duhem et al. 2008, Bino et al. 2010, Aplin et al. 2011). A large number of  
47 studies have tackled mitigation and management measures, such as direct culling aimed at  
48 reducing the ecological and social consequences of overabundant species (Baker and Harris,

49 2006; Beasley et al., 2013; Bosch et al., 2000; Merrill et al., 2006). However, although these  
50 measures have been implemented worldwide, they have often turned out to be expensive  
51 and/or ineffective (Baker and Harris 2006, Oro and Martínez-Abráin 2007, Warburton and  
52 Norton 2009). The main flaw is that management measures often aim to mitigate the  
53 consequences of the human alteration rather than avert the occurrence of the alteration itself.  
54 However, recent European Union (EU) environmental policies are beginning to target the  
55 causes rather than their ‘symptoms’. For example, the final modifications to the Landfill  
56 Waste Council Directive (LWCD; European Commission 2008, E.U. 2009) aim to put an end  
57 to open-air landfill sites. In addition, these policies target a progressive reduction of  
58 predictable subsidies and are expected to trigger population control in some overabundant  
59 species. The exhaustive monitoring of the ecological processes ensuing after the closure of  
60 open-air landfill sites provides a unique perspective and understanding of the consequences to  
61 ecosystems of a forced reduction in supplementary feeding (Steigerwald et al. 2015). Since  
62 seabirds are easily monitored and sensitive to changes in food availability, they provide a  
63 particularly good model for understanding the complexity and the efficacy of recent policy  
64 changes aimed at controlling overabundant species. For instance, changes caused by food  
65 limitation have been previously documented for seabird clutch size, egg volume, body size,  
66 breeding success, fecundity, adult survival, local recruitment, dispersal and population size  
67 (Pons and Migot 1995, Harris et al. 1997, Oro and Pradel 2000, Oro and Furness 2002,  
68 Duhem et al. 2008).

69 Predictable food subsidies together with the protection of suitable breeding areas in recent  
70 years has led to an increase in large opportunistic gull populations (Duhem et al. 2008). Their  
71 growth has caused social annoyance as well as concerns for public health (Hatch 1996), and  
72 have triggered population control measures worldwide (Thomas 1972, Vidal et al. 1998, Bosch  
73 et al. 2000, Brooks and Lebreton 2001a). For instance, yellow-legged gulls *Larus michahellis*

74 (YLG hereafter) in the Mediterranean basin have been subject to numerous culling programs  
75 aimed at controlling their numbers – the ‘symptom’ – by targeting either a reduction in adult  
76 survival rates or breeding performance (Vidal et al. 1998, Brooks and Lebreton 2001a,  
77 Duhem et al. 2008). Because seabirds are long-lived species, the reduction of adult survival is  
78 expected to have important population consequences (Sæther et al. 1996). However, direct  
79 culling had little effect on gull numbers because processes such as earlier recruitment or  
80 density-dependent higher fertility and immigration (Brooks and Lebreton 2001b) were likely  
81 enhanced by high food availability, which might have boosted gulls’ resilience to this type of  
82 perturbation (Oro and Martínez-Abráin, 2007). Although food limitation has some impact on  
83 breeding performance, it is not expected to be particularly useful in controlling long-lived  
84 species; nevertheless, a long-term limitation of resources might be the key to controlling  
85 overabundant species by reducing recruitment (Oro and Martínez-Abráin 2007). When the  
86 two types of measures (food limitation and culling) are used together, their synergic or  
87 cumulative effects may lead to an important reduction in population size, although very little  
88 is known about the potential effects of linked management actions.

89 YLGs are large, colonial and opportunistic seabirds distributed over the whole Mediterranean  
90 basin. YLG are known to exploit landfills to varying extents throughout their distribution  
91 range (Witt et al. 1981, Motis 1989, Bosch et al. 1994, Verdú del Campo et al. 1995, Ramos  
92 et al. 2009). Particularly, Ramos et al. (2011) assessed the importance of landfills on YLG in  
93 the Western Mediterranean basin, and demonstrated that landfill waste represents up to 60%  
94 of the diet of breeding YLG in our study colony. The recent explosion in YLG numbers has  
95 raised conservation concerns and several culling programs have been carried out in different  
96 locations. Despite these control measures, it is still the most abundant seabird in the  
97 Mediterranean (Zotier et al. 1999, Oro and Martínez-Abráin 2007).

98 Here, we assessed the consequences on the ecology of YLG of two anthropogenic  
99 perturbations, 1) the closure of an open-air landfill site due to European Directives (E.U.  
100 2009), which was estimated to represent half of its diet in terms of assimilated biomass  
101 (Ramos et al. 2011); and 2) the use of poison pellets in the study area to eradicate invasive  
102 pest, which caused indirect mortality in YLGs from primary (ingestion of pellets) and  
103 secondary (ingestion of poisoned rodents) poisoning (Mayol et al. 2012a). We investigated  
104 the changes in trophic ecology (dietary shift) and demographic parameters (population size  
105 and survival) of breeding YLGs that were attributable to the two consecutive anthropogenic  
106 perturbations. Life-history theory predicts that under limited food access, long-lived  
107 organisms will forego reproduction to avoid negatively affecting their future survival  
108 (Pugesek and Diem 1990, Oro et al. 1999). Thus, we expected that food limitation would  
109 trigger a dietary shift and differential resource exploitation, affecting breeding performance  
110 (Oro, et al. 1995, Steigerwald et al. 2015) but not individual survival probability. Moreover,  
111 we expected that the inadvertent poisoning event would cause an increase in mortality rate  
112 due to the accidental poisoning of individuals. We expect that the combined effects of one  
113 action affecting reproductive performance and another affecting adult survival might trigger a  
114 decrease in population size. In addition, we expected our results to shed more light on the  
115 effects of consecutive perturbations and to provide a more comprehensive framework for  
116 superabundant species management.

## 117 METHODS

### 118 *Study area and perturbations*

119 Data were collected at Dragonera Natural Reserve, a 300-ha island off the coast of Mallorca  
120 (Balearic archipelago, Spain, 39° 35' 02''N, 02°19'17''E). This protected site hosts the  
121 largest-known YLG breeding colony in the archipelago (McMinn 2010). YLG nests can be

122 found all over the island, with areas of gentle slope and low vegetation having higher density.  
123 The tourism industry on Mallorca (ca.  $10^7$  tourists/year with a population of ca.  $10^6$  residents)  
124 has increased waste production and its availability at a single landfill site for opportunistic  
125 feeders. This anthropogenic subsidy was responsible for the doubling of the YLG Balearic  
126 archipelago population between 1983 (ca. 7500 pairs) and 2000 (ca. 14000 pairs; McMinn  
127 2010). Local managers estimated the number of gulls foraging at the landfill (ca. 32km from  
128 Dragonera) to range between 7300 and 15500 depending on the season and the year (TIRME  
129 2003). Following European Directives (E.U. 2009), the open-air landfill was transformed into  
130 an incineration plant in the winter 2009-2010. This transformation made waste virtually  
131 inaccessible to gulls. In mid winter of the year after the transformation (January and February  
132 2011), an eradication campaign targeting the human-introduced rats (*Rattus rattus*), mice  
133 (*Mus musculus*) and rabbits (*Oryctolagus cuniculus*) was carried out on Dragonera (Mayol et  
134 al. 2012b). This campaign involved the aerial application of Brodifacoum, a second  
135 generation anticoagulant whose main mechanism is blocking epoxy-reductose enzyme  
136 activity. Without generating bait shyness, this leads to lack of blood clotting factors, followed  
137 by hemorrhages and eventually death (Hadler and Buckle, 1992). In the weeks following the  
138 spread of the poison, ca. 800 YLG carcasses were found on the island (Servei de Protecció  
139 d'espècies et al. 2011). This can be considered a minimum estimate given that the search was  
140 not exhaustive and the areas with dense vegetation and surrounding waters were not surveyed  
141 (Servei de Protecció d'espècies et al. 2011).

142 *Trophic level and dietary shift*

143 Nitrogen ( $\delta^{15}\text{N}$ ), carbon ( $\delta^{13}\text{C}$ ) and sulphur ( $\delta^{34}\text{S}$ ) isotopic ratios can be used in ecological  
144 studies to evaluate dietary shifts (Ramos et al. 2011), since analyses of individual feathers  
145 provide unique isotopic information for very specific spatiotemporal periods (Hobson 2008).  
146 We evaluated the nitrogen ( $\delta^{15}\text{N}$ ), carbon ( $\delta^{13}\text{C}$ ) and sulphur ( $\delta^{34}\text{S}$ ) isotopic ratios of the first

147 primary feather (P1) on 68 unique breeding YLG individuals captured (see below) in 2004 ( $N$   
148 = 12), 2008 ( $N$  = 18), 2011 ( $N$  = 18) and 2013 ( $N$  = 20) (Table 2). P1 feathers were collected  
149 during the incubation period (April-May). Feathers were removed by cutting the feather quill,  
150 which causes no damage to the individuals. The P1 feather is replaced by molt at breeding  
151 sites and its isotopic value is an indicator of the diet of the previous breeding season.  
152 Laboratory procedures for preparing and processing feather samples were carried out  
153 following Ramos et al. (2011). Feathers were washed in a 0.25 m sodium hydroxide solution,  
154 rinsed thoroughly in distilled water to remove any surface contaminants, dried in an oven at  
155 60°C to constant mass and ground to a fine powder in a freezer mill (Spex Certiprep 6750;  
156 Spex Industries Inc., Metuchen, NJ, USA) operating at liquid nitrogen temperature.  
157 Subsamples of powdered material were weighed to the nearest  $\mu\text{g}$ , placed in tin capsules and  
158 crimped for combustion for C, N and S isotope determination. Isotopic analyses were carried  
159 out at the Serveis Científico-Tècnics of the University of Barcelona (Spain) by means of a  
160 Thermo-Finnigan Flash 1112(for N and C)/1108 (for S) (CE Elantech, Lakewood, NJ, USA)  
161 elemental analyzer coupled to a Delta-C isotope-ratio mass spectrometer via a CONFLOIII  
162 interface (Thermo Finnigan MAT, Bremen, Germany), and applying IAEA standards (IAEA  
163 CH6, IAEA CH7 and USGS 24 for C, IAEA N1, IAEA N2 and IAEA NO3 for N, and IAEA-  
164 S1, IAEA-S2 and IAEA-S3 for S) every 12 samples to calibrate the system and compensate  
165 for any drift over time. Samples from 2004 were analyzed separately from 2008, 2011 and  
166 2013 but the same instruments and standards were used. Precision and accuracy for  $\delta^{13}\text{C}$   
167 measurements was  $\leq 0.1\text{\textperthousand}$ ,  $\leq 0.3\text{\textperthousand}$  for  $\delta^{15}\text{N}$  and  $\leq 0.3\text{\textperthousand}$  for  $\delta^{34}\text{S}$ .  
168 Results were expressed in delta ( $\delta$ ) notation (Bond and Hobson 2012). We used linear mixed  
169 models (LMM) to evaluate the effects of landfill closure, sex and their interaction (Crawley  
170 2007), with the year as the random effect (Zuur et al. 2009), to account for the effect of  
171 environmental variability on isotopic signatures. In addition, we estimated diet composition

172 before and after landfill closure for males and females by applying Bayesian three-isotope  
173 ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values), three-endpoint (marine, crops and terrestrial environments, and  
174 refuse sites) mixing models to the isotopic values (SIAR, Stable Isotope Analysis in R;  
175 Parnell et al. 2008). Ramos et al. (2011) recently evaluated the spatiotemporal variations the  
176 feeding ecology of YLG on the western Mediterranean region. Prey isotopic signatures were  
177 homogeneous among most of the localities studied, hence we included mean isotopic values  
178 ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$ ) calculated in their study for the main food resources exploited by YLG  
179 in Dragonera (values from Table 5 in Ramos et al 2011). Moreover, we used the consumer-  
180 discrimination factors provided by these authors.

181 *Local survival analysis and estimates of population abundance*

182 Breeding adults were trapped during the incubation period using a tent spring trap (see  
183 Steigerwald et al. 2015). We chose to trap individuals in accessible nests along the main south  
184 path of the island (4.5Km long) to increase resighting probabilities in the following years. In  
185 total we trapped 206 YLG, which were marked using a Darvic plastic band with a unique  
186 alphanumeric code for subsequent individual identification from a distance using spotting  
187 scopes. Marking, resighting of live birds, and recovery of dead animals (99 and 12 cases  
188 respectively) in March/April in 2007–2013 were used to build individual encounter histories  
189 and analyzed using multistate capture-mark-recapture-recovery (CMRR) models to estimate  
190 survival, recapture and recovery probabilities (Brownie and Hines 1993, Lebreton et al.  
191 1999). Since all recoveries came from the colony site, CMRR models cannot distinguish  
192 mortality from permanent emigration to unobservable areas of the island. As a consequence,  
193 our estimates refer to apparent survival (Lebreton et al. 1992). We assessed the goodness-of-  
194 fit test (GOF) for the general model assuming that all parameters vary over time (Jolly-Move  
195 model; Brownie and Hines 1993, Pradel et al. 2003) using the software U-CARE 2.2.2  
196 (Choquet et al. 2005, 2009). The global GOF test revealed no evidence of transient animals,

meaning that there was no difference in the probability of being later reencountered between “new” and “old” individuals encountered at a given time, and that there were no trap-dependence effect (i.e., no difference in the probabilities of being reencountered in the different stages at  $i + 1$  between the animals in the same state at occasion  $i$  whether or not encountered at this date). Thus, the general model adequately explained the data ( $\chi^2 = 37.483$ ,  $df = 35$ ,  $P = 0.356$ ; Table 1). The GOF test for females indicated the presence of transients, but since the global GOF was not statistically significant we used a variance inflation factor,  $\hat{c} = 1.07$ , to account for the remaining heterogeneity (Choquet et al. 2005, 2009). We identified a set of biological hypotheses (Fig. 1) and began by testing effects on a single parameter at a time (Lebreton et al. 1992). We considered the effect of year, sex, landfill closure and the pest eradication campaign on local survival probability (Fig. 1). The landfill closure and pest eradication campaign effects were tested either as punctual or persistent depending on the temporal extent (short vs. long term, respectively) of the effect in the considered hypothesis (Fig. 1). Furthermore, we used the number of days spent searching for marked animals as a predictor of recapture probability and the effort (number of searching days) invested in searching for corpses by the Dragonera Natural Reserve team as a predictor of the recovery rate. We began by simplifying the structure of the recovery rate ( $\lambda$ ) from a general model ( $E_0$ ), assuming all three parameters to be dependent on time and sex. We then modeled recapture ( $p$ ) and finally the survival parameter ( $\phi$ ). Note that models’ rank did not change when the model selection began with a different parameter (results not shown). Models were implemented using the program MARK 7.1 (White and Burnham 1999). Models were selected using the second order Akaike Information Criterion AICc value and, in addition, deviances were scaled using the over-dispersion dispersion parameter (QAICc; Burnham and Anderson 2002). We considered the model with lowest AICc or QAICc and those within two points of  $\Delta$ AICc or  $\Delta$ QAICc (the difference in AICc and QAICc values, respectively) to be

222 equivalent, and we used these models to produce final model-averaged parameter estimates  
223 (mean  $\pm$  SE) (Burnham and Anderson 2002). In this way we included the effects of  
224 parameters obtained from separate models and accounted for model selection uncertainty  
225 (Burnham and Anderson 1998).

226 Each year, we estimated nest density in a 0.32 ha area (0.11% of Dragonera Island surface)  
227 with gentle slope and low vegetation as proxy of population size and for assessing its  
228 fluctuations over the study period. We assumed that despite that nest density might not be  
229 homogeneous within the island, the relative change in its value was a good indicator of  
230 population changes, as the surface occupied by the colony remained invariant. Five to nine  
231 observers walked the delimited area forming a transect line with a distance of ca. 3-5m  
232 between each other and marking all encountered nests. Observers shuffled position within the  
233 line and surveyed the transect a second time to re-capture marked nests and count new ones.  
234 The number of nests in the area was then estimated by the Lincoln-Petersen estimator  
235 (Williams et al. 2001, Seber 2002). We used the “delta method” (Morgan 2000) to  
236 approximate the variance of the mean before and after the landfill closure and the pest  
237 eradication campaign. We then assessed if there was a population change after the events with  
238 a Z-test (Zar 2010).

239 RESULTS

240 *Trophic level and dietary shift*

241 We analyzed nitrogen ( $\delta^{15}\text{N}$ ), carbon ( $\delta^{13}\text{C}$ ) and sulphur ( $\delta^{34}\text{S}$ ) isotopic ratios before and  
242 after the landfill closure (Table 2). The model selection procedure showed no significant  
243 changes in  $\delta^{13}\text{C}$  before and after the landfill closure (Table 3, model M<sub>1</sub>, see Appendix: Table  
244 A1 for estimates). The landfill effect was not retained in the analysis of  $\delta^{15}\text{N}$  (Table 3, M<sub>1</sub>,  
245 Appendix: Table A1 for estimates), although that effect was present in an equivalent model

( $\Delta\text{AICc} = 0.36$  for model  $M_2$ ; Table 3, Appendix: Table A1 for estimates). All retained models for  $\delta^{34}\text{S}$  (Table 3,  $M_2$ ,  $M_4$  and  $M_5$ , see Appendix: Table A1 for estimates) included the landfill effect as important, giving larger  $\delta^{34}\text{S}$  values after landfill closure. Males and females had the same isotopic signature, however a sex effect was accounted for in two of the best three models of  $\delta^{34}\text{S}$  (Table 2,  $M_4$  and  $M_5$ , see Appendix: Table A1 for estimates), indicating a small (not statistically significant) difference in male and female diet. Model results for isotopic contents (Table 3 and Fig. 2), together with the estimated percentage of diet diversity indicated by the SIAR analysis (Fig. 3), revealed changes in resource use after the landfill closure: the marine content of the diet increased while refuse diet content decreased, as expected.

256 *Local survival and population size*

257 The model selection procedure resulted in five models having more than 10% of the QAICc  
258 weight and occurring within 1 point of QAICc value (Table 4), impairing conclusions on the  
259 statistical significance of each single effect. This uncertainty was probably due to the  
260 complexity of the model used to join two types of information (recoveries and recaptures) and  
261 the relatively small dataset available. Nevertheless, model averaging techniques took this  
262 uncertainty into account and delivered weighted estimates of the parameters of interest  
263 according to the model QAICc value. The model with the lowest QAICc value (model  $M_0$ ,  
264 Table 4) indicated a constant survival, i.e. independent of sex and the perturbations or the  
265 years considered. Averaged estimates were calculated for models  $M_{0-3}$  and  $M_5$ , which were  
266 within 2 QAICc points of the one with the lowest value ( $M_0$ ). All these models included the  
267 effect of food limitation and averaged estimates suggest that the closure of the landfill caused  
268 an 8% drop in survival (from 0.71 in 2009, SE = 0.07 to 0.63 in 2010, SE = 0.07). Similarly,  
269 the averaged estimates immediately after the pest eradication program indicated an additional

270 2% drop in apparent survival (from 0.63, SE = 0.07 in 2010 to 0.61, SE = 0.11 in 2011). The  
271 two synergic perturbations caused a 10% drop in survival probability when compared to the  
272 value before the landfill closure.

273 We found no significant differences in either survival between males and females, or over  
274 time (Table 4, M<sub>8-13</sub>). The search for carcasses and the sampling effort (Table 4, M<sub>9</sub> and M<sub>12</sub>  
275 respectively) well predicted recovery and recapture probabilities, respectively. Average  
276 recapture probabilities ranged between 0.24 (SE = 0.06) and 0.47 (SE = 0.07) (Fig. 5b), while  
277 recovery probabilities were constant (0.07, SE = 0.03), except for a 0.18 (SE = 0.09) increase  
278 in 2010 when a specific search for carcasses was conducted (Fig. 5c).

279 Nest survey data clearly showed a decrease in size of the nesting population after the two  
280 perturbations. The number of nests in the surveyed area first decreased by 37% after the  
281 landfill closure (from 92.13 in 2009, SE = 4.01 to 58.05 in 2010, SE = 5.71), and had an  
282 additional drop of 65.99% after the pest eradication campaign (from 58.05 in 2010, SE = 5.71  
283 to 20.19 in 2010, SE = 2.30; Fig. 5). Both perturbations caused a statistically significant  
284 change in nesting population size ( $Z = 13.78, P < 0.00001$  and  $Z = 17.19, P < 0.00001$  for  
285 landfill closure and poisoning campaign, respectively). The two synergic perturbations caused  
286 a 78% drop in nesting population size when compared to the value before the landfill closure  
287 (Fig. 5).

288 DISCUSSION

289 We assessed trophic and demographic changes in YLG after two consecutive anthropogenic  
290 perturbations, namely a food reduction after the closure of an open-air landfill and the  
291 accidental poisoning due to a campaign targeting the eradication of invasive mammals.  
292 Extensive research has been performed on the effects of predictable anthropogenic food  
293 sources across taxa (see reviews in Oro et al. 2013, Newsome et al. 2015). Specifically,

several studies on gulls have assessed the effects of food availability on several parameters such as diet (Ramos et al. 2011), survival (Oro et al. 1999) and population size (Oro et al. 1999, 2004, Duhem et al. 2008). These studies recorded that a decrease in the availability of food subsidies caused changes in resource exploitation and increased dispersal, whereas survival remained constant. However, none of these studies analyzed all these parameters simultaneously, nor did they evaluate the consequences of the combined effect of food limitation and additive mortality on population dynamics.

Predictable anthropogenic food can be a low-quality resource (the so-called ‘junk-food’, see Pierotti and Annett 1991, Annett and Pierotti 1999, Grémillet et al. 2008, Genovart et al. 2010), but gulls appear to adjust their diet in accordance with the availability, rather than with the quality, of foraging resources except when feeding chicks (Pons 1992, Pedrocchi et al. 1996, Oro et al. 2004). During the last few decades, landfills have provided YLG with a vast food surplus, leading to higher carrying capacity and rapid population growth (Duhem et al. 2008). It is likely that when access to this food was restrained, gulls were forced to exploit more energetically demanding and less predictable (unless obtained from fishery discards) marine prey (Bartumeus et al. 2010). Here we present partial evidence of this dietary shift towards marine resources in YLG trophic behavior following a landfill closure. Since we were only interested in changes occurring at a population level, we did not account for the differences between individuals trophic behavior (Navarro et al. 2010). The evidence was clear in sulphur isotope signature: YLG exploited significantly more marine resources after the landfill closure; however, we failed to detect a change in carbon isotope signature. The threshold to detect a change in sulphur isotope signatures lies around 10‰ while it is 3‰ for carbon isotope signatures (see Figure 2 and mean isotopic values in Ramos et al. 2011). We attribute our non-statistically significant difference in carbon isotope signatures to a lack of statistical power, and hence cannot ascertain nor deny a possible effect. However, other YLG

colonies have been observed to follow the same pattern (see Arizaga et al. 2013). The use of  $\delta^{34}\text{S}$  is commonly used to characterize the effect of marine food sources on various species (Lott et al. 2003, Natsumeda et al. 2015). Moreover, Moreno et al. (2010) demonstrated the potential of using  $\delta^{34}\text{S}$  alone to distinguish not only between terrestrial and marine prey, but also between different marine prey species. Pedro et al. (2013) showed that exploitation of waste food by large, opportunistic gulls is a relatively new strategy that appeared less than 100 years ago. It is therefore not surprising that YLG from Dragonera were able to increase their consumption of marine and other terrestrial prey after food from landfill waste became unavailable. Moreover, other studies have also demonstrated a reduction in YLG waste consumption in this study area after the landfill closure (Ramos et al. 2011). It therefore seems reasonable to conclude that a diet change towards a marine diet occurred as a result of the landfill closure.

Low food availability is also known to increase intraspecific competition and reduce the contribution of each individual to the next generation (Begon et al. 1996). Breeding seabirds suffering from food limitation face survival versus reproduction trade-offs, and they are expected to forego current reproduction to guarantee adult survival prospects in order to increase the odds of future generations living under favorable conditions (Pons 1992, Pons and Migot 1995, Oro 1999, Sanz-Aguilar et al. 2008). Previous studies on gulls found severe impacts on breeding performance under different levels of food availability (Pons 1992, Pons and Migot 1995, Oro 1996). Particularly, our colony suffered a significant decrease in breeding performance (clutch size and egg volume) after landfill closure (Steigerwald et al. 2015). Moreover, Steigerwald et al. (2015) suggested that a dietary switch — which we confirmed — might not have been sufficient to fully cover the energy requirements of the local population. Foregoing reproduction to guarantee adult survival acts as a buffer mechanism against environmental variability and allows animals to cope with moderate

344 environmental perturbations. Nevertheless, when food is in very short supply it can even  
345 affect body mass and local adult survival in long-lived seabirds (Oro and Furness 2002). This  
346 appears to be the case for our population, given the recorded drop in YLG body condition  
347 (Steigerwald et al. 2015) along with a slight decrease in local survival rates after landfill  
348 closure. Gulls usually form spatially structured populations (Oro et al. 2003) and given that  
349 previous studies have shown that dispersal occurs following environmental perturbations (Oro  
350 et al. 2004, Fernández-Chacón et al. 2013), we suggest that food limitation has triggered not  
351 only mortality but also permanent emigration (through breeding dispersal) to neighboring  
352 populations (Bosch 2000, Oro 2003).

353 These findings agree with previous work on other seabird species (Oro 1999, Oro et al.  
354 2004, Duhem et al. 2008), which found a close correlation between anthropogenic food  
355 availability and colony size. Our work suggests that the decrease in food availability caused a  
356 dietary shift towards marine resources. The dietary shift was followed by a partial reduction in  
357 breeding performance (Steigerwald et al. 2015), leading to an increase in mortality and  
358 dispersal. Finally, the cumulative effects of poisoning magnified an already severe decrease in  
359 population size through real adult mortality. Despite that many individuals might have died or  
360 emigrated from the study area, those remaining exhibited similar survival compared to pre-  
361 perturbation values. Another possible explanation for why population size and survival follow  
362 different response patterns after these perturbations is that poisoning was intended to cause  
363 non-selective mortality across the whole population, thus also affecting non-breeders and  
364 immature gulls, but our survival estimates came only from breeding adults. Alternatively, the  
365 termination of the waste food surplus might have decreased the carrying capacity of the  
366 system and the population size could therefore have declined to match this new population  
367 ceiling, while also influenced by the additive mortality from poisoning. We predict that  
368 population size will slowly increase in the coming years until it stabilizes at a new

369 demographic equilibrium, however it will not reach the levels recorded before the two  
370 perturbations (Bosch et al. 2000).

371

372 *Implications for the management of overabundant species*

373 The food limitation and the mammal eradication campaign through poisoning were not  
374 specifically intended for the management of YLG populations. However, these actions  
375 allowed us to explore the implications of the combined effect in controlling of consecutive  
376 actions on the management of a so-called ‘overabundant’ species. Many populations of  
377 overabundant species of birds and mammals are subject to extensive management programs  
378 designed to control their numbers (Mate et al. 1998, Twigg and Kent Williams 1999,  
379 Anderson and Devlin 1999, Bosch et al. 2000). These actions mainly aim to either reduce  
380 breeding success (Thomas 1972, Merrill et al. 2006) or to eliminate adults by culling (Bosch  
381 et al. 2000, Baker and Harris 2006). Such management is expensive and ineffective in the  
382 long term if applied in isolation (Merrill et al. 2006, Baker and Harris 2006, Oro and  
383 Martínez-Abráin 2007). Here, we present evidence of how these two consecutively occurring  
384 perturbations have been extremely effective in reducing the population density of a generalist  
385 opportunistic bird, which has not recovered in the three years following these events. Under  
386 strong perturbation pulses (Martínez-Abráin et al. 2012) or intense environmental variability  
387 (Harding et al. 2011), the density dependent responses of demographic parameters appear  
388 insufficient to buffer population changes. Although an isolated perturbation, such as  
389 poisoning, seemed to have an important short-term effect, it is reasonable to believe that it  
390 was the closure of the landfill site that led to a permanent decrease in the carrying capacity of  
391 the system and hence a long-lasting reduction in population numbers, as previously suggested  
392 by Oro and Martínez-Abráin (2007). Cumulative effects of consecutive perturbations are  
393 likely to become a useful tool in the control of overabundant populations. Nevertheless,

394 despite the potential that these results have for the implementation of more effective  
395 management actions of overabundant species, caution must be taken because their long-term  
396 consequences are still unknown.

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## SUPPLEMENTAL MATERIAL

628 **Appendix A:** Results from General Linear Modelling of the landfill closure on  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ 629 and  $\delta^{34}\text{S}$  stable isotope signatures (*Ecological archives* EXXX-XXX-A1).

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A large, semi-transparent watermark is centered on the page. It contains the lowercase letters "esa" in a bold, sans-serif font, with the "e" and "s" partially overlapping. Below "esa", the word "preprint" is written in a larger, italicized, lowercase sans-serif font. A small gray dot is positioned above the letter "i" in "print".

654 TABLE 1. Results of the goodness-of-fit (GOF) tests for the general capture–recapture–  
 655 recovery multistate (CMRR) model for males and females YLG. Test components are listed  
 656 as in Pradel, Wintrebert, & Gimenez (2003) where 3G: Tests for transients presence and M.  
 657 Tests for trap dependence;  $\chi^2$ : chi-squared statistic; df: degrees of freedom;  $\hat{C}$ : inflation factor,  
 658 i.e.,  $\chi^2/\text{df}$ .

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| Males   | Test      | $\chi^2$ | df | p-value | $\hat{C}$ |
|---------|-----------|----------|----|---------|-----------|
|         | 3G.SR     | 2.90     | 5  | 0.72    | 0.58      |
|         | 3G.SM     | 1.66     | 4  | 0.80    | 0.41      |
|         | M. Itec   | 3.54     | 5  | 0.62    | 0.71      |
|         | M. Ltec   | 0.37     | 3  | 0.95    | 0.12      |
|         | Global 3G | 4.55     | 9  | 0.87    | 0.51      |
|         | Global M  | 3.91     | 8  | 0.87    | 0.49      |
| Females | Test      | $\chi^2$ | df | p-value | $\hat{C}$ |
|         | 3G.SR     | 16.02    | 5  | 0.01    | 3.20      |
|         | 3G.SM     | 4.18     | 4  | 0.38    | 1.05      |
|         | M. Itec   | 3.16     | 5  | 0.68    | 0.63      |
|         | M. Ltec   | 5.62     | 4  | 0.23    | 1.41      |
|         | Global 3G | 20.20    | 9  | 0.02    | 2.25      |
|         | Global M  | 8.82     | 9  | 0.45    | 0.98      |

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663 TABLE 2. Mean values ( $\pm$  SE) of nitrogen ( $\delta^{15}\text{N}$ ), carbon ( $\delta^{13}\text{C}$ ) and sulphur ( $\delta^{34}\text{S}$ ) stable  
664 isotopes signatures (‰) of male and female Yellow legged gulls at Dragonera Island before  
665 (2004 & 2008) and after (2011 & 2013) the landfill closure.

666

|                       | Before            | After             |
|-----------------------|-------------------|-------------------|
| <b>Male</b>           |                   |                   |
| $\delta^{15}\text{N}$ | $10.69 \pm 0.12$  | $11.11 \pm 0.29$  |
| $\delta^{13}\text{C}$ | $-19.91 \pm 0.10$ | $-19.64 \pm 0.27$ |
| $\delta^{34}\text{S}$ | $10.85 \pm 0.62$  | $13.95 \pm 0.63$  |
| <b>Female</b>         |                   |                   |
| $\delta^{15}\text{N}$ | $10.50 \pm 0.18$  | $10.91 \pm 0.22$  |
| $\delta^{13}\text{C}$ | $-20.13 \pm 0.21$ | $-19.94 \pm 0.18$ |
| $\delta^{34}\text{S}$ | $11.48 \pm 0.71$  | $14.51 \pm 0.60$  |

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675 TABLE 3. Table summarizing the model selection for isotope signatures of yellow-legged gulls  
 676 breeding in Dragonera Island. LANDFILL: landfill closure effect; SEX: sex effect; '+':  
 677 additive effect; '\*': interaction effect; AICc: corrected Akaike's information criterion; ΔAICc:  
 678 AICc difference with the best model; w: weight. Best model in bold. All models include year  
 679 as random factor.

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| Model notation                          |  | np       | AICc          | ΔAICc       | W           |
|---|--|----------|---------------|-------------|-------------|
| <b><math>\delta^{13}\text{C}</math></b> |  |          |               |             |             |
| <b>M<sub>1</sub></b>                    | $\delta^{13}\text{C}$                                    | <b>1</b> | <b>170.40</b> | <b>0.00</b> | <b>0.58</b> |
| M <sub>2</sub>                          | $\delta^{13}\text{C}_{\text{LANDFILL}}$                  | 2        | 173.20        | 2.75        | 0.15        |
| M <sub>3</sub>                          | $\delta^{13}\text{C}_{\text{SEX}}$                       | 2        | 172.60        | 2.19        | 0.20        |
| M <sub>4</sub>                          | $\delta^{13}\text{C}_{\text{LANDFILL+SEX}}$              | 3        | 175.10        | 4.65        | 0.06        |
| M <sub>5</sub>                          | $\delta^{13}\text{C}_{\text{LANDFILL+SEX+LANDFILL*SEX}}$ | 4        | 177.50        | 7.01        | 0.02        |
| <b><math>\delta^{15}\text{N}</math></b> |  |          |               |             |             |
| <b>M<sub>1</sub></b>                    | $\delta^{15}\text{N}$                                    | <b>1</b> | <b>187.40</b> | <b>0.00</b> | <b>0.43</b> |
| M <sub>2</sub>                          | $\delta^{15}\text{N}_{\text{LANDFILL}}$                  | 2        | 187.70        | 0.36        | 0.36        |
| M <sub>3</sub>                          | $\delta^{15}\text{N}_{\text{SEX}}$                       | 2        | 190.40        | 2.98        | 0.10        |
| M <sub>4</sub>                          | $\delta^{15}\text{N}_{\text{LANDFILL+SEX}}$              | 3        | 190.50        | 3.11        | 0.09        |
| M <sub>5</sub>                          | $\delta^{15}\text{N}_{\text{LANDFILL+SEX+LANDFILL*SEX}}$ | 4        | 192.60        | 5.27        | 0.03        |
| <b><math>\delta^{34}\text{S}</math></b> |  |          |               |             |             |
| <b>M<sub>2</sub></b>                    | $\delta^{34}\text{S}_{\text{LANDFILL}}$                  | <b>2</b> | <b>321.70</b> | <b>0.00</b> | <b>0.33</b> |
| M <sub>4</sub>                          | $\delta^{34}\text{S}_{\text{LANDFILL+SEX}}$              | 3        | 322.00        | 0.35        | 0.28        |
| M <sub>5</sub>                          | $\delta^{34}\text{S}_{\text{LANDFILL+SEX+LANDFILL*SEX}}$ | 4        | 322.10        | 0.39        | 0.28        |

M<sub>1</sub> δ<sup>34</sup>S 1 325.20 3.54 0.06

M<sub>3</sub> δ<sup>34</sup>S SEX 2 325.40 3.69 0.05

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683 TABLE 4. Modelling of survival ( $\Phi$ ), recapture (P) and recovery ( $\lambda$ ) probabilities of yellow-  
 684 legged gulls on Dragonera Island. LANDFILL: landfill effect; T: year effect; B: recovery  
 685 effort; E: recapture effort; PEST: Pest eradication effect; '!': punctual; ' $\infty
 686 effect; '+': additional effect; np: number of estimable parameters in the model; QAICc:  
 687 Akaike's information criterion corrected for sample size, number of parameters and over-  
 688 dispersion;  $\Delta$ QAICc: QAICc difference with the best model; W: weight of the model. Best  
 689 model in bold. Model subscripts refer to hypotheses in Fig. 1.$

|                      | Model notation   | np       | QAICc         | $\Delta$ QAICc | W           |
|----------------------|--|----------|---------------|----------------|-------------|
| <b>M<sub>0</sub></b> | <b><math>\Phi</math>. P<sub>E</sub> λ<sub>B</sub></b>                  | <b>5</b> | <b>579.26</b> | <b>0.00</b>    | <b>0.23</b> |
| M <sub>1</sub>       | $\Phi_{\text{LANDFILL}!} \text{ P}_E \lambda_B$                        | 6        | 579.76        | 0.50           | 0.18        |
| M <sub>3</sub>       | $\Phi_{\text{PEST}!} \text{ P}_E \lambda_B$                            | 6        | 580.17        | 0.91           | 0.15        |
| M <sub>2</sub>       | $\Phi_{\text{LANDFILL}\infty} \text{ P}_E \lambda_B$                   | 6        | 580.18        | 0.92           | 0.15        |
| M <sub>5</sub>       | $\Phi_{\text{LANDFILL}!+\text{PEST}!} \text{ P}_E \lambda_B$           | 7        | 580.21        | 0.95           | 0.14        |
| M <sub>6</sub>       | $\Phi_{\text{LANDFILL}\infty+\text{PEST}!} \text{ P}_E \lambda_B$      | 7        | 581.82        | 2.56           | 0.06        |
| M <sub>7</sub>       | $\Phi_{\text{LANDFILL}\infty+\text{PEST}\infty} \text{ P}_E \lambda_B$ | 8        | 582.34        | 3.08           | 0.05        |
| M <sub>4</sub>       | $\Phi_{\text{PEST}\infty} \text{ P}_E \lambda_B$                       | 6        | 584.38        | 5.11           | 0.02        |
| M <sub>8</sub>       | $\Phi_T \text{ P}_E \lambda_B$   | 10       | 584.88        | 5.62           | 0.01        |
| M <sub>9</sub>       | $\Phi_{T+SEX} \text{ P}_E \lambda_B$                                   | 15       | 592.48        | 13.21          | 0.00        |
| M <sub>10</sub>      | $\Phi_{T+SEX} \text{ P}_T \lambda_B$                                   | 20       | 595.99        | 16.73          | 0.00        |
| M <sub>11</sub>      | $\Phi_{T+SEX} \text{ P}_{T+SEX} \lambda_B$                             | 26       | 608.36        | 29.10          | 0.00        |
| M <sub>12</sub>      | $\Phi_{T+SEX} \text{ P}_{T+SEX} \lambda_{B+SEX}$                       | 28       | 612.4         | 33.14          | 0.00        |
| M <sub>13</sub>      | $\Phi_{T+SEX} \text{ P}_{T+SEX} \lambda_{T+SEX}$                       | 32       | 617.66        | 38.40          | 0.00        |

## 691 FIGURES

692 FIG. 1. Survival probability ( $\Phi$ ): qualitative representation under different biological  
693 hypotheses. Dashed lines ‘a’ and ‘b’ represent the landfill closure and the eradication  
694 campaign respectively. Survival hypotheses are numbered in growing complexity and  
695 assigned to the analogous model on Table 1 (model number in brackets):  $H_0$  ( $M_0$ ),  $H_1$  ( $M_1$ ),  $H_2$   
696 ( $M_2$ ),  $H_3$  ( $M_3$ ),  $H_4$  ( $M_4$ ),  $H_5$  ( $M_5$ ),  $H_6$  ( $M_6$ ),  $H_7$  ( $M_7$ ) and  $H_8$  ( $M_8$ ).

697 FIG. 2. Isotope signatures (‰) of  $\delta^{13}\text{C}$  (a),  $\delta^{34}\text{S}$  (b) and  $\delta^{15}\text{N}$  (c) of male (solid circles) and  
698 female (open circles) yellow-legged gulls breeding on Dragonera Island before (large circles)  
699 and after (small circles) the landfill closure. Tissue: P1 Feathers. Rectangles represent mean  $\pm$   
700 1,96·SE isotopic signature from marine, crops and terrestrial, and waste food sources, as  
701 calculated by Ramos et al. (2011).

702 FIG. 3. Diet estimates of marine, terrestrial and waste resources (true proportions and their  
703 Bayesian credibility intervals including 50, 75 and 95% of the posterior distributions)  
704 estimated by Stable Isotope Analysis in R mixing modeling based on C, N and S isotopic  
705 signatures from the first primary (P1) feathers of yellow-legged gulls from Dragonera Island  
706 before (left) and after (right) landfill closure, in males (upper panel) and females (lower  
707 panel). Sample sizes for males before landfill closure  $N = 23$ , males after  $N = 9$ , females  
708 before  $N = 25$ , and females after  $N = 15$ .

709 FIG. 4. Changes in nest density as a proxy of population size (mean  $\pm$  1.96·SE) of yellow-  
710 legged gulls breeding on Dragonera Island. Dashed lines indicate landfill closure and pest  
711 eradication campaign.

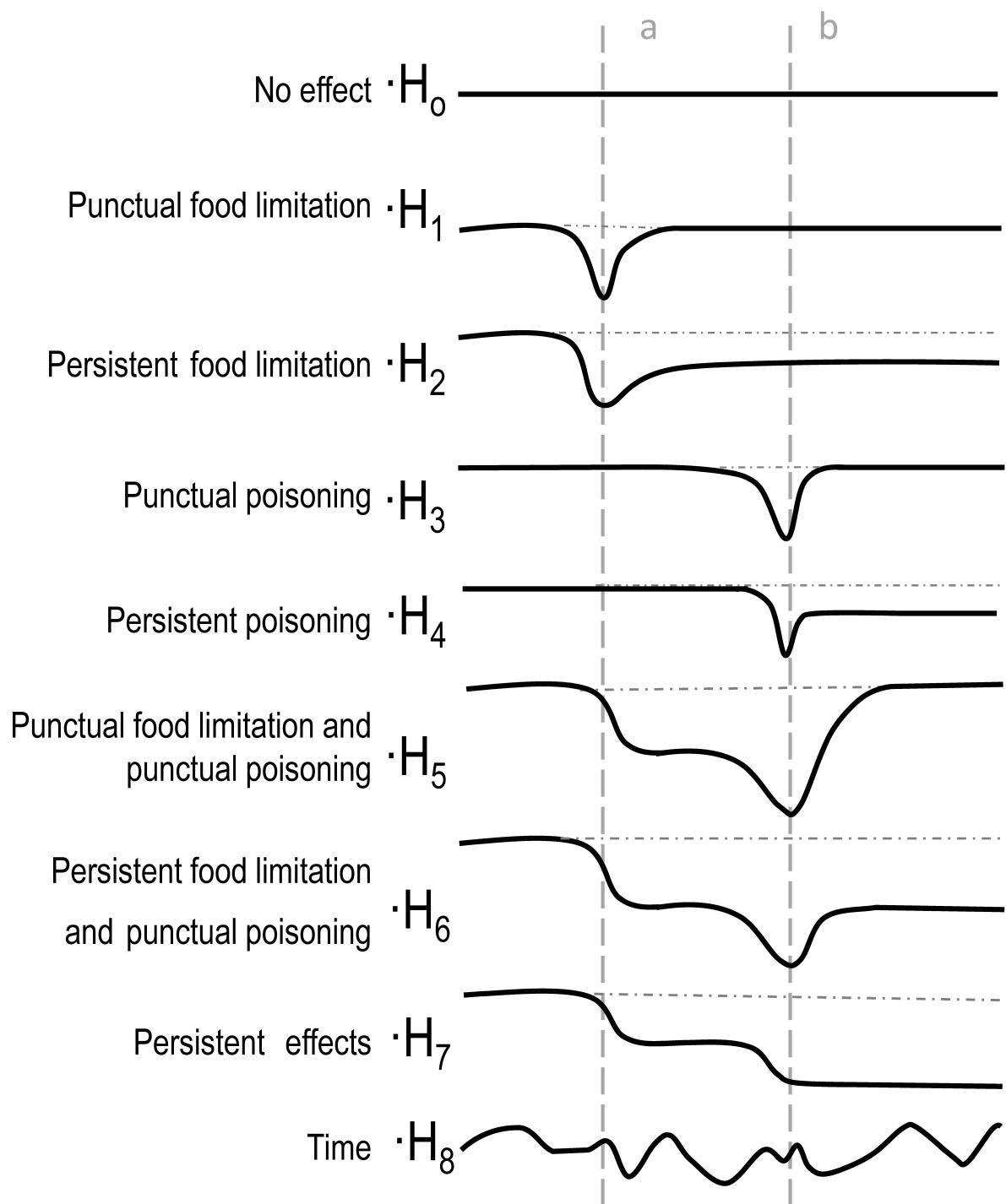
712 FIG. 5. Temporal variability in the estimated probabilities of local survival (a), recapture (b)  
713 and recovery (c) (95% CI) of yellow-legged gulls on Dragonera Island in 2007–2013 as

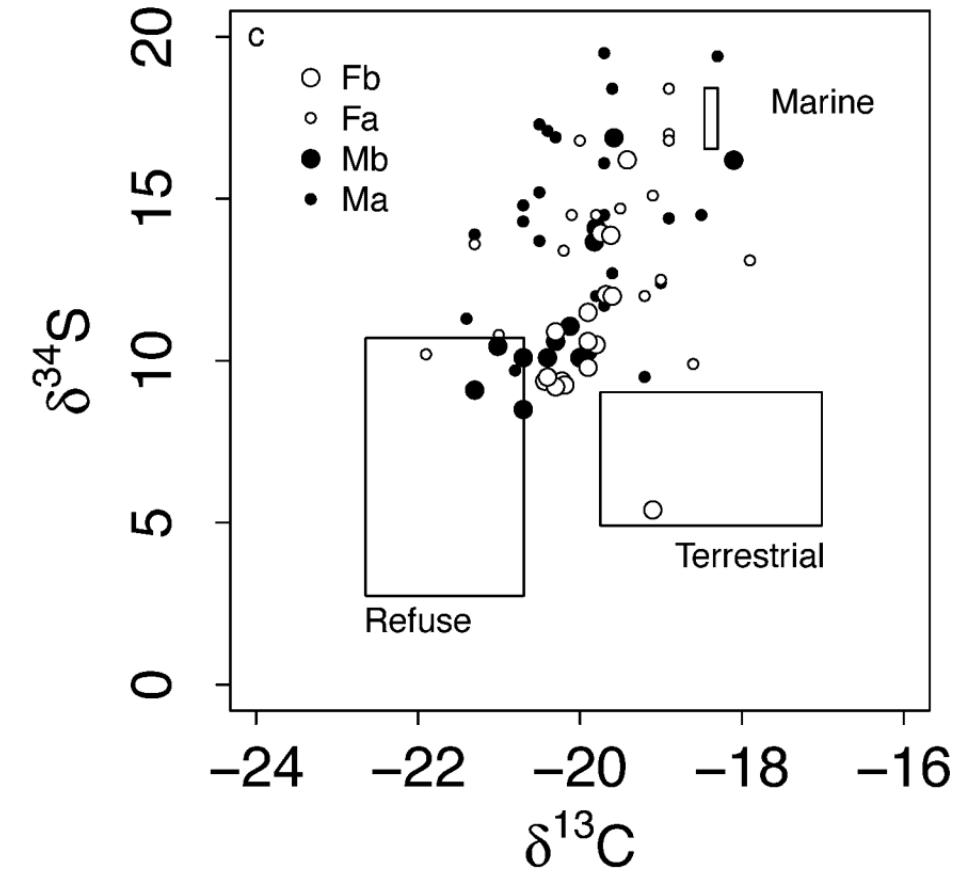
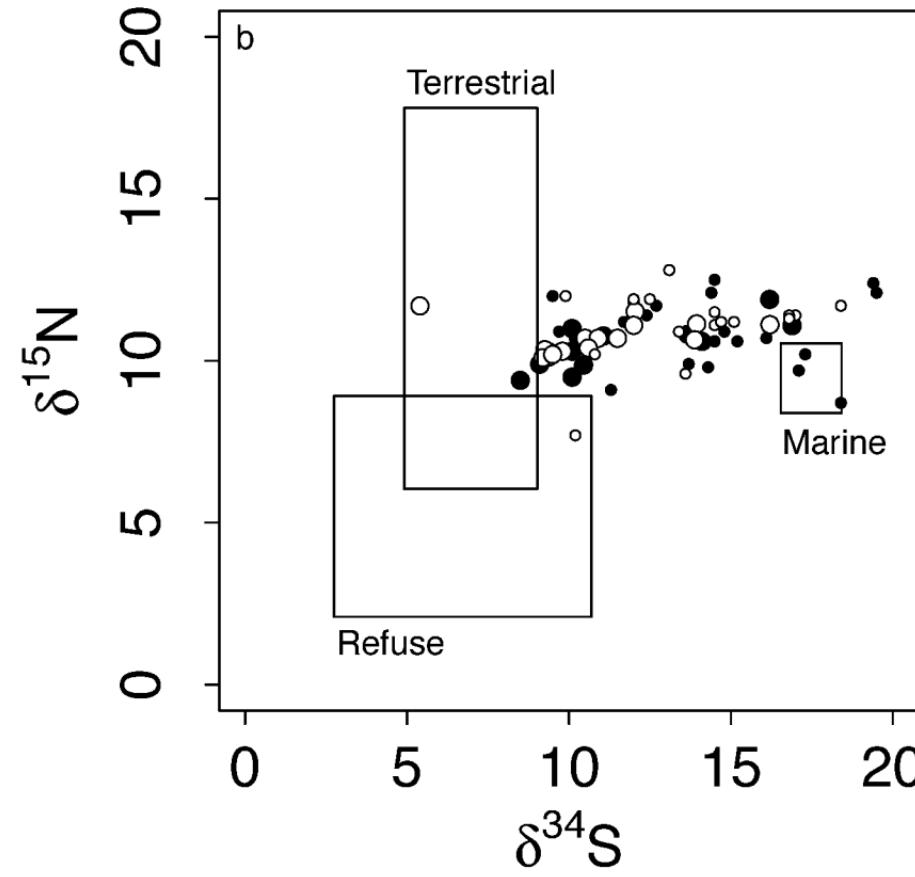
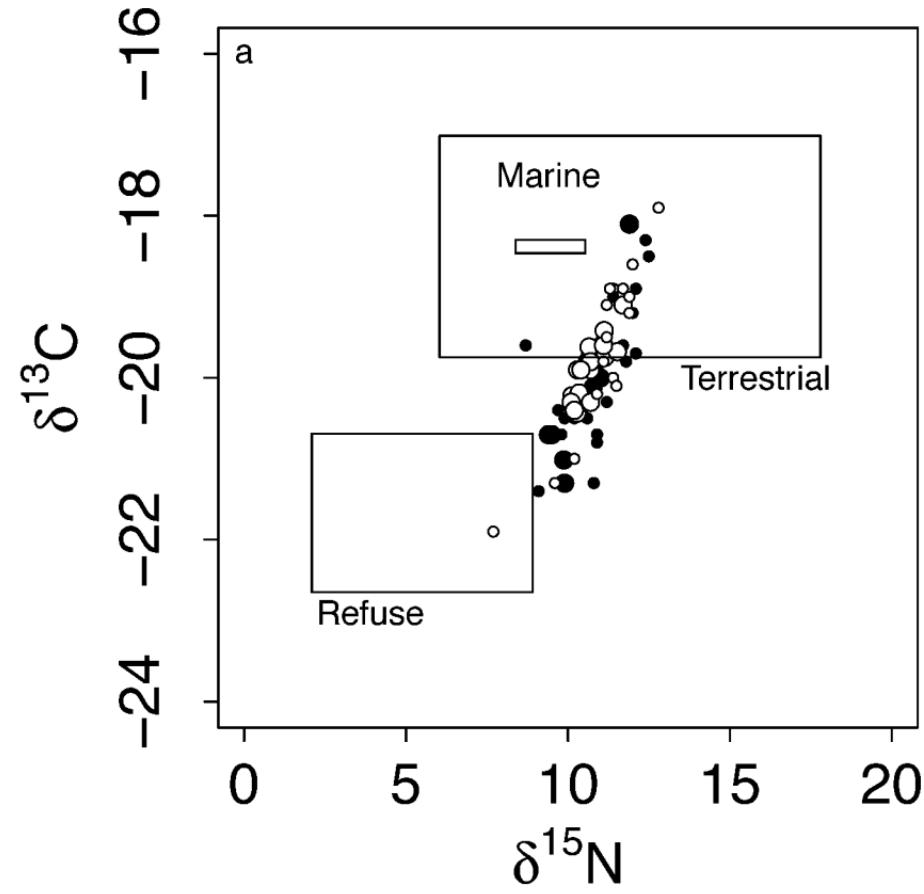
714 estimated by the model averaging of the five best equivalent models with  $\Delta\text{QAICc} < 2$  (Table

715 4).

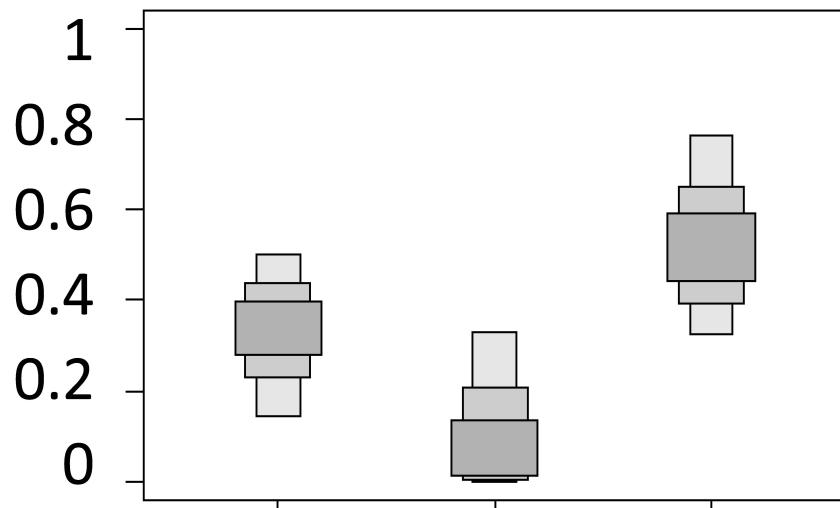
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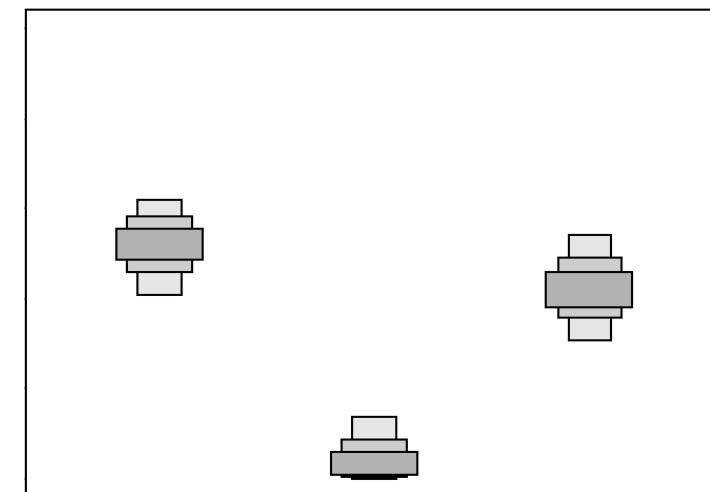
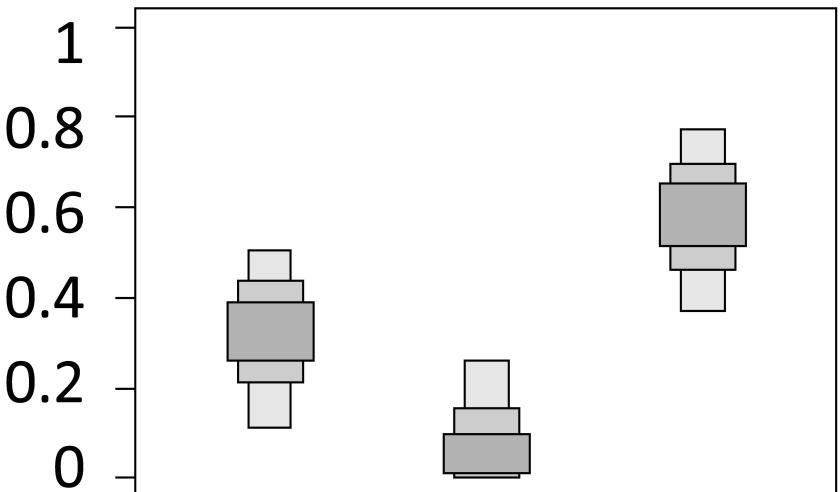
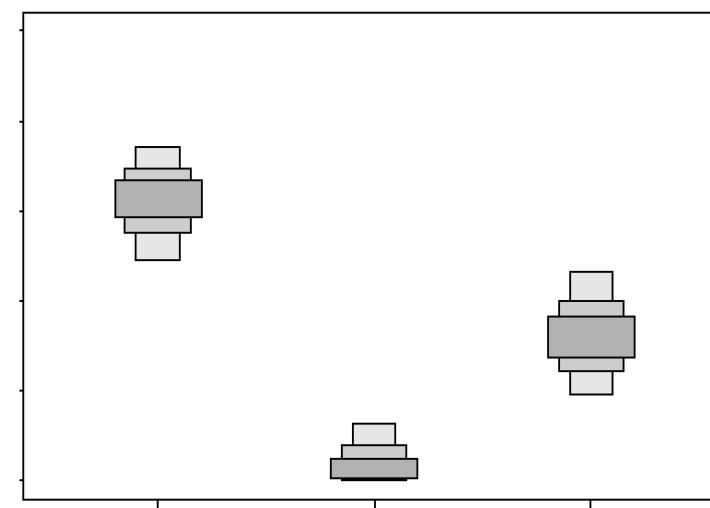




**Before**



**After**



Marine Terrestrial Refuse

Marine Terrestrial Refuse

