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Albatrosses develop attraction to fishing vessels during immaturity but avoid them at old age

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Animals have to develop novel behaviours to adapt to anthropogenic activities or environmental changes. Fishing vessels constitute a recent feature that attracts albatrosses in large numbers. While they provide a valuable food source through offal and bait, they cause mortalities through bycatch, such that selection on vessel attraction will depend on the cost–benefit balance. We examine whether attraction to fishing and other vessels changes through the lifetime of great albatrosses, and show that attraction differed between age classes, sexes and personality. Juveniles encountered fewer vessels than adults, but also showed a lower attraction to vessels when encountered. Attraction rates, especially for fishing vessels, increased through immaturity to peak during adulthood, decreasing with old age. Shy females had lower attraction to vessels and shy males remained at vessels longer, suggesting that bolder individuals may outcompete shyer ones, with positive consequences for mass gain. These results suggest that attraction to vessels is a learned process, leading to an increase with age, and is not the result of preferential attraction to new objects by juveniles. Overall, our findings have important conservation implications as a result of potential strong differential selection on the risk of bycatch for age classes, personality types, populations and species.

1. Introduction

Human activities result in changes in food availability for animals, and often offer novel food resources [1], in the form of waste such as bins, dumps or discards from fisheries. These novel food resources have diverse and variable impacts on individuals and populations [1] through energetic and nutrient supply, but also mortalities, and at the community level they can seriously alter trophic networks [2,3]. These anthropogenic food resources are often associated with specific stimuli such as artificial materials and structures, noise from engines and large multi-specific aggregations that are relatively recent at evolutionary timescales, especially for long-lived vertebrates. From a behavioural-cognitive perspective, this raises the question as to how attraction to these 'novel' food sources can arise in populations—and how animals learn to exploit these new resources is poorly understood.

Adoption of a new foraging behaviour might be favoured by neophilia, the tendency to be attracted to unknown stimuli [4,5]. Individuals could learn to associate these novel stimuli to food, reinforcing their subsequent attraction [6]. Even with low neophilia, learning may be sufficient for individuals to progressively exploit these resources over time, albeit this would be slower to develop and highly age dependent in the population than when higher neophilia is present [7]. Furthermore, neophilia levels might vary within individuals: juveniles often display curiosity towards new objects and can be attracted to an

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object simply because it is unfamiliar, which might be less true of older individuals [8,9].

Attraction to new resources might also vary between individuals: in animal personality research, neophilia is often associated with boldness, aggressivity or exploratory tendencies of individuals [10,11]. This interindividual variability in attraction, which can be heritable, might in turn provide an opportunity for natural selection to operate [12], depending on the fitness consequences of these food resources [13]. If these resources positively affect reproduction (which is not always the case [14,15]) but negatively affect survival (e.g. bycatch), life-history trade-offs may occur. For instance in the case of bycatch risk, young individuals would benefit from avoiding these resources to avoid cost to future reproduction. However, as the value of future reproduction decreases as birds age [16], the risk of bycatch will have a lower impact on lifetime fitness. Allocation trade-offs might also favour the persistence of distinct personalities in the population, if bold individuals use these resources for higher reproductive outputs at higher mortality risks, and shyer individuals use other, lower risk resources [17,18].

Finally, because anthropogenic food resources often generate large multi-specific aggregations [1], they come with intra- and interspecific competition. Attraction to these food resources may also be modulated by the dominance-competitive abilities of individuals. Size, personality or age may affect competitive ability with larger, older and bolder individuals being dominant in large groups.

Albatrosses have been anecdotally attracted by vessels for at least three centuries [19,20], well before the era of industrial fishing, that today attracts many seabirds, including albatrosses, that feed on offal or bait [2,21]. Thus, since the first time albatrosses encountered a vessel, a significant proportion of the adult population of albatrosses has become accustomed to regularly encountering vessels, and is now attracted to and attend vessels [22,23], which they can detect up to 30 km away [24]. Accidental bycatch of albatrosses and petrels by fisheries is very high and these are among the most threatened bird species, with hundreds of thousands killed by long-line fisheries every year [25]. Thus, from a conservation perspective, there is a need to obtain better information on seabirds–fishery interactions [26]. Information on the location of vessels is critical to study bird attraction to them. Even where there are data available on legal vessel activity, many fishing vessels are not declared or illegal and generally have even stronger negative effect on ecosystems through over exploitation of fish stocks and bycatch of non-target species [27,28]. Recently, new loggers allowing the detection of vessels through their radar emissions have been developed, providing locations of interactions between albatrosses and vessels over vast oceanic sectors [22], and by combining them with Automatic Identification System (AIS) information, permit the separation of fishing vessels from other vessels [29]. Studies have shown that attraction to vessels varies among species [23,30], populations [31,32] and individuals [33]. However, the drivers of these differences are not well resolved, and in particular the ontogeny of attraction to boats is unknown.

In this paper, we test a series of hypotheses for the relationship between age, personality and attraction to anthropogenic resources. We examine whether attraction to vessels differs between the juvenile phase, the long period of immaturity, the adulthood and the old age. We predict that if attendance at boats is a learnt behaviour, we expect that attraction would increase progressively through ages, with juveniles being less attracted than adults. In this case, attraction may be higher to fishing vessels that provide food compared to other vessels. If attraction is linked to neophilia in juveniles, we predict that juveniles should be attracted, at least in a similar proportion as adults and presumably equally to fishing or to non-fishing boats. We compare the development of attraction to fishing boats with the development of attraction to non-fishing, commercial boats, that provide no food reinforcement, to decouple neophilia and learning. We also investigate whether boldness and sex of individuals may affect attraction, as well as whether old individuals are more, or less, attracted to vessels than younger individuals: be more attracted to vessels due to an improved experience to acquiring additional food source, or old individuals may be less competitive because of senescence or mortality in fisheries may have selected individual personalities that are less attracted by vessels, resulting in both cases in a low attraction rate in old birds. Finally, we tested differences in mass gains between adults of different age, sex and personality, as a function of their level of attendance to fishing boats, to test for potential fitness consequences. We also examine the potential trade-offs between mortality risks in long-line fisheries and access to food that may underlie age-related attractions.

2. Material and methods

(a) Deployments

A total of 403 wandering (*Diomedea exulans*) and 30 Amsterdam (*Diomedea amsterdamensis*) albatrosses were equipped with XGPS between January 2016 and March 2018 (breeding adults) and with Centurion (breeding adults) and XArgos loggers (juveniles, immatures and failed or post-breeding adults) between November 2018 and March 2020 from Crozet (46°S, 52°E), Kerguelen (50°S, 70°E) and Amsterdam (38°S, 77°E) Islands in the south-western Indian Ocean. In total, 433 individuals of various age were equipped. Details of the XGPS and Centurion-XArgos loggers are given in [22,29].

XGPS (40 g) provide the GPS location of the fitted animal and simultaneously detects radar emissions up to 5 km away [22]. Centurion logger weights 65 g, measures 109 × 30 × 22 mm and records all the information on-board but transmits this instantaneously through Argos the location of the radar detection as soon as a vessel is detected, through its radar emission. Centurions and XGPS recorded fixes every 2 min and the radar detector recorded the presence of radar emissions every 5 min, for a duration of 1 min. The complete information was then downloaded from the logger when the bird had returned to its nest. XGPS and Centurion loggers were deployed on actively breeding birds, which alternate foraging trips at-sea with periods on the nest, making recovery simple.

XArgos loggers (55 g, 109 × 30 × 19 mm) record and send the location of the bird and the summary of the Radar Detector scanning (scan for radar emissions recorded during 1.5 min every 15 min) every hour through Argos. They were deployed on birds for which recovery was not possible because they leave for the sea for several years without returning to land, i.e. on juveniles, immature birds aged 1–10 years, and post-breeding adult birds, which are either adult birds that have successfully finished breeding or failed breeders.

All birds were captured on the colony and the loggers were attached to the back feathers using special tape (Tesa, Germany). For short-term deployment (Centurion loggers on breeding adults), the logger was removed after the bird returned on its nest after one foraging trip. For long-term deployment (XArgos loggers on juveniles, immature and post-breeding adults), the attachment was reinforced by Loctite glue on the contacts between the logger and the tape. XArgos detached from birds through the loss of feathers during moulting process after 3–6 months. The loggers represented 0.46% to 0.93% of the bird body weight (wandering albatrosses weight between 7 and 12 kg, Amsterdam albatross between 6 and 10 kg), i.e. below the recommended maximum 3% of the bird's body mass for loggers attached [34].

Mass gain at sea during a foraging trip was measured in 79 adults breeding birds from Crozet the day they left and the day they returned from the foraging trip.

(b) Vessel information and Automatic Identification System data

For the years 2016–2018, XGPS data provided information on the Radar detections only. AIS data were made available through the Themis interface (CLS Toulouse) for the sector 20–70°S, 10–180°E between December 2018 and May 2020. Through this system, all AIS emissions in the sector are recorded, and the information was downloaded every day from the CLS server and stored in a database. During the study period, more than 250 million AIS locations were obtained. For each AIS location, the following information was available: date, latitude, longitude, Ship Name, IMO number of the vessel (identity of International Marine Organisation), nationality, call sign, speed, heading, type of vessel (fishing, tanker, cargo, pleasure etc.) and activity.

(c) Age and personality

On the three study sites, all individuals were banded every year since 1960 (Crozet), 1981 (Amsterdam) and 1992 (Kerguelen) and sex (determined by molecular sexing and morphology), age (bird banded as chicks) and past reproductive performance of all tracked birds were known from our long-term database [35]. Ages were grouped into classes: juveniles (aged 1 year), immatures 1 (3–4 years), immatures 2 (5–7 years), young adults (8–15 years), adults (16–30 years) and old adults (age more than 30 years). In total, 153 juveniles, 58 immatures, 190 adults and 32 old adults were equipped. Boldness of Crozet adult wandering albatrosses was known from personality tests performed over the past 10 years and is highly repeatable between tests [36]. Personality scores were extracted as individual-level best linear unbiased predictors from a generalized linear mixed model which controlled for observation number and observer [36]. They were grouped into three clear classes based on the three-modal distribution of personality scores (electronic supplementary material, figure S1): shy—intermediate—bold.

(d) Data processing and analyses

For the years 2018–2020, all birds data were then merged with AIS data so that to each bird location was associated with AIS information of any vessel occurring within 5 km (considered as the distance of a bird engaging in a foraging interaction with a nearby boat (i.e. 'attending' it), and corresponding to the range of radar detection for the logger [22], and within 30 km (the maximum distance of detection of a boat by an albatross, considered as an 'encounter' [24]. To determine bird–boat distance and time spent attending and in encounter we use a linear interpolation to identify the AIS location the closest in time from the bird location. Birds attracted to fishing boats come close and stay for at least a couple of hours [37] so that we are confident that a series of consecutive boat locations recorded within the proximity of a bird is not due to inaccurate spatio-temporal matching. We grouped successive encounter locations (without gaps of more than 2 h) as one encounter event. Similarly, all sequential (at least 2 successive) radar detections associated with GPS locations without gaps of more than 2 h were grouped into one attendance event.

Then, the database was processed to associate with each bird location, each radar event, attendance (AIS within 5 km) and encounter (AIS within 30 km) locations, the following parameters: bathymetry and all information on the associated AIS boat (IMO number or identification number for the International Maritime Organization, ship name, activity and nationality). Bathymetry was extracted from the ETOPO1 Global Relief Model from the National Oceanic and Atmospheric Administration using the R package 'marmap' [38]. We selected the bathymetry as the environmental variables that have the most influence on albatross habitat preferences [39]. From the database we calculated, for each individual bird, the number of vessels within 100 km of each bird location, the number encountered (within 30 km) and the time spent encountered, and the number of attendances and time spent attended (within 5 km or with a radar detection). For each encounter event, we estimated attraction as a ratio of time spent attending over the time encountered. For each individual track, we also calculated first the proportion of vessels within 100 km that were encountered and attended, and then from the number of vessels encountered, we estimated the proportion of these vessels was attended.

All data processing was performed in R (R Core Team, 2020). Statistical analyses were performed under Statistica 12 and R (R Core Team, 2020). We used a linear mixed model. The response variables (number of vessels encountered daily, depth of encounters) were fitted to one categorical predictor (age class), and the response variables attraction, attendance duration and mass gain, to age classes, and to sex and personality, with an interaction effect between sex and personality. Bird individual identities were used as random factors. We used χ^2 test to test for the influence of personality on the proportions of individuals attending vessels or not attending vessels.

3. Results

(a) Change with age in co-occurrence and attraction

The numbers of vessels encountered increased with age with juveniles encountering fewer boats than adults overall, and with immature birds having an intermediate number of encounters $F_{5134} = 6.9$, $p = 0.004$ (figure 1*a*). This increase is mirrored by the change in foraging habitat by the different age classes with juveniles foraging over deep oceanic waters, adults foraging over both shallower neritic waters and deep waters, immatures showing a progressive shift between habitats $F_{5309} = 10.5$, $p < 0.001$ (figure 1*b*). Old individuals remained in deeper waters. Juveniles encountered a small proportion of fishing vessels, but the percentage increased when ageing, to reach highest values when adult (figure 1*c*). The proportion of fishing vessels attended increased in parallel (figure 1*c*).

When encountering vessels, attraction rates of juveniles were low and showed no increase during the first months at-sea after fledging ($F_{4,49} = 1.0$, $p = 0.42$) (electronic supplementary material, figure S2), but increased through during immature stage and adulthood ($F_{7109} = 4.0$, $p = 0.001$) (figure 2). However, attraction declined steeply in old age (figure 2). The increase in attraction and decline at old age were more marked for fishing vessels compared to other vessels (figure 2).

The duration of vessel attendance also increased with age, again with a decline at old age ($F_{5112} = 4.2$, $p = 0.005$), whereas for non-fishing vessels, there was no significant difference between age classes ($F_{5,33} = 0.9$, $p = 0.485$) (figure 3).

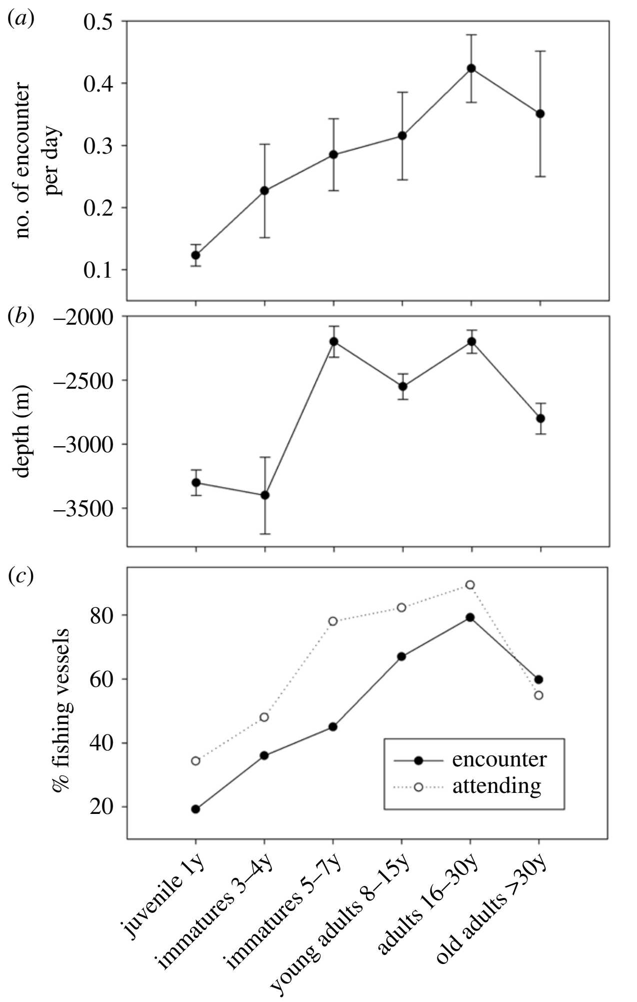

Figure 1. Changes according to age classes in (*a*) number of daily vessel encounters, (*b*) average water depth of encounters and (*c*) proportion among all vessel types of fishing vessels encountered and attended.

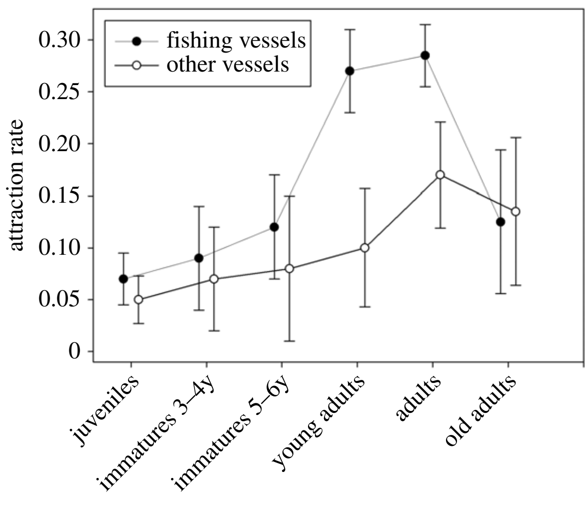

Figure 2. Attraction rates to fishing vessels and to other vessels of wandering albatrosses of different age classes.

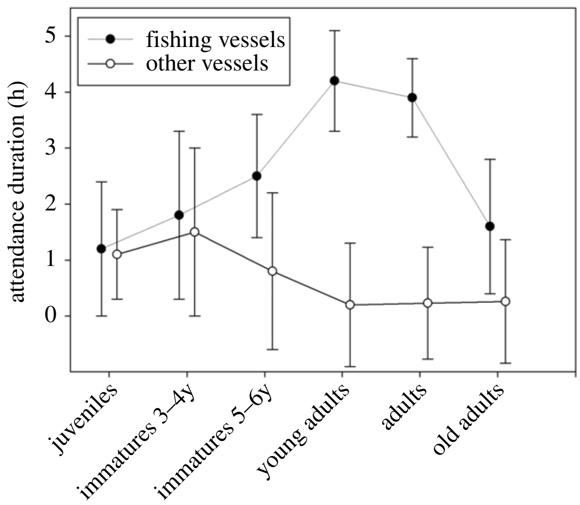

Figure 3. Duration of attendance behind vessels of wandering albatrosses of different age classes.

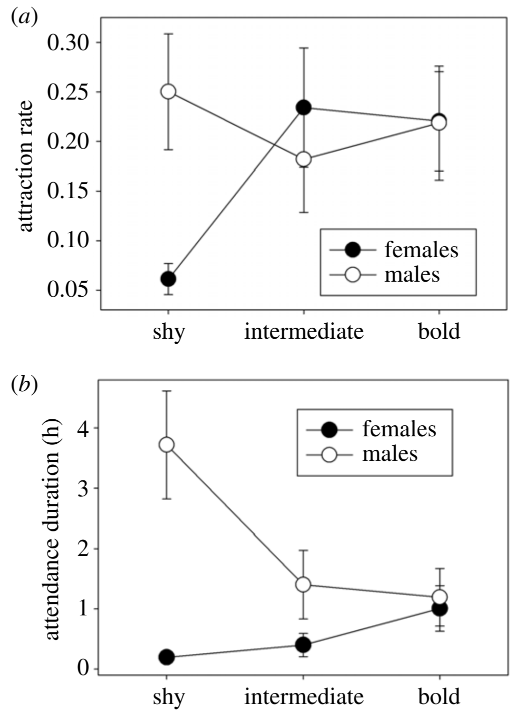

Figure 4. Influence of personality (shy, intermediate and bold) on (*a*) attraction rates and (*b*) attendance duration of males and females wandering albatrosses.

(b) Sex, personality and fitness consequences

Males and females attended vessels in similar proportions ($\chi^2_1 = 0.1$, $p = 0.788$). Males and females had similar attraction rates ($F_{1135} = 0.1$, $p = 0.956$) and spent a similar amount of time attending vessels ($F_{1135} = 0.94$, $p = 0.334$). There was no influence of personality on the proportions of individuals attending vessels or not attending vessels ($\chi^2_2 = 0.5$, $p = 0.782$). Bolder adult females were more attracted to vessels than shy females ($F_{2,18} = 2.6$, $p = 0.0251$), whereas for adult males, the attraction was not influenced by personality ($F_{2,12} = 0.6$, $p = 0.485$) (figure 4), but the duration of attendance was longer for shy males (interaction sex × personality $F_{2202} = 4.2$, $p = 0.016$, figure 4).

The percentage of mass gain (relative to the mass of individual) was higher for males than for females (10.4 ± 8.7% versus 4.2 ± 10.1% of mass at departure at sea) ($F_{1,62} = 6.43$, $p = 0.0017$). Females attending vessels had a higher mass gain than females not attending vessels (8.1 ± 9.4% versus −0.8 ± 9.0%, $F_{1,37} = 6.9$, $p = 0.025$), whereas this was not the case for males ($F_{1,28} = 0.01$, $p = 0.854$). Shy males had a lower mass gain than bold males (5.3 ± 7.3% and 15.6 ± 6.7

respectively, $F_{2,28} = 3.8$, $p = 0.0475$) independently of vessel attendance. There was no difference in mass gain between females of different personalities ($F_{2,29} = 1.1$, $p = 0.325$).

4. Discussion

(a) Attraction, age and personality

Our study provides the first evidence that attraction of an animal to vessels increases through the early life stage to reach highest values at adulthood, indicating that attraction is learnt during the long immature stage. Juvenile individuals, during their first months at sea, encountered fewer boats, but when controlling for the lower number of vessels encountered, they were less attracted to vessels than adults or immature birds, suggesting that the rate of learning will be slow because they encounter few vessels. This low interest in boats encountered seems to discard neophilia as a strong driver of attraction to boats in young birds. The progressive increase in attraction to vessels during immaturity and early adult stage suggests that attraction to vessels increases progressively over the first 15 years of life in albatrosses. Attraction increases during immaturity when individuals more regularly encounter vessels, especially fishing vessels that provide a new food resource (rather than commercial cargos and tankers). During this phase of acquisition of attraction to vessels, juveniles or immatures may be first attracted by other albatrosses attending a vessel, as an innate natural behaviour of being naturally attracted to other congeners. They may then progressively associate the presence of congeners to vessels eventually approaching vessels without the presence of other seabirds. It is also during this phase of learning that they become able to differentiate fishing vessels from other vessels. They reach maximum values at adulthood, when both the encounter rate and the proportion of fishing vessels among the encountered boats are highest, close to the breeding grounds. This progressive increase provides the first evidence that recognition and attraction to fishing boats is probably a learned behaviour acquired progressively (figure 5).

We also show that attraction can be influenced by a personality trait such as boldness. Shy females attended fewer boats and bolder males remained longer at boats once attending. These results align with the prediction that boldness is part of a suite of behaviours including aggression and dominance in competitive situations [11]. Male wandering albatrosses are probably dominant over females [40], likely owing to their larger size, and bolder birds are often dominant to shyer ones. Our results showing that shy females are less likely to attend boats may be driven by their low competitive ability, resulting in competitive exclusion. This appears to have fitness consequences as female birds gain more mass if they are able to attend fishing vessels. For males, only bold males gain mass compared to shy males, whether they attend boats or not. As bold males are predicted to be most dominant, this may explain why shy males spend longest at vessels if they are more likely to be forced out by competition and, thus, spend more time trying to access food made available by vessels. Although attraction to vessels is acquired progressively in the population through the first decade of life, personality may predict whether birds develop an attraction to vessels. Indeed, among adults, not all individuals in the population attended vessels during their foraging trips (28% of adult individuals never approached a vessel), and at least for females, explorative behaviour appears to correlate with boldness, since bold but not shy females approach vessels. Since personality is a heritable trait in wandering albatrosses [36], these differences in attraction between individuals of different personalities may result in a differential selection due to bycatch risk and favoured access to food sources.

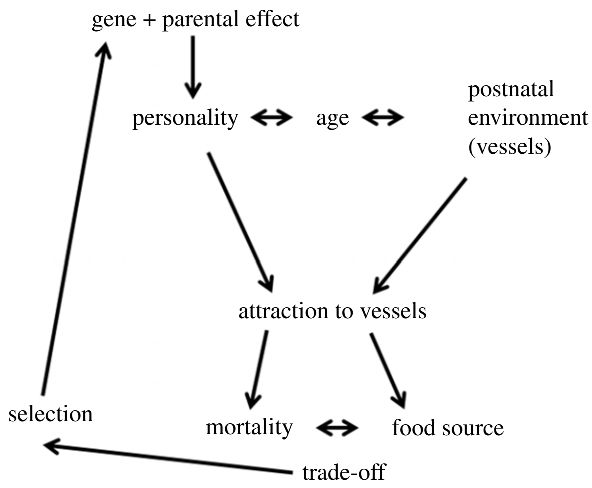

Figure 5. Potential links between attraction to vessels, age and personality and its life-history consequences.

One unexpected result of the study is the decline in attraction and in the duration of vessel attendance at old age. Senescence affects foraging abilities and breeding success [41,42] and decline in foraging and breeding parameters due to senescence is strongly influenced by personality traits [43]. The decline of attraction at old age could be the result of the lower competitive abilities behind vessels of old birds compared to younger adult individuals due to senescence, resulting in older individuals staying at longer distances from vessels than younger individuals [37] or old individuals no longer being attracted by vessels, and ultimately foraging in different areas. This latter hypothesis is supported by the observation that old male wandering albatrosses are the only individuals which forage in distant Antarctic waters where no fisheries occur [44]. Alternatively, decrease in attraction could be the result of selection for individuals that are not attracted by vessels—individual attracted having a higher risk of bycatch in fisheries.

(b) Consequences for conservation

Increasingly we understand the importance of considering individual behaviour in understanding population dynamics and extinction risks (e.g. [45]). Fisheries are a major threat for albatrosses, and bycatch mortality is a major driver of population declines of albatrosses worldwide [46,47]. It has been suggested that bycatch may act as an inadvertent selection pressure against individuals strongly attracted to boats [48], with hopes it might act as evolutionary rescue from extinction. Two lines of evidence have indirectly brought support to this hypothesis in our study populations. First, including hidden individual heterogeneity and selection in demographic modelling of wandering albatross populations helps better explain how the population might have been re-increasing after a strong decline from the 1980s to the year 2000 [48]. Second, in the small remnant population of Amsterdam albatrosses (which went lower than 50 breeding individuals in recent decades), individuals currently display low attraction to fishing boats despite foraging over waters with very high density of fishing boats [29,49]. Here we add another line of evidence, by showing that attraction rate seems indeed heterogeneous between individuals in link with sex and personality which is itself heritable [36].

However, as in many animal interactions with anthropogenic food resources, fisheries have both negative and positive impacts on fitness: despite being the main threat to albatross populations because of bycatch [46,47], fisheries can also be a substantial food resource in particular for reproduction [1]. Here our results suggest that over the lifetime of an albatross, before the individual incurs bycatch mortality, rewards obtained at fisheries can act as strong learning reinforcement to the attraction and interaction behaviour with fishing boats. This reinforcement by fishing boats before mortality might thus slow down selection against this behaviour [50]. Moreover, we found that not only the attraction but also the amount of food (rather positive effects on fitness) obtained from these fisheries is heterogeneous between individuals, in relation to sex and personality. The combination of all these processes, along with trade-offs between reproduction and survival in these long-lived species, should result in a complex selection pressure on attraction behaviour, personality and/or learning capacities. Understanding these processes is, however, needed if we want to accurately predict whether and when evolutionary rescue might occur in natural populations.

5. Conclusion

Our results suggest that attraction to vessels is a behaviour developed during years of immaturity and is under strong but complex selection because of the potential consequences on the trade-off between an easy food source and potential mortality of adults. To our knowledge, while this process was long suspected, our study is the first to directly document the ontogeny and importance of learning for interactions between animals and anthropogenic resources (e.g. see previous reviews in [1,51]). This was enabled by recording for different individuals all encounters and subsequent decisions as to approach boats or not during their first months of life [29]. Our study further detected a link between interaction behaviour and a heritable, heterogeneous individual trait, personality [36]). It is thus an important step towards the understanding of plastic and/or evolutionary responses to threats and benefits of anthropogenic resources to wildlife. It also highlights that more work is required to understand if, and under which conditions, selection on behavioural interactions could act as evolutionary rescue for animals threatened by their use of anthropogenic resources. Finally, our study shows clearly that individual differences (age, sex and personality) matter and need to be accounted for when studying the impact of human activities on the development of new behaviours. In particular, future demographic studies should test for the potential selection of personality types in relation to mortality risks in fisheries.

Ethics. Animal care was performed humanely following rules issued by the Réserve Nationale des Terres Australes. The field procedures and manipulations on Crozet, Kerguelen and Amsterdam, after approval from Comité National de la Protection de la Nature (CNPN), were given permission by the 'Préfet of Terres Australes et Antarctiques Françaises', permit numbers 2018-117 and 2019-106.

Data accessibility. Tracking database and Radar detection events have been deposited in the online open access repository Figshare (https://figshare.com/s/2481d8e6cf4aff484ffe).

Supplementary material is available online [52].

Authors' contributions. H.W.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft and writing—review and editing; A.C.: data curation, formal analysis, methodology and resources; A.P.: data curation, formal analysis, investigation and software; S.C.P.: formal analysis, investigation, writing—original draft and writing—review and editing; J.C.: conceptualization, data curation, formal analysis, resources, software, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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