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

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**Running Title :** Behavioural response of albatrosses to boats

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Collet et al., 2017).

**Abstract:**

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 two species (up to 30km). 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 two 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.

**Keywords**: Comparative behavior, GPS tracking, Seabirds, Vessel Monitoring System data, Predictable Anthropogenic Food Sources, Fisheries.

# 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 (Grünbaum 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 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 two 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 turn-over 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, two 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., 2017). 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 two species of albatross to the same fishing fleet that is operating in two 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 30km (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 5min, never >15min). 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).

69 incubating WA were equipped with GPS loggers recording fixes every 15min. 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 2min: we down-sampled to one fix in every seven, to have a recording frequency of 14min, 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 (>12h) were recorded for BBA, all of which occurred while boats were present within a 350km radius around the focal bird. We assigned the 261 trips to three 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., 2017; 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 1h) 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 10min (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 two 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 < 10km/h) within very close range from boats. The attendance distance threshold for WA was previously estimated at 3km (Collet et al., 2015). To facilitate direct comparisons between species, we used the same 3km 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 3km of a boat, “within attraction range” if located within 30km 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 two such series were separated by less than 4 GPS positions outside the attraction range (i.e. ~1h, 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 three species-breeding stage categories (WA-incubation, BBA-incubation, BBA-chick rearing), as the number of encounter events per trip. We used a two-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 350km 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 modelled 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 1h from a fishing operation. We included as a covariate the average number of boats present within detection range (30km) during the encounter.

For encounters which contained attendance, we compared the attendance behavior between the three 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 3km, rather than simply remaining within 30km), and finally, the average distance from boats when attending them (<3km). For these three 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 while all retained encounters started within 1h 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 30km 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 -1400m 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 to -1400m) when not within attraction range of a boat (>30km). 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. 120km from the -1000m isobath, whereas this isobath is about 15km from the WA Crozet colony. Hence for this analysis we only considered BBA GPS locations that were >120km 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 (Fig.1a,b). WA foraged mainly over oceanic waters but boat attendance occurred over the shelf edge of the Crozet islands (Fig.1a,c). The attraction distance to boats for BBA was 28.6km (95% C.I. 26.0-31.2km; Fig.2a), i.e. similar to that of WA (29.2km, 95% CI: 25.5 – 32.9km, Fig.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; Fig.3a). WA trips were longer in duration than both chick-rearing BBA trips (t=14.198, df=130, p<0.001; Fig.3a) and incubating BBA trips (t=3.996, df=75, p<0.001), which have both been previously reported (Collet et al., 2017; Patrick and Weimerskirch, 2014).

In BBA, 42 trips lasted less than 24h (41 from chick-rearing birds, 1 from an incubating bird), and during these short trips boats were encountered in only two occasions. However 53.1% of BBA tracks that lasted more than 24h (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 >24h 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, Fig.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, Fig.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; Fig.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; Fig.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, Fig.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 10.8h, range 2.0-86.5h), 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 3km) 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; Fig.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, Fig.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; Fig.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 +/- 1.2h, median 1h15min, Fig.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 +/- 31m, Fig.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 (Fig.5b,d), whereas BBA less frequently sat over these waters (Fig 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. Overall, attraction distances were similar between the two 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 targetted 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 procellariiforms (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).

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 30km 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 (Grünbaum 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 50km, 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., in press).

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., 2017). 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 two 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., 2017). 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.

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# Figure Legends

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 (<3km from a boat with speed<10km/h) are shown for WA (B.) and BBA (C.) over the edge of Crozet and Kerguelen shelves respectively (black solid lines indicate 2000m isobaths; see also Fig.5).

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 line indicates null expectations (10/180) for birds not attracted to boats. The black line is the fitted segmented linear regression, with a breakpoint for BBA estimated at 28.6km. The breakpoint estimated for WA from the same methodology was 29.2km (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.

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-slope waters when no boats were within 30km (b), and bathymetry distribution when BBA (c) and WA (d) were sitting within 3km of a boat.