


Integrating immersion with GPS data improves behavioural classification for wandering albatrosses and shows scavenging behind fishing vessels mirrors natural foraging

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Abstract

Advances in biologging techniques and the availability of high-resolution fisheries data have improved our ability to understand the interactions between seabirds and fisheries and to evaluate mortality risk due to bycatch. However, it remains unclear whether movement patterns and behaviour differ between birds foraging naturally or scavenging behind vessels and whether this could be diagnostic of fisheries interactions. We deployed novel loggers that record the GPS position of birds at sea and scan the surroundings to detect radar transmissions from vessels and immersion (activity) loggers on wandering albatrosses *Diomedea exulans* from South Georgia. We matched these data to remotely sensed fishing vessel positions and used a combination of hidden Markov and random forest models to investigate whether it was possible to detect a characteristic signature from the seabird tracking and activity data that would indicate fine-scale vessel overlap and interactions. Including immersion data in our hidden Markov models allowed two distinct foraging behaviours to be identified, both indicative of Area Restricted Search (ARS) but with or without landing behaviour (likely prey capture attempts) that would not be detectable with location data alone. Birds approached vessels during all behavioural states, and there was no clear pattern associated with this type of scavenging behaviour. The random forest models had very low sensitivity, partly because foraging events at vessels occurred very rarely, and did not contain any diagnostic movement or activity pattern that was distinct from natural behaviours away from vessels. Thus, we were unable to predict accurately whether foraging bouts occurred in the vicinity of a fishing vessel, or naturally, based on behaviour alone. Our method provides a coherent and generalizable framework to segment trips using auxiliary biologging (immersion) data and to refine the classification of foraging strategies of seabirds. These results nevertheless underline the value of using radar detectors that detect vessel proximity or remotely sensed vessel locations for a better understanding of seabird–fishery interactions.

Introduction

Incidental mortality (bycatch) in fisheries is one of the major threats to seabird populations worldwide and particularly to albatrosses and petrels (Phillips et al., 2016; Dias et al., 2019). Advances in biologging techniques and the

availability of high-resolution fisheries data through vessel monitoring systems (VMS) and the automatic identification system (AIS) have advanced our understanding of interactions between seabirds and vessels and associated mortality risks (Votier et al., 2010; Granadeiro et al., 2011; Torres et al., 2013). However, there is still an urgent need for better

quantitative predictions of the risk to seabirds from fishery interactions at fine scales, and no studies to date have developed models based on biologging data alone that predict feeding on discards, baited hooks or other anthropogenic resources from vessels. Such models could represent a major step-change in this research field, considering the rapid increase in the availability of biologging data for seabirds (Bernard *et al.*, 2021).

Marine top predators, including seabirds that usually feed on naturally aggregated prey, will often display Area Restricted Search (ARS) behaviour when they encounter profitable patches. This behavioural model is characterised by increased sinuosity and slower speed (Fauchald & Tveraa, 2003; Weimerskirch *et al.*, 2007; Pirota *et al.*, 2018) and increased residence time in productive areas (Weimerskirch, Gault, & Cherel, 2005; Garthe *et al.*, 2016). Seabirds are also known to change their fine-scale movements when they interact with fishing vessels, which also results in ARS behaviour (Torres *et al.*, 2011; Bodey *et al.*, 2014; Corbeau *et al.*, 2019; Grémillet *et al.*, 2019). To discriminate between natural foraging and targeting of vessels requires independent, fine-scale data on seabird movements and the locations of individual vessels. The latter, however, are generally available only within Exclusive Economic Zones (EEZs). Hence, most analyses of seabird–fisheries overlap to date have used aggregated data on fishing effort, such as total longline hooks deployed per 5° grid cell, by month, which is often the highest resolution available from the Regional Fisheries Management Organizations (RFMOs) which manage fishing in the High Seas (Tuck *et al.*, 2011; Small, Waugh, & Phillips, 2013; Clay *et al.*, 2019; Carneiro *et al.*, 2020).

When data are available on bird and vessel movements, a common approach to try to distinguish natural foraging from vessel interactions is to identify periods of active foraging within tracks (based on first-passage time or speed-tortuosity thresholds), overlap those in space and time with vessels, and differentiate natural foraging from vessel interaction based on the presence or absence of nearby fishing vessels (Votier *et al.*, 2010; Torres *et al.*, 2011; Corbeau *et al.*, 2019; Corbeau, Collet, Pajot, *et al.*, 2021b). A second approach focuses on identifying behavioural changes in the vicinity of a fishing vessel by examining the probability of switching from one behavioural state to another (e.g. redirect flight trajectories when in the vicinity of a fishing vessel; Bodey *et al.*, 2014; Collet, Patrick, & Weimerskirch, 2015; Cianchetti-Benedetti *et al.*, 2018; Le Bot, Lescroël, & Grémillet, 2018; Clark *et al.*, 2020b). Although these studies demonstrated that vessels could affect the movements and behaviour of seabirds, it remains unclear whether there is a distinguishable movement pattern, sufficient for predictive discrimination, which is diagnostic of whether the bird is either foraging naturally or scavenging behind a vessel. An approach that offers considerable promise is the use of hidden Markov models (HMMs), which are used increasingly for characterising animal behaviour (McClintock & Michelot, 2018). In seabird ecology, HMMs have been used almost exclusively on location data to distinguish between ARS and transit movements, however, they can also incorporate

auxiliary biologging and environmental data (Leos-Barajas *et al.*, 2017; Patterson *et al.*, 2019; Clay *et al.*, 2020; Conners *et al.*, 2021). In particular, additional sensors could help distinguish searching behaviour from landings to capture prey, the latter potentially signalling a bycatch risk if they take place near vessels and involve targeting of longline baits during setting or hauling. One potential application of these models is to identify characteristic vessel-following behaviour from the complex patterns of activity of seabirds at sea that could improve predictions of seabird–fishery interactions in the absence of independent information on vessel locations.

Wandering albatrosses *Diomedea exulans* at South Georgia have declined catastrophically since the 1970s (Poncet *et al.*, 2017), leading to the development of a conservation Action Plan by the Government of South Georgia and the South Sandwich Islands (GSGSSI), and their listing as a Priority Population by the Agreement on the Conservation of Albatrosses and Petrels (ACAP). Bycatch in fisheries is considered to be their main threat (Pardo *et al.*, 2017; Poncet *et al.*, 2017). Analyses of the spatial overlap at large scales between their at-sea distribution and pelagic and demersal longline fisheries indicated that the population was at highest risk in the Brazil-Falklands confluence zone, particularly from the Japanese and Taiwanese distant-water tuna fleets (Jiménez *et al.*, 2016; Clay *et al.*, 2019). However, overlap metrics are scale dependent and the assumption that co-occurrence of seabirds and fisheries in a region leads to interaction and mortality risk has been regularly highlighted as a potential pitfall (Torres *et al.*, 2013; Weimerskirch *et al.*, 2020; Corbeau, Collet, Orgeret, *et al.*, 2021a) because there is a lack of fine-scale data simultaneously available for both birds and vessels. As such, a thorough understanding of seabird–fishery interactions at much finer scales is highly relevant for conservation and to better target management actions.

Here we used recently developed loggers that record the GPS position of birds at sea and regularly scan the surroundings to detect the presence of radar transmissions from vessels (Weimerskirch *et al.*, 2020). These data may allow recognisable behaviours to be delineated from the movements of the bird that can be matched to the proximity of fishing vessels at that time. Combining these data with immersion (activity) data from geolocator-immersion devices (Phalan *et al.*, 2007; Mackley *et al.*, 2010; Granadeiro *et al.*, 2011; Dean *et al.*, 2013), we used hidden Markov models to characterise foraging behaviour (including landings) in more detail than a location-only model (Clark, Handby, *et al.*, 2020a). We matched these data with the position of individual vessels obtained from the automatic identification system (AIS) and used random forest models to investigate whether wandering albatrosses breeding at South Georgia exhibit clearly identifiable patterns of movement and behaviour that can be associated with either natural foraging or interactions with vessels. If diagnostic, such patterns could then be applied to existing, extensive bird-tracking datasets to quantify the frequency, duration and propensity of individual birds, sexes and life-history stages to interact with fishing vessels, and therefore more accurately assess their risk of bycatch.

Materials and methods

Data collection

We used Tesa® tape to attach 85 GPS-radar loggers (XSputnik; Sextant Technology) to the mantle feathers of breeding adult wandering albatrosses at Bird Island, South Georgia (54°00'S, 38°03'W) and left them attached for one or more foraging trips during incubation (January–February), brood-guard (March–April) and post-guard chick-rearing (July–August) periods in 2020. Loggers recorded a GPS position every 10 min and tested for radar transmissions (within 5 km; Weimerskirch *et al.*, 2018) for 5 min. The same birds were also equipped with a geolocator-immersion logger (Intigeo C-330; Migrate Technology), which recorded salt-water immersion events that lasted ≥ 3 s, providing information on activity patterns (timing and duration of flights and water landings) throughout the foraging trip. Immersion loggers were attached to a plastic ring on the tarsus. Birds were captured on the nest during changeover with the partner (incubation or brood-guard) or after feeding the chick (post-guard). Attachment of the devices always took less than 10 min, and birds typically left the colony shortly after being released to forage at sea. To facilitate logger retrieval during post-guard chick-rearing, a fence was built around the nest on the 3rd day after the adult departed, and nests were visited twice a day thereafter until the adult returned and devices were retrieved (Xavier *et al.*, 2003). If the partner arrived before the instrumented bird returned, the fence was opened temporarily to allow it to deliver the meal to the chick. Total instrument load was *c.* 55 g (0.6 and 0.7 of male and female mean adult body mass, respectively), which was well below the threshold of 3% at which device effects tend to become apparent (Phillips, Xavier, & Croxall, 2003). Tracked birds comprised an even spread of sexes and ages (9–44 years). Breeding success of birds fitted with devices was extremely high (97%) because we targeted experienced breeders (which have higher success than new recruits; Froy *et al.* 2013) and did not deploy until at least the end of the second incubation stint, avoiding the initial period of higher failure post-laying. As such, there was no evidence that the deployments had deleterious effects.

Data processing

GPS data were first filtered to remove locations at the nest and foraging trips were defined as the location between the last GPS fix in the colony prior to departure and the first GPS fix after a return. Unrealistic locations involving travel speeds above 120 km h⁻¹ were removed using the SDLfilter R package (Shimada *et al.*, 2012). Positions were linearly interpolated to a 10-min sampling frequency to regularise the data and fill in occasional gaps. The immersion data were summarised as the number of landings (the total number of dry–wet transitions) and the proportion of time spent on the water surface (wet) in the 10-min interval preceding each GPS location. The number of landings and the proportion of time spent on the water surface were then matched

temporally with GPS data. Albatrosses have low costs of flight and landings, but take-offs from the water surface (wet–dry transitions) involve high energetic cost; birds will only land to feed or to rest, and therefore, the landing rate provides a good indication of foraging effort (Weimerskirch *et al.*, 2000; Phalan *et al.*, 2007; Granadeiro *et al.*, 2011).

Locations of individual fishing vessels within the study area were obtained from Global Fishing Watch (GFW), which combine public vessel registries and machine-learning models to (i) identify fishing vessels in the AIS data and (ii) detect when they are actively fishing, with a fishing detection accuracy of >90% (Kroodasma *et al.*, 2018). For each vessel (AIS) location, the following information was available: unique vessel identifier, date, time, latitude, longitude and fishing score (i.e. the likelihood of fishing from the GFW fishing detection model). All vessel locations within 5 km and 5 min of each interpolated location for the tracked albatrosses were extracted, but only vessels classified as 'actively fishing' were included in the analysis. The temporal resolution of AIS data associated with bird locations within the study area was 7.8 ± 101.9 min (mean \pm SD). Preliminary analyses indicated that including the type of fishing activity (trawling, long-lining etc.) had no effect on the models, and hence the results presented here are from all types of fishing activity pooled.

Behavioural state classification

HMMs are typically used to identify behavioural states from animal movement based on step length and turning angle between subsequent locations, with short-medium step lengths and high turning angles considered to represent foraging (McClintock & Michelot, 2018; Conners *et al.*, 2021). The addition of other data provided by the concurrent deployment of additional sensors may provide increased power to resolve behavioural states (Dean *et al.*, 2013; McClintock & Michelot, 2018; Clark, Handby, *et al.*, 2020). We therefore combined step lengths and turning angles with the number of landings and proportion of time spent on the water surface (extracted from the immersion data) to characterise the principal types of at-sea behaviour of wandering albatrosses using the momentuHMM package in R (McClintock & Michelot, 2018). We modelled the behaviour of all individuals combined, as the inclusion of individual effects in the hidden state process makes little difference in terms of inference (McClintock, 2021).

HMMs require the user to define state-dependent distribution classes and to provide starting values to facilitate parameter estimation. The latter were selected using *k*-means clustering (with *k* = number of states [2–5]; Dean *et al.*, 2013; Clark, Handby, *et al.*, 2020a), with the exception of the proportion of time on the water surface, which was converted into a categorical variable representing low, intermediate and high probability using starting parameters based on obvious breaks in the frequency histogram (Michelot & Langrock, 2019). A gamma distribution was chosen for step lengths, wrapped Cauchy for turning angles, Poisson for number of landings and categorical for the proportion of time on the water surface. We compared the fit between

simple (few states) and complex (many states) models based on the Akaike Information Criterion (AIC) and used the elbow criterion (i.e. the point at which adding additional states no longer results in substantial reductions in AIC) to select the best trade-off between model accuracy and complexity (Dean *et al.*, 2013; Clark, Handby, *et al.*, 2020a). The Viterbi algorithm was then used to estimate the most likely sequence of underlying states from the selected model for each track (McClintock & Michelot, 2018). An expert-driven approach and animations of the trips were used to determine if the models were assigning appropriate sequences of behaviours, that is for a random selection of trips, we compared behaviour states assigned by the models and those from visualisation (Clay *et al.*, 2020).

Behavioural bout identification

We used the results of the HMM to identify behavioural bouts as sequences of positions in the same behavioural state (see Results). In order to smooth the data, bouts that consisted of a single location were reassigned to the same HMM state as the previous and subsequent location if the HMM states of the previous and subsequent locations were identical. Wandering albatrosses attend fishing vessels for several hours (Weimerskirch *et al.*, 2020); therefore, we excluded behavioural bouts of short duration (< 5 locations) from the analyses (this only accounted for 8% of the data), as these were likely to indicate transit through the same area as vessels, and not an interaction. We then characterised each behavioural bout using several metrics, including the type of bout (based on HMM classification), the mean, maximum and minimum overall speeds, duration, cumulative and maximum distances travelled and straightness of movement (a measure of maximum distance divided by cumulative distance). Based on the majority of time spent, the bout was assigned to daylight (including twilight) or darkness, according to the timing of civil twilight (when the sun is 6° below the horizon) that were previously assigned to each GPS position. We calculated the total number of landings and the proportion of locations with landing attempts, and the proportion of time spent on the water, for the duration of the bout. We also extracted from GFW whether any of the vessels within 5 km were actively fishing at any time during the bout.

Discriminating between natural foraging vs. foraging behind vessels using machine learning

We used a machine-learning algorithm to test whether we could accurately predict if a bird was foraging in the vicinity of a vessel using the results of the HMM analysis and the behavioural bout classification. Our response variable was binary and indicated whether each bout coincided with detection of radar from a vessel and if that vessel was actively fishing within the bout (detected by AIS). For this, we calculated the proportion of GPS locations in each bout that coincided with radar detection and the proportion of locations in each bout that were classified as actively fishing. We then used various thresholds to determine whether a behavioural bout was

associated with an actively fishing vessel to overcome the uncertainty inherent in both the radar detection and AIS classifications. Ninety-one per cent of bouts with radar detections were also associated with AIS data, whereas only 49% of bouts with actively fishing vessels inferred from AIS were associated with radar detection. This is similar to results in a previous study using the same technology, which indicated that 46.6% of AIS locations within 5 km of birds resulted in radar detection (Weimerskirch *et al.*, 2020). We considered a bout to be indicative of attending a fishing vessel at different thresholds; these were when 0%, 5%, 10%, 20% or 50% of locations in that bout were associated with radar detection, and when 0%, 5%, 10%, 20% or 50% of locations in that bout were associated with a nearby vessel classified as actively fishing. We report the prevalence (proportion of bouts classified as 'attending a fishing vessel') for each combination of thresholds in TABLE 2. We then fitted each random forest model based on a conditional inference framework accounting for correlated predictors (Hothorn, Hornik, & Zeileis, 2006a) to test whether the behavioural states derived from the HMM had predictive power to distinguish between bouts with and without nearby vessels that were actively fishing. We fitted this model in a binary classification framework with the R package party (Hothorn, Hornik, & Zeileis, 2006b). We specified an internal cross-validation structure to ensure that data from the same individuals were used either for fitting or evaluating trees in the forest, which emulates a random effect in linear models and accounts for the serial autocorrelation of bouts performed by the same individual (Buston & Elith, 2011). We used a random subset of 65% of data without replacement to build single trees and validated our model by applying the output to the remaining data to estimate the accuracy of predictions. We present the predictive accuracy of each random forest model as the proportion of cross-validated bouts that were correctly predicted and the sensitivity of the random forest models as the proportion of bouts with actively fishing nearby vessels that were correctly predicted.

The importance of variables was calculated using a permutation procedure that assesses the loss in model predictive accuracy (Strobl *et al.*, 2008; Janitza, Strobl, & Boulesteix, 2013; Hapfelmeier *et al.*, 2014). For easier interpretation, the variable importance was standardised, with the most important variable assigned a relative importance of 100% (Oppel, Powell, & Dickson, 2009; Oppel *et al.*, 2017). If behavioural metrics derived from tracking data have sufficient predictive information to distinguish foraging behind vessels in seabirds, we would expect the sensitivity of the model to be high (>75% correct classifications). All analyses were performed in R 3.6.3 (R Core Team, 2019). Unless indicated otherwise, all data are presented as means \pm SD.

Results

Foraging trip characteristics

We tracked 30, 28 and 27 individual wandering albatrosses during incubation, brood-guard and post-guard chick-rearing, respectively (Fig. 1). GPS and radar data were incomplete

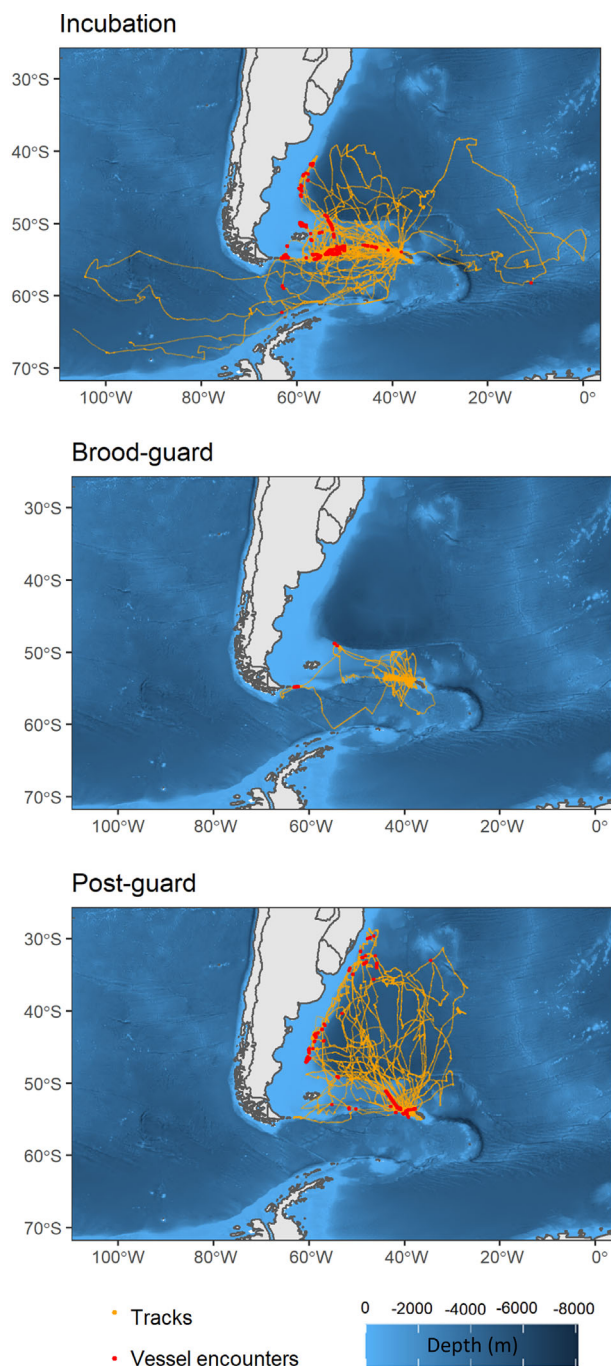


Figure 1 Foraging trips of wandering albatrosses tracked from Bird Island, South Georgia, during incubation, brood-guard and post-guard chick-rearing in 2020, overlaid on bathymetry. Red dots represent locations where albatrosses encountered vessels, either detected by bird-borne radar or from satellite AIS data indicating actively fishing vessels.

for a few trips because of battery depletion (one in incubation, three in brood-guard and six in post-guard chick-rearing). Some individuals were tracked for multiple trips in

brood-guard and post-guard chick-rearing. Overall, we obtained a total of 29, 29 and 23 complete trips that lasted for 12.6 ± 6.4 days during incubation (range 3–39 days), 3.2 ± 1.8 during brood-guard (range 2–9 days) and 8.0 ± 6.2 days during post-guard chick-rearing (range 1–24 days), respectively. Of the 85 individuals tracked, devices on 45 birds (53%) detected vessel radar during at least one trip, and 26 (58%) of these birds encountered actively fishing vessels (Fig. 1). Vessel radar was not detected by devices on twelve birds that encountered actively fishing vessels according to the AIS data.

Behavioural models

The inspection of AIC for candidate HMMs with 2–5 states suggested that a four-state HMM adequately described the dominant behavioural patterns of wandering albatrosses at sea (Additional File 1). The four behavioural states consisted of a travelling state characterised by directed flight with high speeds and low variance in turning angles, few landings and no immersion; a resting state with very slow travel speeds, intermediate variance in turning angles, no landings and always wet; and two ARS states characterised by slow speeds and high variance in turning angles, either without immersion (ARS without landings) or at least one landing (ARS with landings) (Fig. 2; TABLE 1). We classified a total of 4349 bouts of consistent behaviour from the 85 tracked individuals. The duration of bouts of ARS with landings was *c.* three times shorter than those of ARS without landings. On average, the proportion of foraging trips that was spent travelling, resting, in ARS without landings and ARS with landings was 40%, 23%, 23% and 14%, respectively (TABLE 1).

Natural foraging vs. foraging behind vessels

Vessel encounters (radar detections and AIS locations from actively fishing vessels) occurred during all behavioural states (Fig. 3), with a higher number of ARS with landings bouts associated with vessel encounters than expected (TABLE 1; $\chi^2 = 98.404$; $p < 0.001$). However, despite the unequal frequency of vessel encounters among different behavioural bouts, we found no predictable pattern associated with foraging behind vessels because the distributions of travel speeds, turning angles, landings and immersion values overlapped when comparing bouts of behavioural states with and without vessel encounters (Fig. 3). The use of metrics extracted from combined GPS and immersion data in the HMMs did not reveal a state indicative of foraging behind vessels (as indicated by radar and AIS locations from actively fishing vessels). Our results showed a higher percentage of bouts associated with vessel encounters for the ARS with landings state (30.8%) when compared to the ARS without landings state (9.6%); nonetheless, the majority of bouts in the ARS with landings state were not associated with vessels, suggesting that this state mostly reflected natural foraging behaviour.

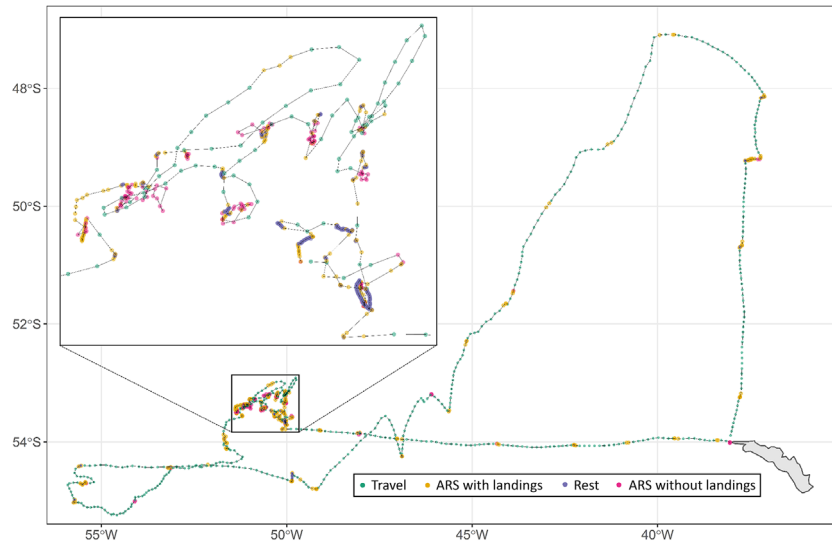


Figure 2 Example of one foraging trip of a wandering albatross tracked from Bird Island, South Georgia, during incubation in 2020, with regularised GPS locations coloured by behaviours derived from the 4-state hidden Markov model (HMM).

Table 1 Parameter estimates of the state-dependent probability distributions from the four-state hidden Markov model (HMM) of tracked wandering albatrosses from South Georgia based on GPS and immersion (activity) data. The table also includes the proportion of time spent in each state (% locations) and mean \pm SD of bout durations and the proportion of bouts with vessel encounters (radar detections and AIS locations from actively fishing vessels).

Behavioural state	Bout duration (hrs)	% Bouts with vessel encounter	Speed (km/h)	Angle conc.	<i>N</i> landings	Probability of wet			% Locations
						[0–0.2]	[0.2–0.8]	[0.8–1]	
Travel	3.31 \pm 3.05	3.87	44.68 \pm 15.5	0.92	0.02	1	0	0	40
Rest	3.41 \pm 3.01	12.93	1.59 \pm 1.08	0.8	0	0	0	1	23
ARS w/o landings	4.48 \pm 5.91	9.60	5.63 \pm 6.10	0.77	0	1	0	0	23
ARS with landings	1.55 \pm 1.22	30.80	13.80 \pm 16.19	0.72	2.62	0.12	0.36	0.52	14

Travel speeds are derived from step lengths and do not represent flight (ground) speeds of birds in the respective behavioural states. Turning angle is the angle concentration parameter (higher values indicate less variance and less convoluted tracks). The number of landings represents the total number of dry–wet transitions. The probability of wet indicates the probabilities from low (0) to high (1) that time was spent on the sea surface.

The random forest models had collectively very low sensitivity and were unable to identify bouts associated with nearby, actively fishing vessels regardless of the thresholds used for the proportion of radar detections and the proportion of locations for which a nearby vessel was classified as actively fishing (TABLE 2). However, even under the lowest thresholds, an actively fishing vessel was nearby only for about 7.4% of the 4349 bouts included in the analysis (TABLE 2); this low prevalence resulted in an overall high predictive accuracy because a model predicting there was no fishing vessel nearby would correctly classify >95% of bouts. Thus, we were unable to accurately predict whether foraging bouts occur in the vicinity of a fishing vessel, or naturally, based on movement metrics.

Discussion

This study investigated whether it is possible to detect a characteristic signature from movement and activity data that

would indicate the interaction of wandering albatrosses with fishing vessels, rather than natural foraging. Although integrating immersion and GPS data allowed us to identify two different ARS-type behaviours, neither could unambiguously indicate vessel following and associated scavenging in this species. Our results suggest that wandering albatrosses approach actively fishing vessels infrequently, and their movement and activity metrics during those encounters are not fundamentally different from their broad range of natural foraging behaviours during different stages of the breeding season (Phalan *et al.*, 2007; Froy *et al.*, 2015; Jiménez *et al.*, 2016). We therefore conclude that it is currently not possible to infer vessel attendance and thus bycatch risk from seabird movement and activity data alone using the methods presented here. Regardless, bird-borne radar loggers clearly improve our ability to infer interactions (Weimerskirch *et al.*, 2018, 2020; Corbeau *et al.*, 2019; Grémillet *et al.*, 2019; this study).

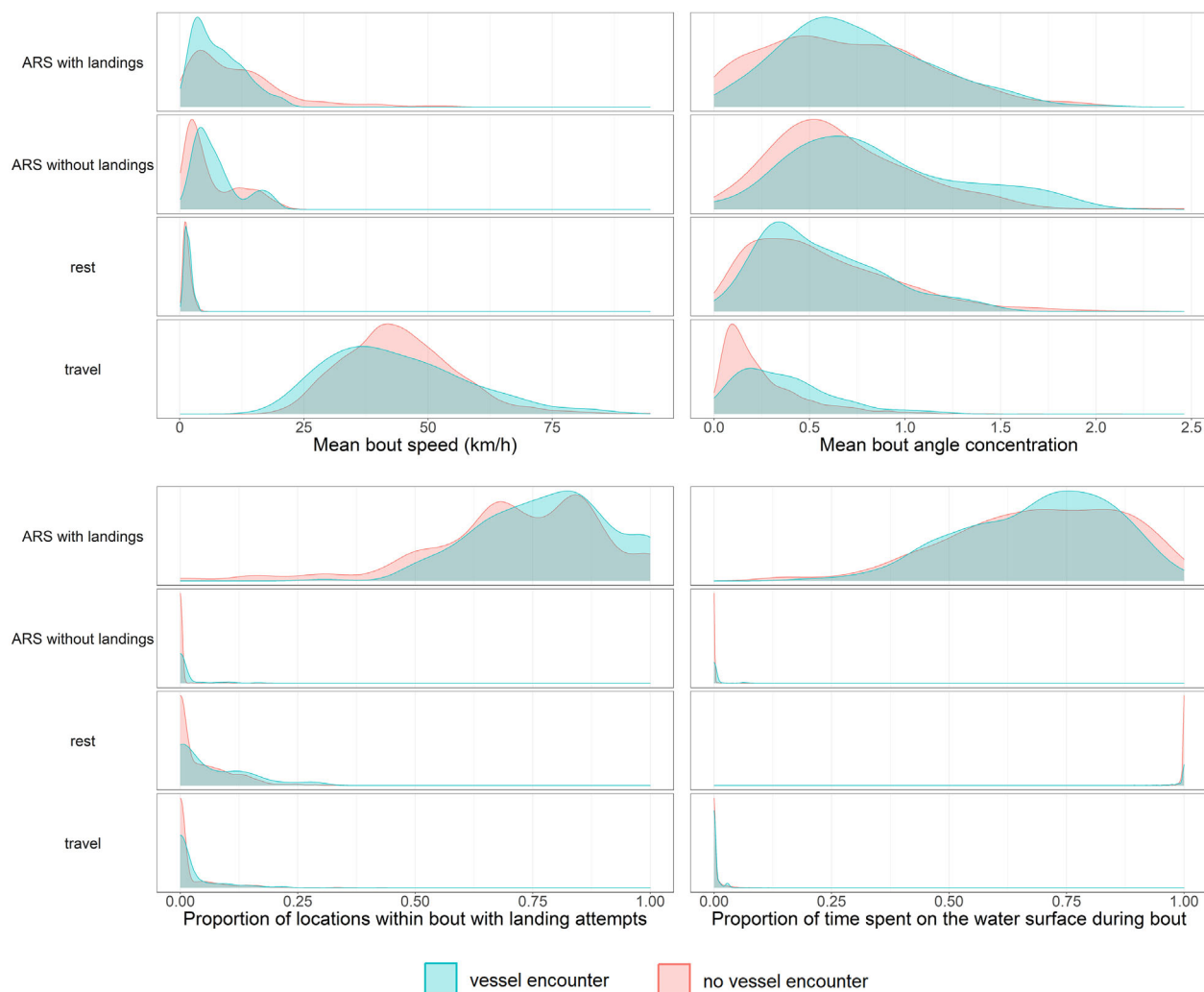


Figure 3 State-dependent density histograms of a) observed speed, b) angle concentration, c) the number of landings, and d) proportion of time spent on the water surface of wandering albatrosses tracked from South Georgia for each behaviour bout. Different colours indicate the proportion of locations within each state that were associated (green) or not (pink) with vessels (either detected by bird-borne radar or from satellite AIS data indicating actively fishing vessels).

Although seabird–fisheries interactions have been the focus of many studies worldwide (Votier *et al.*, 2010; Granadeiro *et al.*, 2011; Patrick *et al.*, 2015; Weimerskirch *et al.*, 2020), as far as we are aware, previous studies have not identified a diagnostic pattern of movement associated with scavenging behind vessels that would allow for predictions. Indeed, the few studies exploring this topic have found contrasting results. Granadeiro *et al.* (2011) found no difference in movement or at-sea activity patterns of black-browed albatrosses *Thalassarche melanophris* when foraging naturally or in close proximity to trawl vessels around the Falkland Islands. In contrast, Torres *et al.* (2011) found that white-capped albatrosses *T. steadi* from the Auckland Islands moved in straighter paths and at slower speeds when following a squid trawler than when foraging naturally. Similarly, wandering albatrosses from the Crozet Islands moved with greater sinuosity in the presence of longline fishing vessels

(Weimerskirch *et al.*, 2018; Corbeau *et al.*, 2019). However, even though mean values for movement metrics may differ significantly between birds foraging naturally or behind vessels, predicting vessel interactions is problematic when these occur very infrequently and birds display movement patterns that also occur during natural foraging.

Wandering albatrosses are known to adopt diverse strategies, including in-flight searching for prey, and sit-and-wait on the sea surface (Weimerskirch, Wilson, & Lys, 1997; Phalan *et al.*, 2007; Weimerskirch *et al.*, 2007). When foraging in flight, albatrosses often adopt ARS (Torres *et al.*, 2011). However, previous studies showed that ARS behaviour in wandering albatrosses after prey capture did not last long and only occurred after ingestion of a large item (Weimerskirch *et al.*, 2007). Indeed, over a larger scale, the most effective search strategy for wandering albatrosses is apparently to follow a nearly straight path, using ARS only when

Table 2 Prevalence (P) and predictive accuracy (A) of random forest models aiming to distinguish between behavioural bouts of tracked wandering albatrosses from South Georgia with and without actively fishing nearby vessels as identified from radar transmissions and vessel AIS locations from Global Fishing Watch (GFW)

Radar threshold	AIS threshold				
	0	0.05	0.1	0.2	0.5
0	–	P: 0.074 A: 0.926	P: 0.068 A: 0.932	P: 0.057 A: 0.943	P: 0.036 A: 0.964
0.05	P: 0.064 A: 0.936	P: 0.033 A: 0.967	P: 0.031 A: 0.969	P: 0.027 A: 0.973	P: 0.019 A: 0.981
0.1	P: 0.056 A: 0.944	P: 0.028 A: 0.972	P: 0.027 A: 0.973	P: 0.024 A: 0.976	P: 0.018 A: 0.982
0.2	P: 0.043 A: 0.957	P: 0.023 A: 0.977	P: 0.023 A: 0.976	P: 0.021 A: 0.979	P: 0.016 A: 0.984
0.5	P: 0.023 A: 0.977	P: 0.014 A: 0.986	P: 0.014 A: 0.986	P: 0.014 A: 0.986	P: 0.011 A: 0.989

The sensitivity of all models was zero. Different thresholds of % radar transmissions and % of locations with a nearby vessel classified as actively fishing were used to classify a bout as attending an actively fishing vessel; the prevalence (P) indicates the proportion of these bouts out of the total sample of 4349 bouts from 85 individuals.

they encounter a particularly favourable environment (Weimerskirch *et al.*, 2007; Corbeau *et al.*, 2019). The inclusion of immersion data in our HMM allowed two ARS states to be identified, both involving slow speeds and high turning angles, but with one state including landings indicative of prey capture attempts; this would not otherwise be detectable with location data only. Therefore, our models represent an improvement on previous approaches using auxiliary biologging data for validation purposes only. Landings (determined from immersion data) provide a reliable indicator of attempts at prey capture, as albatrosses should otherwise avoid incurring the high energetic cost of the subsequent take-off (Weimerskirch *et al.*, 2000). Resting on the water – the only other reason to land on the water surface – appears to be confined to darkness when low light levels limit the opportunities for in-flight searching for prey (Phalan *et al.*, 2007; Mackley *et al.*, 2010). This will be the case whether scavenging behind a fishing vessel or targeting natural prey. That the speed of the state ARS with landings was considerably higher on average, and more variable, than the speed during ARS without landings, may be explained by a few rapid movements of actively foraging birds, and also by the resolution of the GPS locations (10 min, possibly failing to capture the total distance travelled [and thus speed] during circular movements in the state ARS without landings).

Our inability to determine from movements or activity whether particular foraging bouts occurred only in the vicinity of an actively fishing vessel suggests that wandering albatrosses may perceive and react to fishing vessels and favourable foraging patches essentially in the same way, using visual or olfactory cues (Nevitt, 2000; Weimerskirch

et al., 2007; Collet, Patrick, & Weimerskirch, 2015). Foraging behind a vessel may be simply an extension of natural foraging for a generalist species such as the wandering albatross. Indeed, parallels have been drawn between scavenging behaviour and interactions with other types of predictable anthropogenic food sources (Collet, Patrick, & Weimerskirch, 2017). Species that have more specialised foraging strategies may respond differently to vessels. For instance, Collet, Patrick, & Weimerskirch, (2017) showed that black-browed albatrosses were more strongly attracted to fishing vessels and showed a higher level of active interaction than wandering albatrosses which overlapped with the same fleet. Moreover, many studies investigating seabird–fisheries interactions show differences in the degree of interaction with vessels according to species (Collet, Patrick, & Weimerskirch, 2017), population (Granadeiro *et al.*, 2011), sex (Jiménez *et al.*, 2016) and individual (Votier *et al.*, 2010; Granadeiro, Brickle, & Catry, 2014; Patrick *et al.*, 2015). The large variability among individuals may obscure patterns that may indicate foraging in association with a vessel based on movement and activity data alone.

Wandering albatrosses from South Georgia range widely in the southwest Atlantic during the breeding season, mostly in pelagic waters except during brood-guard when trips tend to be restricted to the South Georgia shelf and shelf-slope (Handley *et al.*, 2020). Their extensive foraging range is such that birds encounter many fishing fleets with a variety of operational and gear characteristics (Jiménez *et al.*, 2014, 2020; Phillips *et al.*, 2016). High overlaps between foraging wandering albatross and pelagic longline fisheries are reported in the Brazil-Falklands confluence (Bugoni *et al.*, 2008; Jiménez *et al.*, 2014, 2016), particularly with the Taiwanese and Japanese fleets (Jiménez *et al.*, 2016; Clay *et al.*, 2019). They also overlap with demersal longline fisheries, but this is generally restricted to a continental shelf or shelf-break habitats (Clay *et al.*, 2019). The diversity of fisheries, fleets and operational characteristics, including time of setting in relation to day/night time and the use of mitigation measures, combined with environmental conditions, are known to influence the likelihood of interactions (Jiménez *et al.*, 2014). Therefore, variation in attendance, movement and landing patterns behind different types of fishing vessel, and when foraging on diverse natural prey, may generate behavioural signatures which are specific to each of these circumstances. The diversity of fishing operations that may be attended by albatrosses is likely to further reduce the predictive power of any generic model trying to distinguish between vessel following and foraging on natural prey.

Conclusions

An inability to predict vessel attendance based on movement and activity data alone underlines the value of using multiple sources of information, including bird-borne radar and fine-scale vessel movements for a better understanding of seabird–fishery interactions. Furthermore, our method provides a coherent and generalizable framework to segment trips using auxiliary biologging (immersion) data, which

allow prey capture attempts to be quantified. Other sensors such as accelerometers and magnetometers may also provide useful data for improving predictions. Incorporation of data on wind conditions might also be valuable, as this modulates flight and foraging decisions of albatrosses and other seabirds (Clay *et al.*, 2019). We caution that the bird-borne radar did not always record vessels that were nearby according to the AIS data, indicating that direct detection of interactions is not straightforward. Nonetheless, radar detectors can provide invaluable tools when fine-scale data on vessels are unavailable and they can improve our understanding of the scale of undeclared fishing. They can also be used to support remote surveillance of the oceans. The ability to predict seabird–fisheries interactions would be invaluable for risk assessments and for improving the targeting of resources for bycatch mitigation and compliance-monitoring, contributing to the conservation of many highly threatened albatrosses and petrels (Phillips *et al.*, 2016).

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References

- Bernard, A., Rodrigues, A.S.L., Cazalis, V. & Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conserv. Lett.*, **14**, e12804.
- Bodey, T.W., Jessopp, M.J., Votier, S.C., Gerritsen, H.D., Cleasby, I.R., Hamer, K.C., Patrick, S.C., Wakefield, E.D. & Bearhop, S. (2014). Seabird movement reveals the ecological footprint of fishing vessels. *Curr. Biol.*, **24**, R514–R515.
- Bugoni, L., Mancini, P.L., Monteiro, D.S., Nascimento, L. & Neves, T.S. (2008). Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the southwestern Atlantic Ocean. *Endanger. Species Res.*, **5**, 137–147. <http://dx.doi.org/10.3354/esr00115>
- Buston, P.M. & Elith, J. (2011). Determinants of reproductive success in dominant pairs of clownfish: A boosted regression tree analysis. *J. Anim. Ecol.*, **80**, 528–538.
- Carneiro, A.P.B., Pearmain, E.J., Opper, S., Clay, T.A., Phillips, R.A., Bonnet-Lebrun, A.-S., Wanless, R.M. *et al.* (2020). A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology. *J. Appl. Ecol.*, **57**, 514–525.
- Cianchetti-Benedetti, M., Dell’Omo, G., Russo, T., Catoni, C. & Quillfeldt, P. (2018). Interactions between commercial fishing vessels and a pelagic seabird in the southern Mediterranean Sea. *BMC Ecol.*, **18**, 54.
- Clark, B.L., Handby, T., Leat, E. & Weber, S.B. (2020a). First three-dimensional tracks for the Ascension Frigatebird *Fregata aquila* highlight the importance of altitude for behavioural studies. *Seabird*, **32**, 1–19.
- Clark, B.L., Vigfúsdóttir, F., Jessopp, M.J., Burgos, J.M., Bodey, T.W. & Votier, S.C. (2020b). Gannets are not attracted to fishing vessels in Iceland—Potential influence of a discard ban and food availability. *ICES J. Mar. Sci.*, **77**, 692–700. <http://dx.doi.org/10.1093/icesjms/fsz233>
- Clay, T.A., Joo, R., Weimerskirch, H., Phillips, R.A., den Ouden, O., Basille, M., Clusella-Trullas, S., Assink, J.D. & Patrick, S.C. (2020). Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. *J. Anim. Ecol.*, **89**, 1811–1823.
- Clay, T.A., Small, C., Tuck, G.N., Pardo, D., Carneiro, A.P.B., Wood, A.G., Croxall, J.P., Crossin, G.T. & Phillips, R.A. (2019). A comprehensive large-scale assessment of fisheries bycatch risk to threatened seabird populations. *J. Appl. Ecol.*, **56**, 1882–1893.
- Collet, J., Patrick, S.C. & 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, S.C. & Weimerskirch, H. (2017). A comparative analysis of the behavioral response to fishing boats in two albatross species. *Behav. Ecol.*, **28**, 1337–1347.
- Connors, M.G., Michelot, T., Heywood, E.I., Orben, R.A., Phillips, R.A., Vyssotski, A.L., Shaffer, S.A. & Thorne, L.H. (2021). Hidden Markov models identify major movement modes in accelerometer and magnetometer data from four albatross species. *Mov. Ecol.*, **9**, 7.
- Corbeau, A., Collet, J., Fontenille, M. & Weimerskirch, H. (2019). How do seabirds modify their search behaviour when encountering fishing boats? *PLOS ONE*, **14**, e0222615.
- Corbeau, A., Collet, J., Orgeret, F., Pistorius, P. & Weimerskirch, H. (2021a). Fine-scale interactions between boats and large albatrosses indicate variable susceptibility to bycatch risk according to species and populations. *Anim. Conserv.*, **24**, 689–697. <http://dx.doi.org/10.1111/acv.12676>
- Corbeau, A., Collet, J., Pajot, A., Joo, R., Thellier, T. & Weimerskirch, H. (2021b). Differences in foraging habitat result in contrasting fisheries interactions in two albatross populations. *Mar. Ecol. Prog. Ser.*, **663**, 197–208.
- Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M. & Guilford, T. (2013). Behavioural mapping of a pelagic seabird: Combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *J. R. Soc. Interface*, **10**, 20120570. <http://dx.doi.org/10.1098/rsif.2012.0570>
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G. & Croxall, J.P. (2019). Threats to seabirds: A global assessment. *Biol. Conserv.*, **237**, 525–537.
- Fauchald, P. & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, **84**, 282–288.

- Froy, H., Lewis, S., Catry, P., Bishop, C.M., Forster, I.P., Fukuda, A., Higuchi, H., Phalan, B., Xavier, J.C., Nussey, D.H. & Phillips, R.A. (2015). Age-related variation in foraging behaviour in the wandering albatross at South Georgia: No evidence for senescence. *PLOS ONE*, **10**, e0116415.
- Froy, H., Phillips, R.A., Wood, A.G., Nussey, D.H. & Lewis, S. (2013). Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following senescence. *Ecol. Lett.*, **16**, 642–649.
- Garthe, S., Schwemmer, P., Paiva, V.H., Corman, A.-M., Fock, H.O., Voigt, C.C. & Adler, S. (2016). Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the Wadden Sea. *PLOS ONE*, **11**, e0159630.
- Granadeiro, J.P., Brickle, P. & Catry, P. (2014). Do individual seabirds specialize in fisheries' waste? The case of Black-browed albatrosses foraging over the Patagonian shelf. *Anim. Conserv.*, **17**, 19–26.
- Granadeiro, J.P., Phillips, R.A., Brickle, P. & Catry, P. (2011). Albatrosses following fishing vessels: How badly hooked are they on an easy meal? *PLOS ONE*, **6**, e17467.
- Grémillet, D., Collet, J., Weimerskirch, H., Courbin, N., Ryan, P.G. & Pichegru, L. (2019). Radar detectors carried by cape gannets reveal surprisingly few fishing vessel encounters. *PLOS ONE*, **14**, e0210328.
- Handley, J.M., Pearmain, E.J., Opper, S., Carneiro, A.P.B., Hazin, C., Phillips, R.A., Ratcliffe, N., Staniland, I.J., Clay, T.A., Hall, J., Scheffer, A., Fedak, M., Boehme, L., Pütz, K., Belchier, M., Boyd, I.L., Trathan, P.N. & Dias, M.P. (2020). Evaluating the effectiveness of a large multi-use MPA in protecting key biodiversity areas for marine predators. *Diversity and Distributions*, **26**, 715–729. <http://dx.doi.org/10.1111/ddi.13041>
- Häpfelmeier, A., Hothorn, T., Ulm, K. & Strobl, C. (2014). A new variable importance measure for random forests with missing data. *Stat. Comput.*, **24**, 21–34.
- Hothorn, T., Hornik, K. & Zeileis, A. (2006a). Unbiased recursive partitioning: A conditional inference framework. *J. Comput. Graph. Stat.*, **15**, 651–674.
- Hothorn, T., Hornik, K. & Zeileis, A. (2006b). Party: A laboratory for recursive part(y)itioning. <http://CRAN.R-project.org/>
- Janitza, S., Strobl, C. & Boulesteix, A.-L. (2013). An AUC-based permutation variable importance measure for random forests. *BMC Bioinformatics*, **14**, 119.
- Jiménez, S., Domingo, A., Brazeiro, A., Defeo, O., Wood, A.G., Froy, H., Xavier, J.C. & Phillips, R.A. (2016). Sex-related variation in the vulnerability of wandering albatrosses to pelagic longline fleets. *Anim. Conserv.*, **19**, 281–295.
- Jiménez, S., Domingo, A., Winker, H., Parker, D., Gianuca, D., Neves, T., Coelho, R. & Kerwath, S. (2020). Towards mitigation of seabird bycatch: Large-scale effectiveness of night setting and Tori lines across multiple pelagic longline fleets. *Biol. Conserv.*, **247**, 108642.
- Jiménez, S., Phillips, R.A., Brazeiro, A., Defeo, O. & Domingo, A. (2014). Bycatch of great albatrosses in pelagic longline fisheries in the Southwest Atlantic: Contributing factors and implications for management. *Biol. Conserv.*, **171**, 9–20.
- Kroodtsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C. & Worm, B. (2018). Tracking the global footprint of fisheries. *Science*, **359**, 904–908.
- Le Bot, T., Lescoë, A. & Grémillet, D. (2018). A toolkit to study seabird–fishery interactions. *ICES J. Mar. Sci.*, **75**, 1513–1525. <http://dx.doi.org/10.1093/icesjms/fsy038>
- Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T.A., Watanabe, Y.Y., Murgatroyd, M. & Papastamatiou, Y.P. (2017). Analysis of animal accelerometer data using hidden Markov models. *Methods Ecol. Evol.*, **8**, 161–173. <http://dx.doi.org/10.1111/2041-210x.12657>
- Mackley, E., Phillips, R.A., Silk, J., Wakefield, E., Afanasyev, V., Fox, J. & Furness, R. (2010). Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar. Ecol.-prog. Ser. - MAR ECOL-PROGR SER*, **406**, 291–303.
- McClintock, B.T. (2021). Worth the effort? A practical examination of random effects in hidden Markov models for animal telemetry data. *Methods Ecol. Evol.*, **12**, 1475–1497. <http://dx.doi.org/10.1111/2041-210x.13619>
- McClintock, B.T. & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.*, **9**, 1518–1530. <http://dx.doi.org/10.1111/2041-210x.12995>
- Michelot, T. & Langrock, R. (2019). A short guide to choosing initial parameter values for the estimation in moveHMM 10.
- Nevitt, G. (2000). Olfactory foraging by Antarctic Procellariiform seabirds: Life at high Reynolds numbers. *Biol. Bull.*, **198**, 245–253.
- Opper, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Manolopoulos, A., Kret, E., Velevski, M., Popgeorgiev, G.S. & Nikolov, S.C. (2017). Landscape factors affecting territory occupancy and breeding success of Egyptian vultures on the Balkan Peninsula. *J. Ornithol.*, **158**, 443–457.
- Opper, S., Powell, A.N. & Dickson, D.L. (2009). Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck. *J. Anim. Ecol.*, **78**, 524–531.
- Pardo, D., Forcada, J., Wood, A.G., Tuck, G.N., Ireland, L., Pradel, R., Croxall, J.P. & Phillips, R.A. (2017). Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. *Proc. Natl. Acad. Sci.*, **114**, E10829–E10837.
- Patrick, S.C., Bearhop, S., Bodey, T.W., Grecian, W.J., Hamer, K.C., Lee, J. & Votier, S.C. (2015). Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. *J. Avian Biol.*, **46**, 431–440. <http://dx.doi.org/10.1111/jav.00660>

- Patterson, A., Gilchrist, H.G., Chivers, L., Hatch, S. & Elliott, K. (2019). A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecol. Evol.*, **9**, 3030–3045.
- Phalan, B., Phillips, R.A., Silk, J.R.D., Afanasyev, V., Fukuda, A., Fox, J., Catry, P., Higuchi, H. & Croxall, J.P. (2007). Foraging behaviour of four albatross species by night and day. *Mar. Ecol. Prog. Ser.*, **340**, 271–286. <http://dx.doi.org/10.3354/meps340271>
- Phillips, R.A., Gales, R., Double, M.C., Favero, M., Quintana, F., Tasker, M.L., Weimerskirch, H., Uhart, M. & Wolfaardt, A. (2016). The conservation status and priorities for albatrosses and large petrels. *Biol. Conserv.*, **201**, 169–183.
- Phillips, R.A., Xavier, J.C. & Croxall, J.P. (2003). Effects of satellite transmitters on albatrosses and petrels. *Auk*, **120**, 1082–1090. <https://doi.org/10.1093/auk/120.4.1082>
- Pirotta, E., Edwards, E.W.J., New, L. & Thompson, P.M. (2018). Central place foragers and moving stimuli: A hidden-state model to discriminate the processes affecting movement. *J. Anim. Ecol.*, **87**, 1116–1125.
- Poncet, S., Wolfaardt, A.C., Black, A., Browning, S., Lawton, K., Lee, J., Passfield, K., Strange, G. & Phillips, R.A. (2017). Recent trends in numbers of wandering (*Diomedea exulans*), black-browed (*Thalassarche melanophris*) and grey-headed (*T. chrysostoma*) albatrosses breeding at South Georgia. *Polar Biol.*, **40**, 1347–1358.
- R Core Team. (2019) *R: A language and environment for statistical computing*. Vienna: Austria.
- Shimada, T., Jones, R., Limpus, C. & Hamann, M. (2012). Improving data retention and home range estimates by data-driven screening. *Mar. Ecol. Prog. Ser.*, **457**, 171–180. <http://dx.doi.org/10.3354/meps09747>
- Small, C., Waugh, S.M. & Phillips, R.A. (2013). The justification, design and implementation of ecological risk assessments of the effects of fishing on seabirds. *Mar. Policy*, **37**, 192–199. <http://dx.doi.org/10.1016/j.marpol.2012.05.001>
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T. & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC Bioinformatics*, **9**, 307.
- Torres, L.G., Sagar, P.M., Thompson, D.R. & Phillips, R.A. (2013). Scaling down the analysis of seabird-fishery interactions. *Mar. Ecol. Prog. Ser.*, **473**, 275–289. <http://dx.doi.org/10.3354/meps10071>
- Torres, L.G., Thompson, D.R., Bearhop, S., Votier, S., Taylor, G.A., Sagar, P.M. & Robertson, B.C. (2011). White-capped albatrosses alter fine-scale foraging behavior patterns when associated with fishing vessels. *Mar. Ecol. Prog. Ser.*, **428**, 289–301.
- Tuck, G.N., Phillips, R.A., Small, C., Thomson, R.B., Klaer, N.L., Taylor, F., Wanless, R.M. & Arrizabalaga, H. (2011). An assessment of seabird–fishery interactions in the Atlantic Ocean. *ICES J. Mar. Sci.*, **68**, 1628–1637. <http://dx.doi.org/10.1093/icesjms/fsr118>
- Votier, S.C., Bearhop, S., Witt, M.J., 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.
- Weimerskirch, H., Collet, J., Corbeau, A., Pajot, A., Hoarau, F., Marteau, C., Filippi, D. & Patrick, S.C. (2020). Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. *Proc. Natl. Acad. Sci.*, **117**, 3006–3014.
- Weimerskirch, H., Filippi, D.P., Collet, J., Waugh, S.M. & Patrick, S.C. (2018). Use of radar detectors to track attendance of albatrosses at fishing vessels. *Conserv. Biol.*, **32**, 240–245.
- Weimerskirch, H., Gault, A. & Cherel, Y. (2005). Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology*, **86**, 2611–2622.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P. (2000). Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. Lond. B Biol. Sci.*, **267**, 1869–1874.
- Weimerskirch, H., Pinaud, D., Pawlowski, F. & Bost, C. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am. Nat.*, **170**, 734–743.
- Weimerskirch, H., Wilson, R. & Lys, P. (1997). Activity pattern of foraging in the wandering albatross: A marine predator with two modes of prey searching. *Mar. Ecol. Prog. Ser.*, **151**, 245–254.
- Xavier, J.C., Croxall, J.P., Trathan, P.N. & Wood, A.G. (2003). Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Mar. Biol.*, **143**, 221–232.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Akaike Information Criterion (AIC) calculated for hidden Markov models (HMMs) with an increasing number of behavioural states.

Table S1. Relative variable importance of random forest models aiming to distinguish between behavioural bouts with and without nearby fishing vessels as identified from radar contacts and AIS data (Global Fishing Watch; GFW) based on different thresholds.