Original Article

A comparative analysis of the behavioral response to fishing boats in two albatross species

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Anthropogenic food resources have significantly modified the foraging behavior of many animal species. They enhance large multi-specific aggregations of individuals, with strong ecological consequences. It is challenging to predict how individuals or species can differ in their reaction to these resources. For instance, there are wide variations in seabird species abundance behind fishing boats, and individual variations in interaction rates. Whether this is reflecting variations in fine-scale encounter rates or rather variations in attraction strength is poorly quantified. Here we compare the response of Wandering (WA) and Black-browed (BBA) albatrosses to fishing boats operating in sub-Antarctic waters. We use GPS tracking data from both birds and boats (Vessel Monitoring System). Attraction distances were similar between the 2 species (up to 30 km). BBA foraged further from fishing grounds and encountered boats less frequently than WA, but once they encountered a boat BBA were more strongly attracted (80% vs. 60% chance) and had a higher level of active interaction, compared to WA. Furthermore, in the absence of boats, BBA were rarely observed foraging over the habitat where the fisheries mainly operate, in contrast with WA. We thus report qualitative and quantitative differences in the response of these 2 species to the same fishing fleet. WA, the larger, more dominant and more generalist species was unexpectedly less attracted to fishing vessels. Comparing our results with previously published studies, we suggest that energetic requirements of individuals may be a crucial predictor for assessing risks of interactions with anthropogenic food resources.

Key words: comparative behavior, fisheries, GPS tracking, seabirds, predictable anthropogenic food sources, vessel monitoring system data.

INTRODUCTION

Human activities generate large amount of food available for wildlife, especially since the industrial revolution (Oro et al. 2013). Many such subsidies are concentrated in large quantities within highly predictable patch (in time and/or space). They include for instance dumps, fisheries discards, piles of carcasses or garden bird feeders (reviewed in Oro et al. 2013) and are, often referred to as Predictable Anthropogenic Food Sources (PAFS).The concentration of animals at these places is often higher than in more "natural" feeding contexts, with important and well-described consequences on individual behavior (Gilbert et al. 2016; Uyeda et al. 2015), epidemiology (Becker et al. 2015), population (Bino et al. 2010; Garthe et al. 1996; James et al. 2017) or community dynamics (Cortés-Avizanda et al. 2012; Heath et al. 2014; Newsome et al. 2015; Votier et al. 2004b). However some individuals foraging close to these food sources may never or rarely be attracted to them (Bodey et al. 2014; Newey et al. 2009; Skov and Durinck

2001). In addition to individual variation within populations or species, some species are never attracted to PAFS within their range (Hawkins 1982; Nevitt et al. 2004; Petyt 1995; Ramsay et al. 1997). Understanding the causes of this variation at the individual and species level is an important subject for research in behavioral sciences.

It is often believed that generalists rather than specialists, and/or larger and more dominant species are more likely to exploit PAFS. However, this view may not be supported by empirical data (see Oro et al. 2013). Alternatively, species or individuals could first differ in detection capacities, either qualitatively (sensory channels) or quantitatively. For instance, albatrosses and petrels are among the usual and most threatened ship-following species worldwide (Croxall et al. 2012). They are known to strongly rely on olfaction compared to other seabirds, and may be using distinct odor cues (Nevitt 2008; Nevitt et al. 1995). Large seabird species such as gannets or albatrosses can also use visual detection of conspecifics to detect food sources (Grunbaum and Veit 2003; Thiebault et al. 2014). Second, the ability to successfully forage at PAFS may be variable among individuals and species and in turn affect the

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attraction probability. Observations onboard fishing boats clearly demonstrate the range of differences in foraging behavior exhibited by different seabird species. The capture mode (plunge-diving, surface seizing, kleptoparasitism), the dominance rank within the seabird aggregation, the aggressiveness of individuals and the selectivity in prey item size all vary widely between species and individuals (Arcos 2002; Ashford et al. 1995; Cherel et al. 1996; Hudson and Furness 1989). This can have an impact on inter and intra-species competition level. The time and energy constraints affecting foraging can also differ within species depending on the breeding stage or status (e.g. incubating vs. chick-rearing adults), or the age or sex of individuals (e.g. Weimerskirch et al. 1993; Weimerskirch 1995). Optimal foraging theory predicts that all of these factors could affect foraging decisions such as the probability to join a foraging patch at a vessel, the time individuals spend in a patch, or their position within aggregations (Giraldeau and Caraco 2000; Stephens and Krebs 1986). A similar reasoning has recently been published to describe the natural history of scavengers (Kane et al. 2016), and indeed parallels are often drawn between scavenging behavior and interactions with PAFS. On the other hand because PAFS were developed recently (on evolutionary time scales) they may act as ecological traps (Schlaepfer et al. 2002; Sherley et al. 2017). In such a case, behavioral reactions to boats may not strongly differ between individuals or species (but see Barbraud et al. 2013).

The interaction between seabirds and fishing boats has been the focus of a tremendous number of studies worldwide. Currently, there are large efforts to assess on a coarse-scale (10s of km) the overlap between bird foraging areas and known fishing fleet target areas (Pichegru et al. 2009; Croxall et al. 2013; Tuck et al. 2015). This approach is motivated by acute conservation issues caused by seabird-fisheries interactions and associated mortality consequences (Anderson et al. 2011; Bicknell et al. 2013; Cury et al. 2011), as well as by the apparent reliance on this food resource for many populations (Bicknell et al. 2013). This approach nevertheless implicitly assumes that 2 populations or species with similar coarse-scale overlap with fisheries will show the same level of interaction. Yet for centuries, observers onboard boats have reported not only differences in seabird behavior (see above) but also large variation in species occurrence and abundance (e.g. Cherel et al. 1996; Hudson and Furness 1989; see Tickell 2000 for historical accounts in albatrosses), that did not necessarily reflect broader local seabird abundance (e.g. Bugoni et al. 2011; Oro and Ruiz 1997; Stempniewicz 1994; Weimerskirch et al. 2000). This suggests biases in behavioral attractions.

Accurately quantifying this bias in species composition from onboard observations is however challenging (Skov and Durinck 2001). Similarly, we can rarely infer the rates of individual turnover behind boats from onboard observations. Indeed it is very difficult to recognize and focus on particular individuals for extended periods of time or over the large distances they can cover when following boats (Bodey et al. 2014; Collet et al. 2015; Skov and Durinck 2001). As a result it is difficult to determine whether seabird aggregations are the outcome of a fraction of local individuals remaining for long times or a succession of individuals making up a large proportion of the local seabird community. On the latter issue, 2 lines of studies have brought complimentary information: diet studies assessing the amount of fisheries items consumed by individuals; and more recently analyses of fine spatio-temporal associations between individual birds and boats. The latter can now be assessed through simultaneous GPS tracking of birds and fishing boats. These studies reveal important variations in the amount of interactions with boats at the individual (Bodey et al. 2014; Granadeiro et al. 2011; Patrick et al. 2015; Ramos et al. 2009; Torres et al. 2013a; Votier et al. 2004a 2010), population (Granadeiro et al. 2013; Tew Kai et al. 2013) and species levels (Blaber et al. 1995; Bugoni et al. 2010). These studies however rarely quantified interaction opportunities of sampled individuals (i.e., whether they flew within detection range of a boat). Hence it is still challenging to determine whether individuals with low interaction rates or low discards levels in their diet "ignored" boats or simply did not encounter them at fine enough scales to detect them (Collet et al. 2017a). This question seems to have rarely been addressed in other PAFS systems (but see works on white storks: Gilbert et al. 2016; griffon vultures: Monsarrat et al. 2013; hares: Newey et al. 2009; or shearwaters: Soriano-Redondo et al. 2016).

Here, we compare the behavioral response to longline fishing boats between Wandering albatrosses (*Diomedea exulans*, hereafter WA) from Crozet Islands and Black-Browed albatrosses (*Thalassarche melanophrys*, BBA) from Kerguelen Islands, at different stages of their breeding season. Both are large size species known to interact with fishing boats in large extent worldwide (e.g. Granadeiro et al. 2013; Tuck et al. 2015). They breed on sub-Antarctic islands, often sympatrically, but they differ in habitat preferences during breeding: BBA are neritic-slope foragers remaining over shelf waters (Cherel and Weimerskirch 1995; Wakefield et al. 2011; Weimerskirch et al. 1997), while WA exploit a much wider range of bathymetric conditions, from sub-Antarctic shelf waters to subtropical and Antarctic oceanic areas (Weimerskirch et al. 2014). Both are surface-feeding seabirds, although BBA but not WA can occasionally dive to a few meters under the surface (Prince et al. 1994). It has been suggested that the smaller size of BBA may limit the size of food items they can swallow compared to WA (Ashford et al. 1995; Cherel et al. 1996). At boats, WA always dominate BBA during agonistic interactions (Weimerskirch et al. 1986). The dominance and wider diet of WA may lead to the hypothesis that they should forage more frequently at boats. However, this is not fully supported by onboard observations suggesting that BBA are more active within aggregations at boats (Ashford et al. 1995; Cherel et al. 1996).

We examine the response of these 2 species of albatross to the same fishing fleet that is operating in 2 sectors of the Southern Ocean: Kerguelen waters when BBA are incubating and rearing chicks, and then Crozet waters, when WA are incubating. We used fine-resolution GPS tracking data from seabirds coupled with GPS positions of vessels, recorded several times per hour (from Vessel Monitoring System and additional data on fishing operations). WA are attracted to boats at distances up to 30 km (Collet et al. 2015). We first assess whether this attraction distance is similar in BBA. Second we use these estimates as thresholds to statistically compare whether species differed in their probability to be attracted to boats they encountered, in their individual residence time once attracted and in their position within the seabird aggregation (distance from the boat when attending it). Finally, we compare to what extent each species "naturally" exploits the habitat used by boats when no boats were close by to assess how important boats are in habitat choice.

MATERIAL AND METHODS

Bird tracks

GPS loggers (I-GotU Mobile Technology) were deployed on breeding adult albatrosses, in December 2011–January 2012 for black-browed albatrosses at Cañon des Sourcils Noirs, Kerguelen, and

in January–March 2011 and 2012 for wandering albatrosses at Possession Island, Crozet Archipelago. Birds were caught on their nest and GPS loggers were attached to their back feathers with adhesive Tesa tape. Birds were released as soon as possible (generally within 5 min, never >15 min). They left the colony shortly after being released, to forage at sea, and were captured again on their nest upon their return to recover loggers. The mass of attached devices was c. 1% of the mass of BBA, c. 0.3% of the mass of WA, i.e. well below the 3% threshold suggested to effect bird behavior (Phillips et al. 2003). All procedures had been approved and authorized by the Ethics Committee of IPEV (Institut Paul-Emile Victor), the Comité de l'Environnement Polaire, and the administration of Terres Australes et Antarctiques Françaises (TAAF).

Sixty-nine incubating WA were equipped with GPS loggers recording fixes every 15 min. 72 incubating trips were recorded for this species, all of them occurred while boats were operating on the Crozet shelf. For BBA, GPS loggers were programmed to record positions every 2 min: we down-sampled to 1 fix in every 7, to have a recording frequency of 14 min, comparable to that of WA. 77 chick-rearing BBA and 9 BBA in late incubation phase were equipped, with several consecutive trips recorded particularly during chick-rearing. A total of 189 trips (>12 h) were recorded for BBA, all of which occurred while boats were present within a 350 km radius around the focal bird. We assigned the 261 trips to 3 species-breeding stage categories for our analyses: BBA incubation ($n = 12$), BBA-chick rearing ($n = 177$), and WA incubation ($n = 72$).

Preliminary analyses did not reveal sex effects on analyzed parameters of boat interactions (WA: Collet et al. 2017a; BBA: Patrick and Weimerskirch 2014 and Weimerskirch et al, unpublished data). Hence, sex was not considered in the analyses presented here.

Boat data

VMS data (GPS fixes every 1 h) was provided by the Pecheker database (Gasco 2011), as longline fleets legally operate in French subantarctic waters off Kerguelen and Crozet. The same 7 boats operate every year in the Kerguelen EEZ until January and then in the Crozet EEZ until March, complying with fishing practices regulations (Journal Officiel des Terres Australes et Antarctiques Françaises 2010). In addition, for both Kerguelen and Crozet operations, we had the date, time and location of all lines set and hauled which we integrated into the VMS tracking data. The legislation imposes that line setting occurs only at night to limit bird interactions during these operations. Most interactions thus occurred during line hauling. Boat tracks were then interpolated to obtain a location every 10 min (as a trade-off between minimizing the ratio of real/interpolated boat positions, and minimizing the time lag between birds and boats locations).

Birds attraction and attendance distance thresholds

To analyze behavioral responses of seabirds to boats, we distinguished between encountering (i.e. entering within detection-attraction range) and attending boats (i.e. sitting within short distance from them). We first quantified encounter rates in each species, accounting for boat density and bird foraging trip duration. We then compared the response of the 2 species after boats had been encountered (e.g. probability of attending, time spent attending per encounter). To define an encounter, we estimated at what distance birds could potentially be attracted to boats ("attraction distance threshold"). This was done in Collet et al. (2015) for WA, and

here we used the same methodology for BBA: we calculated the maximal distance at which birds were observed flying in the direction of boats (i.e., within 10°) more than expected from chance (i.e., 10/180 as expected for a uniform distribution of directions; Collet et al. 2015). We defined "attendance behavior" as birds sitting (speed < 10 km/h) within very close range from boats. The attendance distance threshold for WA was previously estimated at 3 km (Collet et al. 2015). To facilitate direct comparisons between species, we used the same 3 km threshold for both BBA and WA.

Comparison of behavioral responses of birds

Once each bird position had been assigned a status ("attendance" if sitting on the water within 3 km of a boat, "within attraction range" if located within 30 km of a boat, "none" in any other circumstances), we defined an encounter event as a series of consecutive locations remaining within the attraction range of a boat. When 2 such series were separated by less than 4 GPS positions outside the attraction range (i.e. ~1 h, the "time-to-return" threshold), we grouped them as a single encounter. An encounter event thus represents one "opportunity", seized or not, to attend a boat.

We compared encounter chances between the 3 species-breeding stage categories (WA-incubation, BBA-incubation, BBA-chick rearing), as the number of encounter events per trip. We used a 2-step GLMM to account for zero-inflation: a binomial model evaluating the probability to encounter at least one boat, followed by a negative binomial GLMM evaluating the number of encounters per trip for trips with at least one encounter. We included as covariates the trip duration and the average number of boats present within 350 km of the bird during the trip.

To compare the strength of attraction to boats between species, for each encounter event we determined whether there was at least one attending location during the encounter. We modeled this proportion in relation to the species-breeding stage category, using a GLMM with a binomial structure. Almost all BBA encounter events started within 1 hour of a fishing operation; hence, there was not enough variability at the start of encounters to test effects of boat activity on the probability of attraction, and this variable was not included in models. For consistency between species, we discarded WA encounter events that started more than 1 h from a fishing operation. We included as a covariate the average number of boats present within detection range (30 km) during the encounter.

For encounters which contained attendance, we compared the attendance behavior between the 3 species-breeding stage categories. Three response variables were used: the total duration of the encounter (which contained attendance events), the proportion of this encounter duration spent attending boats (sitting within 3 km, rather than simply remaining within 30 km), and finally, the average distance from boats when attending them (<3 km). For these 3 models, we also included the average number of boats present within detection range during the encounter, and a variable accounting for vessel fishing activity during the encounter. Indeed though all retained encounters started within 1 h of a fishing activity (see above), some ended well after the end of fishing activities. This fishing-activity covariate was the proportion of the whole encounter duration where the boat was actively fishing (rather than transiting). We tested for the interactions between boat activity and species, but removed it from final models when non-significant. We did not test the interaction between species and average number of boats as it was not variable enough to be biologically meaningful. We used a negative binomial structure for models of encounter duration and proportion

of time attending boats (with encounter duration as an offset), and a Gaussian structure for the average distance when attending.

Habitat selection with or without boats

To determine the extent of "natural" foraging that occurs in areas where boats are present, we first examined the duration of encounters (remaining within 30 km of a vessel) not containing attendance behavior, with a negative binomial GLMM.

Furthermore, we also compared the tendency of species to select habitats exploited by boats when no boats were present. Boats tended to operate over shelf-slope waters, so that most bird attendance occurred over waters between −600 and −1400 m deep (see Results). Since albatrosses are active during the day (Weimerskirch and Guionnet 2002), we developed a model using the number of daylight locations spent in areas of shelf-slope depth as the response variable (−600 km to −1400 m) when not within attraction range of a boat (>30 km). This was offset against the total number of trip locations during daylight. Explanatory variables included the species (BBA or WA) with a binary variable evident of whether a bird was sitting on the water (as a proxy for foraging attempt) or flying

(as a proxy for habitat encountered). BBA colony at Kerguelen is located c. 120 km from the −1000 m isobath, whereas this isobath is about 15 km from the WA Crozet colony. Hence for this analysis we only considered BBA GPS locations that were >120 km from the colony to discard parts of tracks which were too close to the colony to encounter shelf slopes. This is a more conservative analysis, and qualitative results remained unchanged when including all BBA GPS locations. Likewise, we only considered WA GPS locations that were over the Crozet shelf area.

All analyses were carried out in R, using lme4 (Bates et al. 2015) and nlme (Pinheiro et al. 2016) for statistical models, packages geosphere (Hijmans et al. 2015) and tripEstimation for track analyses (Sumner and Wotherspoon 2010), and marmap (Pante and Simon-Bouhet 2013) for mapping.

RESULTS

During incubation and chick rearing, BBA foraged mainly over the Kerguelen shelf, and boat attendance occurred mainly on the shelf edge (Figure 1a and b). WA foraged mainly over oceanic waters but
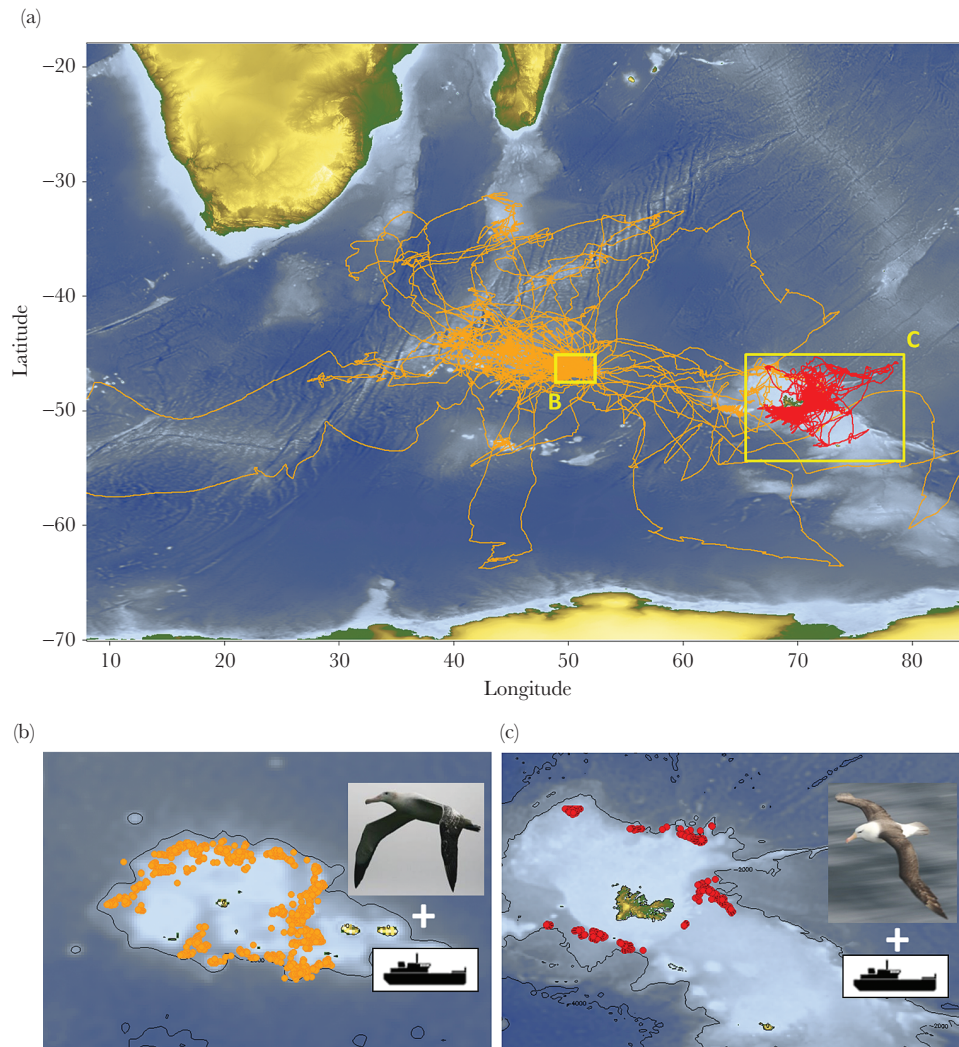

Figure 1
All studied tracks (a) from incubating WA from Crozet (orange) and chick-rearing and incubating BBA from Kerguelen (red). Colors reflect bathymetry, with lighter blues indicating shallower shelf waters. All bird GPS locations identified as "attending" boats (<3 km from a boat with speed<10 km/h) are shown for WA (b) and BBA (c) over the edge of Crozet and Kerguelen shelves respectively (black solid lines indicate 2000 m isobaths; see also Figure 5).

boat attendance occurred over the shelf edge of the Crozet islands (Figure 1a and c). The attraction distance to boats for BBA was 28.6 km (95% CI: 26.0–31.2 km; Figure 2a), i.e., similar to that of WA (29.2 km, 95% CI: 25.5–32.9 km, Figure 2b ; Collet et al. 2015). Trips were shorter in duration for chick-rearing BBA than for incubating BBA ($t = 5.655$, df = 118, $P < 0.001$; Figure 3a). WA trips were longer in duration than both chick-rearing BBA trips ($t = 14.198$, df = 130, $P < 0.001$; Figure 3a) and incubating BBA trips ($t = 3.996$, df = 75, $P < 0.001$), which have both been previously reported (Collet et al. 2017a; Patrick and Weimerskirch 2014).

In BBA, 42 trips lasted less than 24 h (41 from chick-rearing birds, 1 from an incubating bird), and during these short trips boats were encountered in only 2 occasions. However 53.1% of BBA tracks that lasted more than 24 h (78 out of 147 tracks, involving 64.3% of all tracked BBA individuals) contained at least one boat encounter. The probability of encountering at least one boat during a BBA trip >24 h increased with trip duration ($z = 2.396$, $P = 0.02$) and tended to be higher for incubating BBA than chick-rearing BBA ($z = 1.878$, $P = 0.06$, Figure 3b). In contrast, up to 86.1% of all WA tracks (62 out of 72) contained at least one boat encounter, which is more than for chick-rearing BBA ($z = 2.586$, $P < 0.01$, Figure 3b) but statistically similar to the proportion for incubating BBA ($z = -0.133$, $P = 0.89$). Overall the probability to encounter at least one boat tended to increase with the average number of boats present in the area (0.33 ± 0.18, $z = 1.854$, $P = 0.06$).

The number of encounters within one trip, when >0, was not related to trip duration ($z = -1.066$, $P = 0.29$) nor the average number of boats in the area ($z = 0.623$, $P = 0.53$). BBA mostly had only one encounter per trip (average when >0: 1.42 ± 0.79; Figure 3b) with no difference between reproductive stages ($z = 0.625$, $P = 0.53$). WA generally had several encounters per trip (average when >0: 3.47 ± 2.03; $z = 5.299$, $P < 0.001$; Figure 3b). In BBA, 79.1% of boat encounters resulted in boat attendance, a much higher proportion than for WA (57.8%, $z = -2.560$, $P = 0.01$, Figure 4a). There was no difference in this proportion between chick-rearing and incubating BBA ($z = 0.548$, $P = 0.58$). The number of boats within the detection range during the encounter had a positive effect on the probability of attending one of the boats (2.16 ± 1.03, $z = 2.095$, $P = 0.04$).

The duration of encounters which resulted in attendance behavior was variable (median 10.8 h, range 2.0–86.5 h), with no difference

between species ($z = -0.786$, $P = 0.43$) nor breeding stage in BBA ($z = -0.120$, $P = 0.91$). Encounter events lasted longer when more boats were within detection range (0.66 ± 0.07, $z = 9.467$, $P < 0.001$) and for WA (1.06 ± 0.29, $z = 3.704$, $P < 0.001$), but not for BBA, ($z = 0.175$, $P = 0.86$) encounter events were longer when boats were actively fishing. The proportion of the total encounter duration which was actually spent attending boats (sitting within 3 km) was higher when boats were actively fishing (0.78 ± 0.20, $z = 3.970$, $P < 0.001$) for both BBA and WA ($z = 0.713$, $P = 0.48$). WA spent a lower proportion of the encounter duration attending boats than chick-rearing BBA ($z = -5.794$, $P < 0.001$; Figure 4c), but we did not detect differences between incubating WA and incubating BBA ($z = 0.388$, $P = 0.31$). Incubating BBA proportionally spent less time attending boats compared to chick-rearing BBA ($z = -2.145$, $P = 0.03$, Figure 4c). The number of boats within detection range had no effects on this proportion ($z = -0.050$, $P = 0.96$).

When attending boats, chick-rearing BBA were found closer to boats than WA ($t = 4.859$, df = 79, $P < 0.001$; Figure 4d) but not closer than incubating BBA ($t = 1.336$, df = 79, $P = 0.19$). The average distance from boats when attending was not affected by the number of boats within attraction range ($t = -0.629$, df = 43, $P = 0.53$) nor by their fishing activity ($t = -1.650$, df = 43, $P = 0.11$), in both species ($t = -0.525$, df = 42, $P = 0.60$). Encounters that did not contain attendance were generally short (2.1 ± 1.2 h, median 1 h 15 min, Figure 5a) and did not differ in duration between species nor reproductive stages (chick-rearing BBA vs. WA: $z = 1.150$, $P = 0.25$; vs incubating BBA: $z = -0.139$, $P = 0.89$). The duration did not depend on the number of boats within detection range ($z = 1.446$, $P = 0.15$) nor on their fishing activity ($z = 0.125$, $P = 0.90$).

Attendance behavior occurred mainly over shelf-slope waters (mean -1140 ± 31 m, Figures 1 and 5b, e, f) where fisheries operate around Crozet and Kerguelen. When no boats were present within detection ranges, WA regularly sat on the surface (a pre-requisite for feeding) over shelf-slope waters (Figure 5b, d), whereas BBA less frequently sat over these waters (Figure 5b, c; $t = 3.605$, df = 244, $P < 0.001$).

DISCUSSION

We showed clear differences in the behavioral response to boats between chick-rearing BBA in Kerguelen and incubating WA in Crozet, which interact with the same toothfish longline fleet.
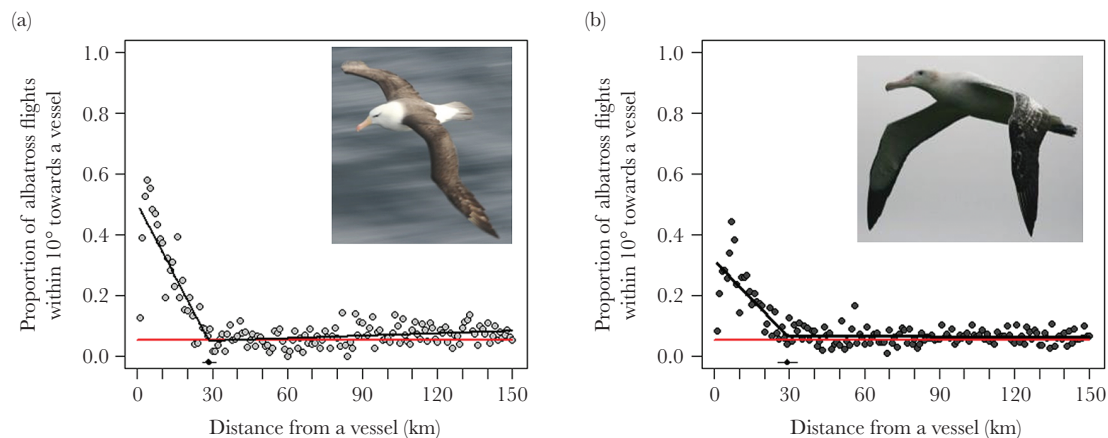

(a) (b)

Figure 2
Proportion of flights directed (<10°) towards a boat for BBA (a) and for WA (b, re-drawn from Collet et al. 2015), as a function of the distance from boats. The red, straight line indicates null expectations (10/180) for birds not attracted to boats. The broken black line is the fitted segmented linear regression, with a breakpoint for BBA estimated at 28.6 km. The breakpoint estimated for WA from the same methodology was 29.2 km (Collet et al. 2015).
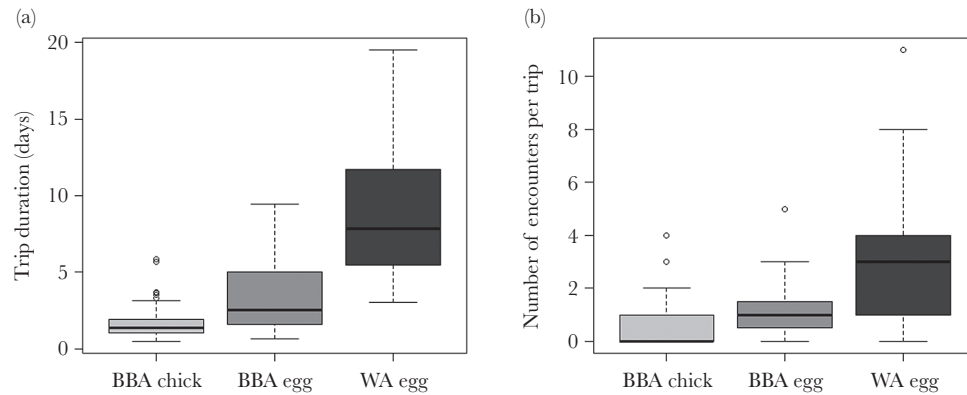
Figure 3

Trip duration (a) and numbers of encounter per trip (b) for the different species and breeding stages. Trip duration had only limited and non-linear influence on the number of encounters during trips (see Results).
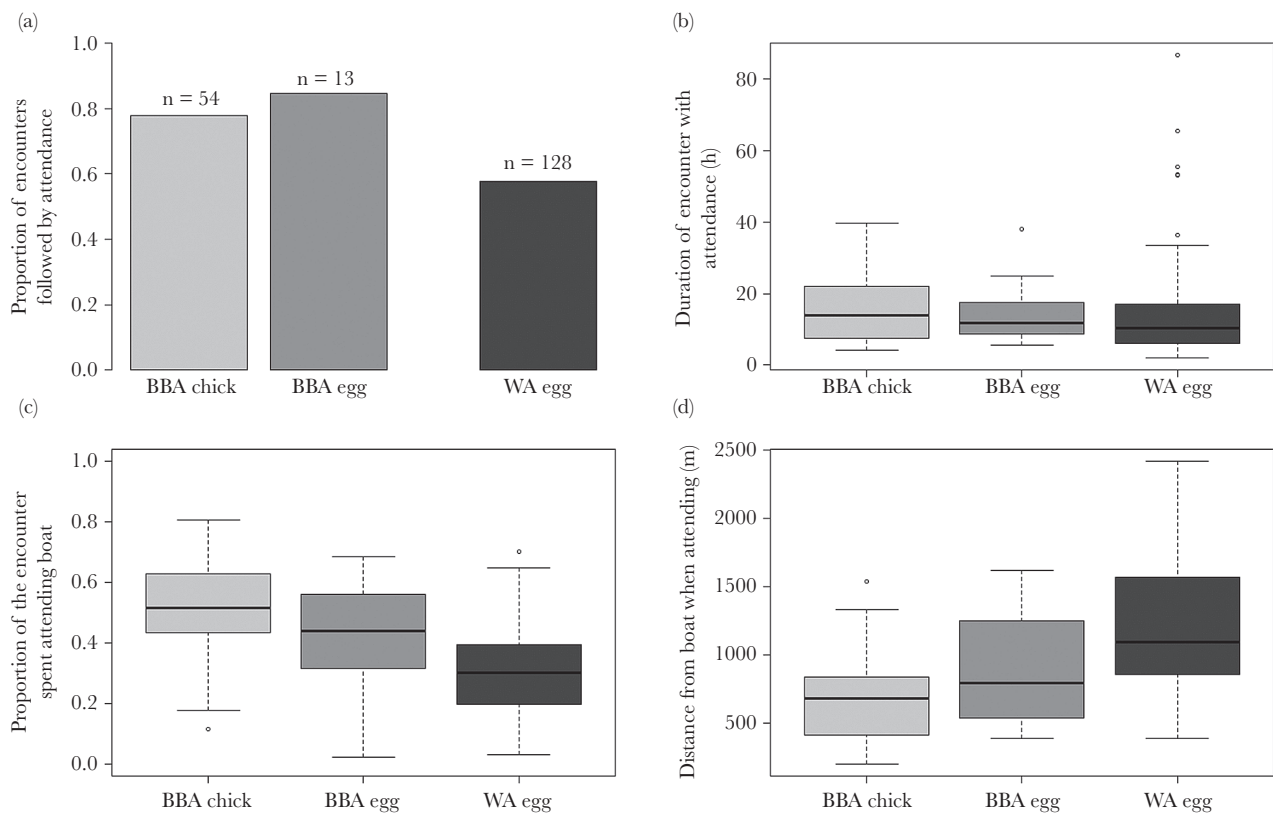

Figure 4

Probability to be attracted (a) and behavior when attending: total duration of encounters (b), proportion of the encounter duration spent attending (c) and average distance from boats when attending (d) for different species and breeding stages.

Overall, attraction distances were similar between the 2 species. However, BBA encountered boats less frequently than WA; but once boats were encountered, BBA showed stronger attractions and more active interactions with boats, compared to WA. In addition, we found evidence that WA naturally foraged over shelf-slope waters where fisheries mainly operate, whereas BBA targeted these areas mainly to attend boats.

It is generally considered that larger, more dominant species and generalist species are more likely to attend PAFS (Bicknell et al. 2013, but see Oro et al. 2013). In our system, WA clearly dominate all agonistic interactions over BBA and any other species present at boats (Weimerskirch et al. 1986). Moreover, WA can forage over a wide variety of marine habitats (Weimerskirch et al. 2014), compared to BBA which seem to be mainly restricted to neritic waters (Cherel and Weimerskirch 1995; Copello et al. 2014; Wakefield et al. 2011; Weimerskirch et al. 1997). Hence, our results suggest that the smaller and less generalist species was actually the more strongly attracted to boats. In Spain, it was shown that shearwaters could extensively attend boats, despite being outcompeted and dominated by gull species (Arcos 2002) which are traditionally seen as more generalists than procellariformes (see also Oro et al. 2013). Our results also seem consistent with onboard observations of the behavior of birds close to boats. Indeed BBA tend to be more actively involved in multi-species feeding aggregations than WA (Ashford et al. 1995; Cherel et al. 1996).
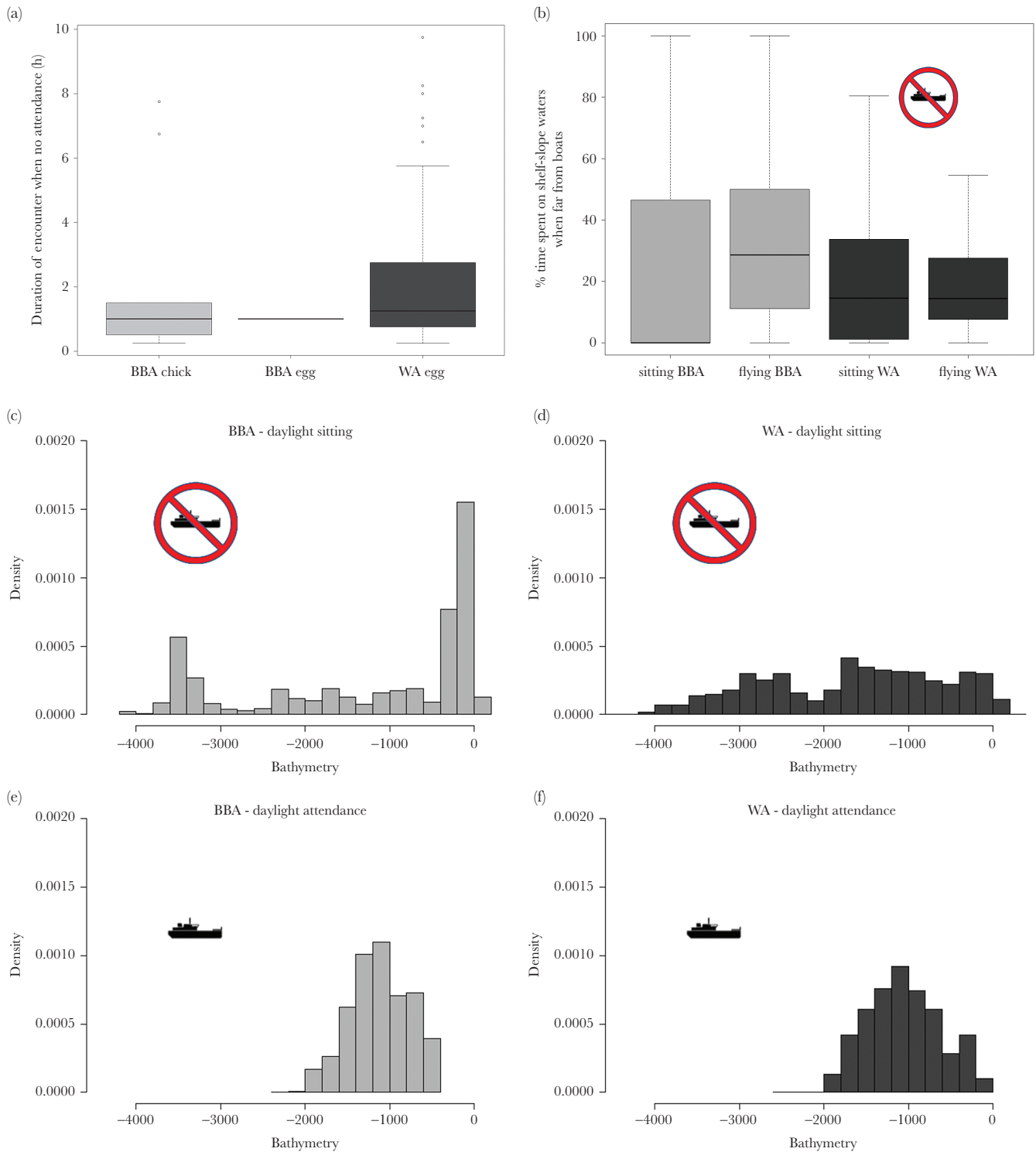
Figure 5

Behavior when not attending: duration of encounters when no attendance occurred (a), proportion of the trip duration spent sitting or flying over shelf-slopewaters when no boats were within 30 km (b), and bathymetry distribution when BBA (c) and WA (d) were sitting >30km from any boat compared to bathymetry distribution when BBA (e) and WA (f) were sitting within 3 km of a boat.

Seabirds provisioning young chicks are more constrained energetically than incubating individuals (Ricklefs 1983; Weimerskirch and Lys 2000). It is striking to note that here the most constrained birds, i.e. BBA brooding chicks, were more strongly attracted to boats. In Spain, during breeding white storks increased efforts to

join and forage on dumps, compared to the non-breeding season (Gilbert et al. 2016). Cape gannets and griffon vultures were shown to switch on PAFS mainly when natural prey were scarcer (Monsarrat et al. 2013; Tew Kai et al. 2013). Scopoli's shearwaters in the Mediterranean Sea increased feeding on baited hooks

from longlining boats when the density of trawling boats decreased (Soriano-Redondo et al. 2016). At Kerguelen, boats are generally encountered relatively far from the BBA colony, such that encounters were more likely for birds foraging further. During the chick-rearing season, these may be individuals pushed out in less profitable waters by more dominant individuals (Patrick and Weimerskirch 2014). Indeed, shyer BBA in this population have been found to be more likely to range over shelf-slope areas (Patrick and Weimerskirch 2014), although no difference in their overlap with boats was detected. We also showed that although BBA less frequently sat on the water (a pre-requisite for feeding) on shelf-slope areas when no boats were present, they still spent a non-trivial part of their trip flying over these areas. The relatively low boat density in the region implied that very few sampled BBA individuals encountered boats across several of their consecutive trips, limiting opportunities to test for individual repeatability in this behavior (Patrick et al. 2015). Further work is needed to evaluate whether the BBA which attend boats in Kerguelen could be the less competitive individuals, forced to forage in lower quality waters. More generally, if PAFS especially attract animals with higher energetic requirements at the expense of more natural food, it may exacerbate issues related to the nutritional quality of these food resources (Grémillet et al. 2008 2016).

Alternatively, part of the behavioral differences between species reported here may be caused by differential detection capacities beyond direct visual scope (Martin 1998; Martin and Prince 2001; Nevitt et al. 2004, 1995). The maximum distance of direct attraction was similar between BBA and WA, and higher than other estimates from seabird species in the North Sea (Skov and Durinck 2001). This distance of 30 km roughly corresponds to the distance beyond which boats would fall below the horizon line for a flying albatross (Collet et al. 2015), although WA have been reported to reach higher flight heights than BBA when soaring (Pennycuick 1982). While this suggests that both species strongly rely on visual detection of boats, they could also be attracted by indirect cues such as local enhancement through seabird aggregations around boats. BBA have been shown to react to local enhancement (Grunbaum and Veit 2003), but whether this may also be the case for WA is unknown. Our analyses also do not exclude the hypothesis of a potential olfaction mechanism for attraction from further distances (Mardon et al. 2010; Nevitt et al. 2008, 1995), beyond visual scope. Birds might be able to detect a food source through its smell without being able to accurately target it (i.e. within 10° accuracy) before seeing it. Anecdotal dynamic visualization of concurrent WA-boat tracks suggests attractive responses could at times occur as far as 50 km, clearly beyond horizon distance. The direct approach reported here may thus at times only represent the final stage of attraction. Such inter-species differences in mechanisms of large scale detection of food patch are known for vultures, and thought to be the cause of community disruptions now that highly predictable "vulture restaurants" are available (Cortés-Avizanda et al. 2012). On the other hand, we also reported differences between breeding stages in BBA. Although sample sizes were small, it suggests that detection capacities are not solely responsible for all observed differences.

Another important question arising from our results is the extent to which habitat selection analyses can be quantitatively biased by not accounting for the presence of PAFS. BBA are considered in the literature as shelf and shelf-slope foragers (Cherel et al. 2000; Copello et al. 2014; Wakefield et al. 2011; Weimerskirch et al. 1997). Diet analyses of chick-rearing BBA in our study population indicated a significant but relatively low prevalence of fish and invertebrate prey known to occur on slope but not shelf waters (Cherel et al. 2000). However an important part of these slope-water prey are also found in the gut content of *Dissostichus eleginoides* (Cherel et al. 2004), the main target species of the fishing boats in the area. Slope-water prey found in BBA gut contents may, at least partly, reflect secondary ingestion (Cherel and Klages 1998, but see Xavier et al. 2012). Indeed our results suggest that most of the time spent sitting at the sea surface of shelf-slope waters by BBA occurred around boats, and that these areas were not "naturally" selected by individuals when no boats were present, in contrast to WA. The recent development of GPS loggers able to record radar emissions from encountered boats could help quantify the risk of bias in habitat selection analyses for other populations, even when VMS data is not available, which is commonly the case (Weimerskirch et al. forthcoming).

Finally, our results have also strong implications for the conservation of seabird species. First, many populations worldwide are at risk of being caught in long lines (Anderson et al. 2011). Our results emphasize the need to directly quantify the behavioral response of seabirds at boats if we are to accurately estimate interaction risks quantitatively (Croxall et al. 2013; Torres et al. 2013b). Overlaying seabirds foraging areas over large scale maps of fishing activity enables us to estimate whether a population is at risk of encountering boats. Our results however show that the response to encountered boats can largely vary beyond encounter chances, and are currently challenging to predict, even qualitatively. Second, our results also highlight that even after mitigation measures are implemented to limit food availability to seabirds, and reduce bycatch risks, seabirds can still be strongly attracted to boats. In the particular case of the toothfish fishery operating in the French EEZs, it is important to quantify the amount of food seabirds can actually obtain now that mitigation measures have efficiently been implemented to reduce albatross bycatch (Delord et al. 2005; Journal Officiel des Terres Australes et Antarctiques Françaises 2010, sec. Annexe II-Exercice de la pêche). Indeed, lines are set only at night, so that baits are not accessible to diurnal albatrosses, to avoid them being hooked. In addition, fishermen are required to limit discards at maximum, and to restrict them to periods when boats are not hauling lines, which is when BBA and WA are more actively attending boats (see also Collet et al. 2017a). Being able to quantify the amount of food that albatrosses can obtain from the fishery is the next step to be able to interpret the differences in attraction between species.

In conclusion, we stress that more studies should attempt to describe individual foraging decisions relative to PAFS and the factors affecting them. Indeed our results clearly demonstrate that the attraction probability once in the vicinity of fishing boats, the residence time and the spatial distribution when attending boats, can largely vary between 2 similar species and during periods with different energetic requirements for the same species. This is in contrast with a study at the intra-specific scale in WA that overall showed minor variations across individuals of different age and sex (Collet et al. 2017a). We suggest that "hungry" individuals, with higher energetic needs and/or scarcer natural prey, rather than generalist species, may be the ones most likely to attend PAFS (Gilbert et al. 2016; Monsarrat et al. 2013; Tew Kai et al. 2013) given these food sources often present low nutritional quality (Grémillet et al. 2008). Furthermore, we show that despite huge efforts in French EEZs to limit the overlap between albatrosses and fisheries, attendance at vessels is still high. Such empirical studies are necessary to fuel a better theoretical understanding and a more

accurate predictive power of these interactions of wildlife with human activities in an era of rapid global changes.

REFERENCES

Anderson OR, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O, Black A. 2011. Global seabird bycatch in longline fisheries. Endanger Species Res. 14:91–106.

Arcos JM. 2002. Foraging ecology of seabirds at sea: significance of commercial fisheries in the NW Mediterranean. Barcelona (Spain): Universitat de Barcelona.

Ashford JR, Croxall JP, Rubilar PS, Moreno CA. 1995. Seabird interactions with longlining operations for Dissostichus eleginoides around South Georgia, April to May 1994. CCAMLR Sci. 2:111–121.

Barbraud C, Tuck GN, Thomson R, Delord K, Weimerskirch H. 2013. Fisheries bycatch as an inadvertent human-induced evolutionary mechanism. PLoS ONE. 8:e60353.

Bates D, Machler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67:1–48.

Becker DJ, Streicker DG, Altizer S. 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. Ecol Lett. 18:483–495.

Bicknell AWJ, Oro D, Camphuysen KCJ, Votier SC. 2013. Potential consequences of discard reform for seabird communities. J Appl Ecol. 50:649–658.

Bino G, Dolev A, Yosha D, Guter A, King R, Saltz D, Kark S. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. J Appl Ecol. 47:1262–1271.

Blaber SJM, Milton DA, Smith GC, Farmer MJ. 1995. Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. Mar Ecol Prog Ser. 127:1–13.

Bodey TW, Jessopp MJ, Votier SC, Gerritsen HD, Cleasby IR, Hamer KC, Patrick SC, Wakefield ED, Bearhop S. 2014. Seabird movement reveals the ecological footprint of fishing vessels. Curr Biol. 24:R514–R515.

Bugoni L, Griffiths K, Furness R. 2011. Sex-biased incidental mortality of albatrosses and petrels in longline fisheries: differential distributions at sea or differential access to baits mediated by sexual size dimorphism? J Ornithol. 152:261–268.

Bugoni L, McGill RAR, Furness RW. 2010. The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. J Exp Mar Biol Ecol. 391:190–200.

Cherel Y, Duhamel G, Gasco N. 2004. Cephalopod fauna of subant-arctic islands: new information from predators. Mar Ecol Prog Ser. 266:143–156.

Cherel Y, Klages N. 1998. A review of the food of albatrosses. In: Albatross Biology and Conservation. Chipping Norton (UK): Surrey Beatty & Sons. p. 113–136.

Cherel Y, Weimerskirch H. 1995. Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. Mar Ecol Prog Ser. 129:295–300.

Cherel Y, Weimerskirch H, Duhamel G. 1996. Interactions between long-line vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. Biol Conserv. 75:63–70.

Cherel Y, Weimerskirch H, Trouve C. 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. Mar Ecol Prog Ser. 207:183–199.

Collet J, Patrick SC, Weimerskirch H. 2017a. Behavioral responses to encounter of fishing boats in wandering albatrosses. Ecol Evol. 7:3335–3347.

Collet J, Patrick SC, Weimerskirch H. 2015. Albatrosses redirect flight towards vessels at the limit of their visual range. Mar Ecol Prog Ser. 526:199–205.

Collet J, Patrick SC, Weimerskirch H. 2017b. Data from: a comparative analysis of the behavioural response to fishing boats in two albatross species. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.qm28r.

Copello S, Pon JPS, Favero M. 2014. Spatial overlap of Black-browed albatrosses with longline and trawl fisheries in the Patagonian Shelf during the non-breeding season. J Sea Res. 89:44–51.

Cortés-Avizanda A, Jovani R, Carrete M, Donázar JA. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. Ecology. 93:2570–2579.

Croxall J, Small C, Sullivan B, Wanless R, Frere E, Lascelles B, Ramirez I, Sato M, Yates O. 2013. Appropriate scales and data to manage seabird-fishery interactions: Comment on Torres et al. (2013). Mar Ecol Prog Ser. 493:297–300.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int. 22:1–34.

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJ, Furness RW, Mills JA, Murphy EJ, Osterblom H, Paleczny M, et al. 2011. Global seabird response to forage fish depletion–one-third for the birds. Science. 334:1703–1706.

Delord K, Gasco N, Weimerskirch H, Barbraud C, Micol T. 2005. Seabird mortality in the Patagonian toothfish longline fishery around Crozet and Kerguelen Islands, 2001–2003. CCAMLR Sci. 12:53–80.

Garthe S, Camphuysen K, Furness RW. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar Ecol Prog Ser. 136:1–11.

Gasco N. 2011. Contributions to marine science by fishery observers in the French EEZ of Kerguelen, Proceedings of the 1st international Science Symposium on the Kerguelen Plateau (Concarneau, 2010), The Kerguelen Plateau, Marine Ecosystem and Fisheries. 93–98 p.

Gilbert NI, Correia RA, Silva JP, Pacheco C, Catry I, Atkinson PW, Gill JA, Franco AM. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (Ciconia ciconia) from a partially migratory population. Mov Ecol. 4:7.

Giraldeau LA, Caraco T. 2000. Social foraging theory. Princeton (NJ): Princeton University Press.

Granadeiro JP, Brickle P, Catry P. 2013. Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. Anim Conserv. n/a-n/a. doi:10.1111/acv.12050.

Granadeiro JP, Phillips RA, Brickle P, Catry P. 2011. Albatrosses Following Fishing Vessels: How Badly Hooked Are They on an Easy Meal? PLoS ONE. 6:e17467.

Grémillet D, Péron C, Kato A, Amélineau F, Ropert-Coudert Y, Ryan PG, Pichegru L. 2016. Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem. Mar Biol. 163:1–11.

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJ, Ryan PG. 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proc R Soc B Biol Sci. 275:1149–1156.

Grunbaum D, Veit RR. 2003. Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? Ecology. 84:3265–3275.

Hawkins JM. 1982. Gannets feeding behind trawler. Notornis. 29:22.

Heath MR, Cook RM, Cameron AI, Morris DJ, Speirs DC. 2014. Cascading ecological effects of eliminating fishery discards. Nat Commun. 5:3893.

Hijmans RJ, Williams E, Vennes C. 2015. geosphere: Spherical Trigonometry. R package version 1.4–3. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://cran.r-project.org/package=geosphere.

Hudson AV, Furness RW. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis. 131:225–237.

James RS, Scott DM, Yarnell RW, Overall ADJ. 2017. Food availability and population structure: How do clumped and abundant sources of carrion affect the genetic diversity of the black-backed jackal? J Zool. 301:184–192.

Journal Officiel des Terres Australes et Antarctiques Françaises. 2010. Arrêté n° 2010–53 du 30 août 2010 prescrivant les règles encadrant l'exercice de la pêche à la légine (Dissostichus eleginoides), aux raies (Bathyraja eatonii, Bathyraja irrasa, Raja taaf), au grenadier (Macrourus carinatus), autorisée dans les zones économiques exclusives de Crozet et de Kerguelen.

Kane A, Healy K, Guillerme T, Ruxton GD, Jackson AL. 2016. A Recipe for Scavenging in Vertebrates - the natural history of a behaviour. Ecography. 40:324–334.

Mardon J, Nesterova AP, Traugott J, Saunders SM, Bonadonna F. 2010. Insight of scent: experimental evidence of olfactory capabilities in the wandering albatross (Diomedea exulans). J Exp Biol. 213:558–563.

Martin GR. 1998. Eye structure and amphibious foraging in albatrosses. Proc R Soc Lond B Biol Sci. 265:665–671.

Martin GR, Prince PA. 2001. Visual fields and foraging in procellariiform seabirds: sensory aspects of dietary segregation. Brain Behav Evol. 57:33–38.

Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? PLoS ONE. 8:e53077.

Nevitt G, Reid K, Trathan P. 2004. Testing olfactory foraging strategies in an Antarctic seabird assemblage. J Exp Biol. 207:3537–3544.

Nevitt GA. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. J Exp Biol. 211:1706–1713.

Nevitt GA, Losekoot M, Weimerskirch H. 2008. Evidence for olfactory search in wandering albatross, Diomedea exulans. Proc Natl Acad Sci. 105:4576–4581.

Nevitt GA, Veit RR, Kareiva P. 1995. Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. Nature. 376:680–682.

Newey S, Allison P, Thirgood SJ, Smith AA, Graham IM. 2009. Using PIT-tag technology to target supplementary feeding studies. Wildl Biol. 15:405–411.

Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2015. The ecological effects of providing resource subsidies to predators. Glob Ecol Biogeogr. 24:1–11.

Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol Lett. 16:1501–1514.

Oro D, Ruiz X. 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. ICES J Mar Sci J Cons. 54:695–707.

Pante E, Simon-Bouhet B. 2013. marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS One. 8:e73051.

Patrick SC, Bearhop S, Bodey TW, Grecian WJ, Hamer KC, Lee J, Votier SC. 2015. Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. J Avian Biol. 46:431–440.

Patrick SC, Weimerskirch H. 2014. Personality, foraging and fitness consequences in a long lived seabird. PLoS One. 9:e87269.

Pennycuick CJ. 1982. The Flight of Petrels and Albatrosses (Procellariiformes), Observed in South Georgia and its Vicinity. Philos Trans R Soc B Biol Sci. 300:75–106.

Petyt C. 1995. Behaviour of seabirds around fishing trawlers in New Zealand subantarctic waters. Notornis. 42:99–115.

Phillips RA, Xavier JC, Croxall JP, Burger AE. 2003. Effects of satellite transmitters on albatrosses and petrels. Auk. 120:1082–1090.

Pichegru L, Ryan PG, Le Bohec C, Van der Lingen CD, Navarro R, Petersen S, Lewis S, Van der Westhuizen J, Grémillet D. 2009. Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. Mar Ecol Prog Ser. 391:199–208.

Pinheiro J, Bates D, DebRoy S, Sarkar D; R Core Team. 2016. nlme: Linear and nonlinear mixed effects models. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://cran.r-project.org/package=nlme.

Prince PA, Huin N, Weimerskirch H. 1994. Diving depths of albatrosses. Antarct Sci. 6:353–354.

Ramos R, Ramírez F, Sanpera C, Jover L, Ruiz X. 2009. Diet of Yellow-legged Gull (Larus michahellis) chicks along the Spanish Western Mediterranean coast: the relevance of refuse dumps. J Ornithol. 150:265–272.

Ramsay K, Kaiser MJ, Moore PG, Hughes RN. 1997. Consumption of Fisheries Discards by Benthic Scavengers: Utilization of Energy Subsidies in Different Marine Habitats. J Anim Ecol. 66:884–896.

Ricklefs RE. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Stud Avian Biol. 8:84–94.

Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. Trends Ecol Evol. 17:474–480.

Sherley RB, Ludynia K, Dyer BM, Lamont T, Makhado AB, Roux JP, Scales KL, Underhill LG, Votier SC. 2017. Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. Curr Biol. 27:563–568.

Skov H, Durinck J. 2001. Seabird attraction to fishing vessels is a local process. Mar Ecol Prog Ser. 214:289–298.

Soriano-Redondo A, Cortés V, Reyes-González JM, Guallar S, Bécares J, Rodríguez B, Arcos JM, González-Solís J. 2016. Relative abundance and distribution of fisheries influence risk of seabird bycatch. Sci Rep. 6:37373.

Stempniewicz L. 1994. Marine birds drowning in fishing nets in the Gulf of Gdansk (southern Baltic): Numbers, species composition, age and sex structure. Ornis Svec. 4:123–132.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton (NJ): Princeton University Press.

Sumner M, Wotherspoon S. 2010. tripEstimation: Metropolis sampler and supporting functions for estimating animal movement from archival tags and satellite fixes. R Package Version 00-33 [cited 2011 June 1]. Available from: https://cran.r-project.org/web/packages/tripEstimation/index.html.

Tew Kai E, Benhamou S, van der Lingen CD, Coetzee JC, Pichegru L, Ryan PG, Gremillet D. 2013. Are Cape gannets dependent upon fishery waste? A multi-scale analysis using seabird GPS-tracking, hydro-acoustic surveys of pelagic fish and vessel monitoring systems. J Appl Ecol. 50:659–670.

Thiebault A, Mullers RH, Pistorius PA, Tremblay Y. 2014. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. Behav Ecol. 25:1302–1310.

Tickell WLN. 2000. Albatrosses. Mountfield (Sussex): Pica Press.

Torres LG, Sagar PM, Thompson DR, Phillips RA. 2013a. Scaling down the analysis of seabird-fishery interactions. Mar Ecol Prog Ser. 473:275–289.

Torres LG, Sagar PM, Thompson DR, Phillips RA. 2013b. Scale-dependence of seabird-fishery data analysis and management: Reply to Croxall et al. (2013). Mar Ecol Prog Ser. 493:301–304.

Tuck GN, Thomson RB, Barbraud C, Delord K, Louzao M, Herrera M, Weimerskirch H. 2015. An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? J Appl Ecol. 52:950–959.

Uyeda LT, Iskandar E, Kyes RC, Wirsing AJ. 2015. Encounter rates, agonistic interactions, and social hierarchy among garbage-feeding water monitor lizards (Varanus salvator bivittatus) on Tinjil Island, Indonesia. Herpetol Conserv Biol. 10:753–764.

Votier SC, Bearhop S, Ratcliffe N, Phillips RA, Furness RW. 2004a. Predation by great skuas at a large Shetland seabird colony. J Appl Ecol. 41:1117–1128.

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J Appl Ecol. 47:487–497.

Votier SC, Furness RW, Bearhop S, Crane JE, Caldow RWG, Catry P, Ensor K, Hamer KC, Hudson AV, Kalmbach E, Klomp NI, Pfeiffer S, Phillips RA, Prieto I, Thompson DR. 2004b. Changes in fisheries discard rates and seabird communities. Nature. 427:727–730.

Wakefield ED, Phillips RA, Trathan PN, Arata J, Gales R, Huin N, Robertson G, Waugh SM, Weimerskirch H, Matthiopoulos J. 2011. Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. Ecol Monogr. 81:141–167.

Weimerskirch H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. Oecologia. 102:37–43.

Weimerskirch H, Capdeville D, Duhamel G. 2000. Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. Polar Biol. 23:236–249.

Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L. 2014. Lifetime foraging patterns of the wandering albatross: life on the move! J Exp Mar Biol Ecol. 450:68–78.

Weimerskirch H, Filippi DP, Collet J, Waugh SM, Patrick SC. Forthcoming 2017. Use of radar detectors to track attendance of albatrosses at fishing vessels. Conserv Biol.

Weimerskirch H, Guionnet T. 2002. Comparative activity pattern during foraging of four albatross species. Ibis. 144:40–50.

Weimerskirch H, Jouventin P, Stahl JC. 1986. Comparative ecology of the six albatross species breeding on the Crozet Islands. Ibis. 128:195–213.

Weimerskirch H, Lys P. 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. Polar Biol. 23:733–744.

Weimerskirch H, Mougey T, Hindermeyer X. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. Behav Ecol. 8:635–643.

Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. Auk. 110:325–342.

Xavier JC, Cherel Y, Roberts J, Piatkowski U. 2012. How do cephalopods become available to seabirds: can fish gut contents from tuna fishing vessels be a major food source of deep-dwelling cephalopods? ICES J Mar Sci J Cons. 70:46–49.