Agreement on the Conservation of Albatrosses and Petrels

**Thirteenth Meeting of the Seabird Bycatch Working Group**

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# Bait colour preference of seabirds to better understand vulnerabilities to anthropogenic pressures

***Elliot Styles, Karen Blake and Lauren Roman***

## ABSTRACT

Colour plays a key role in predator–prey interactions, influencing both predator behaviour and prey responses, thereby driving natural selection and evolutionary change. Birds, including seabirds, are predators that are well regarded for their visual acuity, relying on sight to see cryptic and often small prey in complex environments. Seabirds are also highly susceptible to mortality from anthropogenic pressures while foraging, including from ingestion of plastic at sea and bycatch in fisheries. To better understand this vulnerability as it relates to colour, we explore colour preference both in an a posteriori context, by reviewing the literature on colour selectivity occurring after interaction (i.e. necropsies) and then testing these findings experimentally in an a priori context. Specifically, we conducted bait colour preference trials with wild seabirds off Tasmania, Australia. Wild pelagic seabirds were offered edible baits coloured either white, yellow, red, green, black or blue, and their order of consumption was documented. We conducted 117 trials, of which 80.06% (562) of baits were eaten by seven seabird species. Of these, most baits were taken by shy-type albatrosses, *Thalassarche cauta* and *T. steadii*, and kelp gulls, *Larus dominicanus*. White bait was eaten significantly more often than other examined colours. Blue bait was rejected significantly more often than other colours. The presence of interspecific competition affected the frequency of baits eaten by each species. Both species showed a statistically significant colour preference order, favouring white first, warm colours (yellow and red) second, followed by green and black, with blue as least preferred. Our results support overarching as well as species-specific colour preferences and patterns, which we propose are dependent on foraging strategies, taxonomy and life-history stages. This data provides useful information on what choices seabirds make when foraging, with implications for both plastic ingestion and use of blue-dyed bait as a bycatch mitigation measure.

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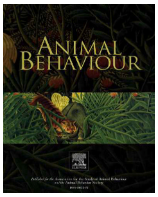

# Bait colour preference in seabirds as a way to better understand vulnerability to anthropogenic pressures

Elliot Styles [a, *], Karen Dick [b], Lauren Roman [a]

[a] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia
[b] BirdLife Tasmania, Hobart, Australia

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Colour plays a key role in predator—prey interactions, influencing both predator behaviour and prey responses, thereby driving natural selection and evolutionary change. Birds, including seabirds, are predators that are well regarded for their visual acuity, relying on sight to see cryptic and often small prey in complex environments. Seabirds are also highly susceptible to mortality from anthropogenic pressures while foraging, including from ingestion of plastic at sea and bycatch in fisheries. To better understand this vulnerability as it relates to colour, we explore colour preference both in an a posteriori context, by reviewing the literature on colour selectivity occurring after interaction (i.e. necropsies) and then testing these findings experimentally in an a priori context. Specifically, we conducted bait colour preference trials with wild seabirds off Tasmania, Australia. Wild pelagic seabirds were offered edible baits coloured either white, yellow, red, green, black or blue, and their order of consumption was documented. We conducted 117 trials, of which 80.06% (562) of baits were eaten by seven seabird species. Of these, most baits were taken by shy-type albatrosses, *Thalassarche cauta* and *T. steadii*, and kelp gulls, *Larus dominicanus*. White bait was eaten significantly more often than other examined colours. Blue bait was rejected significantly more often than other colours. The presence of interspecific competition affected the frequency of baits eaten by each species. Both species showed a statistically significant colour preference order, favouring white first, warm colours (yellow and red) second, followed by green and black, with blue as least preferred. Our results support overarching as well as species-specific colour preferences and patterns, which we propose are dependent on foraging strategies, taxonomy and life-history stages. This data provides useful information on what choices seabirds make when foraging, with implications for both plastic ingestion and use of blue-dyed bait as a bycatch mitigation measure.

Colour plays an important role in predator—prey interactions (Stevens & Ruxton, 2019). Avian predators use colour to discern prey from complex backgrounds, often using colour cues to select for (Götmark, 1996; Götmark & Olsson, 1997) or avoid prey, a trait that can be inherited (Lindström et al., 1999) or learned (Ham et al., 2006; Mastrota & Mench, 1995). Seabirds contend with unique circumstances associated with foraging at the sea surface, such as surface glare and altered depth and angle perceptions by light refraction (Bozhevolnyi, 2017). Therefore, they use several senses to seek out food at sea, foraging via both pursuit of living prey as well as scavenging (Ceia & Ramos, 2015). Olfactory cues are used to distinguish oceanographic indicators of productivity over large spatial scales (thousands of square kilometres) coupled with visual cues to target foraging opportunities over smaller scales (tens of kilometres; Nevitt, 2008). To date, information about the way seabirds use colour cues in foraging remains relatively sparse (Martí et al., 2020).

Seabirds are exposed to prey and nonprey items (e.g. plastic debris) encompassing a variety of colours in a fairly uniform sea surface foraging environment (Bozhevolnyi, 2017; Roman, Hardesty, et al., 2020). Consequently, seabirds have become vulnerable to multiple at-sea threats while foraging, including the ingestion of plastic debris (Croxall et al., 2012; Wilcox et al., 2015) and entanglement or bycatch when birds target baited hooks in longline fisheries (Cocking et al., 2008; Melvin et al., 2014).

Physical and contextual cues, including size, shape, colour and movement, likely affect a bird's decision to consume prey and other items encountered while foraging (Dell'Ariccia et al., 2014;

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* Corresponding author.
*E-mail address:* elliot.styles@utas.edu.au (E. Styles).

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Roman et al., 2016). Considering the high incidences of plastic ingestion in seabirds (Kühn & van Franeker, 2020), item colour may be one of the indicators for a seabird when making foraging decisions. The link between the colour of plastic ingested and colour of preferred prey have previously been noted but not explored in detail (Roman et al., 2016).

The consumption of plastic debris by seabirds poses a threat to individuals around the world (Roman, Butcher, et al., 2021; Wilcox et al., 2015). Many studies report on the plastic colour preference of a variety of seabird species, supported by the colour distribution of plastics retrieved during necropsies (Hidalgo-Ruz et al., 2021; Lavers & Bond, 2016; Provencher et al., 2017; Roman et al., 2016). A necropsy (or other seabird by-product, such as boluses) is conducted/collected a posteriori to the seabird death, exposing a knowledge gap whereby it is impossible to know what colour of plastic items were available to the seabird prior to its death. A study conducted a priori (before) the death of a bird, in which the range of colours available to an individual are known or controlled for, would be more informative to understand colour preferences than a posteriori studies. These a posteriori studies suggest there is a preference in colour from seabirds rather than random selection based on visibility (i.e. brightness). While visibility may play a minor role (that is, some colours may blend into the water better), the selective ingestion of certain colours indicates that mistaken identity, instead of ease of detection, could be a primary driver for plastic ingestion in seabirds. Colour preferences in seabirds may be further differentiated based on species-specific diets that reflect variances in foraging methods, body size, and ecological niches, with potential prey ranging from zooplankton, small fish and squid to scavenged carrion (Croxall, 1987).

Seabird bycatch from fisheries, including those employing longlining methods, is one of the biggest threats to seabirds globally, particularly those in the order Procellariiformes (tube-nosed seabirds; Melvin et al., 2014; Tuck et al., 2001; Weimerskirch et al., 1997). To understand the role of colour in deterring seabirds from consuming baits, trials and research on colour-dyed baits in fisheries have indicated blue-dyed baits may be useful (Cocking et al., 2008; Gilman et al., 2003, 2016; Lydon & Starr, 2005). However, further research is required to support blue dye as a deterrent. Due to a lack of evidence for the effectiveness of blue-dyed bait in reducing seabird bycatch, the Agreement on the Conservation of Albatrosses and Petrels (ACAP), an international body that advises fisheries on best practices for reducing seabird bycatch, released a statement in November 2023 declaring, ‘Use of blue-dyed bait is explicitly not recommended by ACAP, which states for this measure that there is “No experimental evidence of effectiveness in pelagic longline fisheries”’ (Agreement on the Conservation of Albatrosses and Petrels, 2023). Existing experimental evidence shows a 68% reduction in bird interactions with blue-dyed squid compared to uncoloured squid, with an overall higher efficacy of dye when applied to squid baits rather than fish baits in a longline trial (Cocking et al., 2008). This study supports the potential for coloured bait to be applied in fisheries; however, there is insufficient evidence for advisory or governing bodies to recommend blue dye as a bycatch mitigation measure, and other colours are yet to be tested.

This study aimed to experimentally investigate the colour preferences of seabirds by delivering a controlled availability of coloured baits, therefore eliminating the biases present in a posteriori studies. Specifically, we aimed to (1) review the literature on plastic ingestion by seabirds to explore the evidence for colour preferences; (2) test experimentally in wild seabirds whether different species exhibit preferences in bait colours that are consumed; and (3) test whether different species have an order of preference in the coloured baits that they consume. We also explored whether interspecific competition has an effect on these choices. From these experiments, we hope to gain new insights into how seabird vulnerability to consuming plastic debris and to bycatch in longline fisheries would be affected using different colour baits.

## METHODS

### *Literature Review for Seabird Colour Preference*

Given the limited information on seabird colour preference as it relates to fisheries, we sought existing data on seabird colour preference by reviewing the literature on the plastic colours that are ingested by seabirds belonging to the order Procellariiformes. To do this, we used data available in an international plastic ingestion database. This provided a framework to make a higher-level comparison of the frequency at which certain colour groups are consumed by seabirds against the rates of availability of these colours in the ocean. To conduct this review, we used the Global Plastic Ingestion Initiative (GLOVE) compiled by Monteiro et al. (2022), which is an open-access database of research conducted on plastic ingestion by wild animals, spanning 1981–2021 (Monteiro et al., 2022). To accurately compare the frequency of plastic colours ingested by seabirds, retrieved from the GLOVE database, against the baseline availability of plastics in the same colours on the sea surface, we compared and aligned colour categories with a recent study of global plastic colour trends as collected at the sea surface (Table S1, Martí et al., 2020). Martí et al. (2020) grouped their findings by a set of broad colour categories: transparent/translucent, white, black, grey, amber, reddish and bluish-green (Table S2). These categories were also applied for reporting of the GLOVE results. A detailed methodology of how this literature research was conducted is available in the Text S1.

These results aimed to provide context for the bait experiment conducted in this study, helping to provide a coarse overview of potential patterns in colour preferences among seabirds. These results are not intended to be analysed or interpreted in depth, given the temporal and geographic mismatches between the collection of seabird plastic ingestion and plastic at the sea surface data.

### *Field Colour Preference Testing*

The experimental component of this study was conducted alongside regular monthly seabird pelagic surveys at the continental shelf to the southeast of the state of Tasmania, Australia (−43.043, 148.038; Fig. 1). In this location, the continental shelf is accessible approximately 15 kilometres from the mainland, providing a unique opportunity to conduct behavioural experiments using wild populations of pelagic seabird species. These seabird pelagic surveys operated under the Southern Ocean Seabird Study Association Inc. (SOSSA), which coordinated pelagic surveys across four sites in southern Australia until early 2024. The seabird pelagic trips in Tasmania have been operating for over 25 years but more frequently over the past decade (up to 25 trips annually), differing from other SOSSA survey locations in that the birds are observed only (that is, not captured, handled or banded) during surveys.

The experiments took place across seven, day-long, seabird pelagic trips during the Austral spring and summer (November 2023–February 2024), departing at 0700 hours and returning at approximately 1500 hours each day. The pelagic seabird surveys are conducted by travelling via boat to the continental shelf, then ‘burleying’ while the boat drifts, a process whereby a mixture of tuna oil and minced Australian salmon, *Arripis trutta*, are placed in

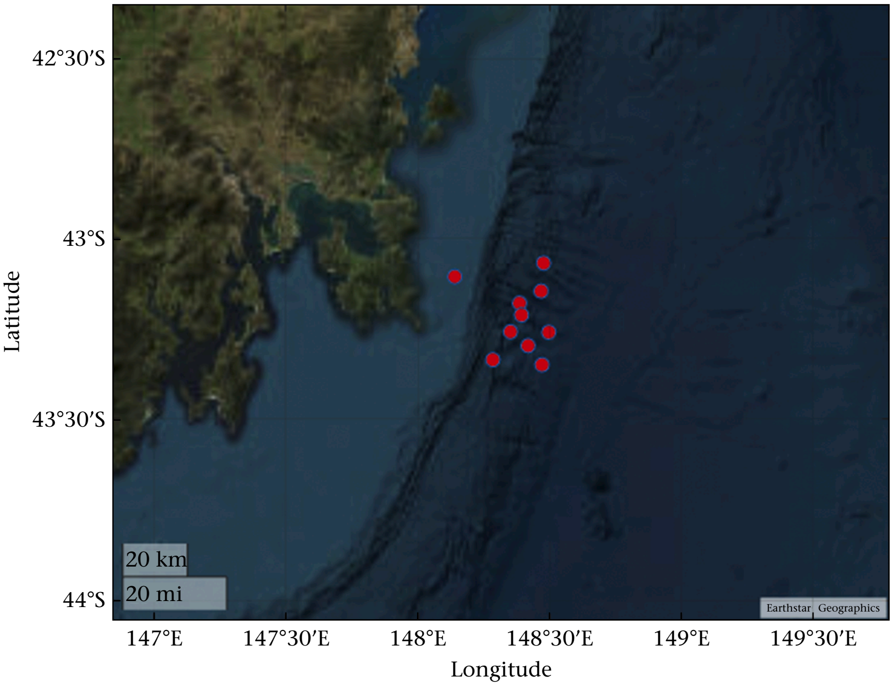

**Figure 1.** Study locations from this study conducted at the continental shelf to the southeast of the state of Tasmania, Australia. Most trials were conducted at depths of 500–1200 m.

the water as an olfactory attractant for seabirds. Skins from domestic chickens, *Gallus domesticus*, a human food-grade poultry product, are also placed in the water as a visual attractant. The vessel will typically visit three locations along the shelf in a day, drifting at each site for up to three hours.

Feeding trials involved offering baits of six colour variants to wild seabirds and recording their colour preferences. To conduct the feeding trials, a subset of the freshly defrosted chicken skins was separated at the beginning of the trip, cut into roughly 5 $cm^2$ portions and coloured either yellow, red, green, black, blue or white/tan (being the natural/white-tan colour of the undyed skins; hereafter referred to as ‘white’) with human-grade food dye. Approximately five drops of dye was used per 30 to 40 pieces of bait (Fig. S1). These colours were chosen to reflect the most common colour ‘categories’ of plastic found at sea (Martí et al., 2020; Roman et al., 2016), with blue also tested given its historical use in fisheries for seabird bycatch mitigation. The chicken skins were chosen for the baits in this study because they have already been routinely used as a visual attractant during approximately 25 years of pelagic seabird surveys, therefore posing no known additional risk to the birds. Furthermore, chicken skins are naturally light in colour, therefore taking on the dye well, and are buoyant, giving the best chances of identifying the colour choices of birds in changing wind and swell conditions.

The dispersal of the bait was conducted in a stop and trial format; the vessel stopped up to three times on each trip at different points along the shelf in a north–south orientation, covering water depths from 50–1200 m. At each stop, trials were carried out consisting of the simultaneous dispersal of one bait of each of the six colours, from the stern of the boat. These trials were recorded on paper and filmed for five minutes or until all pieces were eaten, whichever came first. The baits were deployed by a custom-made device consisting of a lightweight long pole with a flat, square foam paddle (Fig. S1). This enabled the bait to be gently lowered into the water close to the boat, minimising the chance of scaring birds and reducing the spread of excess food dye. The baits were loaded onto the dispersal device in a haphazard order before each deployment and were further mixed by the ocean movement at the stern of the boat. Alongside a camera person filming, a skilled observer recorded the order the colours were eaten in and the respective species that ate each colour, with a second observer calling interactions (Fig. 2). The camera footage allowed for quality control to retrospectively verify data recorded in the journal and to record the average (± SD) trial length and the time taken for first and last baits to be eaten from bait deployment. Typically, 20–40 trials were conducted at each stop, depending on sea conditions and the number of birds present at the boat. At each stop, metadata including latitude and longitude, cloud cover, swell size (m), depth (m), wind speed (km/h) and wind direction were recorded (Table S3). As all trials occurred in quick succession at a stop, metadata was only recorded for each stop, not each trial.

### Ethical Note

This study was undertaken with approval from the University of Tasmania's Animal Ethics Committee (Project ID: 29355). The study was undertaken in Commonwealth waters and did not require further permission under the Australian Environment Protection and Biodiversity Act 1999, as per following the Significant Impact Guidelines 1.1 – Matters of National Environmental Significance, which indicated that the proposed study would not likely have a significant impact on the environment and/or a matter of national environmental significance. As this study was conducted in natural conditions with species present on the day, species and number of individuals could not be controlled. We assume each seabird that attended the boat with each stop was a new individual, as the small number of uniquely coloured or banded birds observed generally in this pelagic tour are rarely seen more than once. However, some individuals participated in multiple trials within a stop, and it was not possible to account for this statistically as those of the same species look too similar to identify individuals. Given there were no prior similar studies, planning

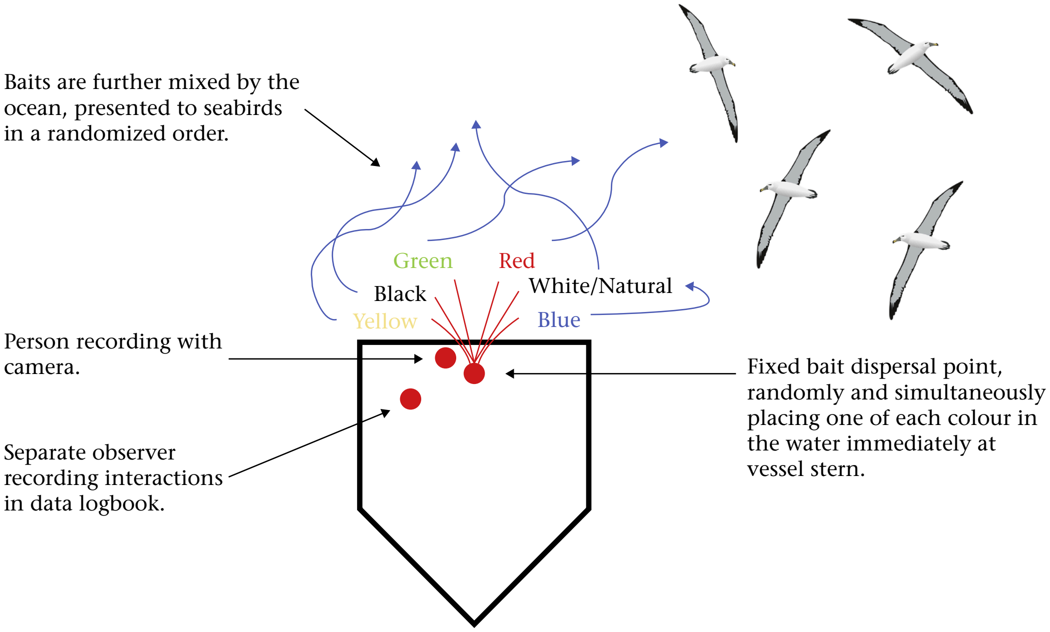

**Figure 2.** Schematic of at-sea procedure for bait deployment and trial data collection (i.e. trial 1 of 20, stop 1 of 3, trip 1 of 7).

regarding animal welfare was meticulously conducted, ensuring minimal opportunities for adverse animal welfare events to occur. Human-grade chicken skins and food dye were used in the study, with the chicken skins being used on the boat for over 25 years without incidence. To ensure the welfare of the wild birds, their behaviour was constantly monitored, ensuring no birds were experiencing any adverse effects either from the bait or from competition created during feeding. Even during feeding, the birds were left to exhibit natural behaviour. Furthermore, a workflow was established that would notify the relevant authorities should an adverse event occur, to be then instructed on how to proceed. There were no adverse events recorded during the study.

### Statistical Methods

To test the statistical significance of which colour baits the birds ate and their order of preference against random chance, we adopted the following null hypotheses. (1)$H_{O1}$: bait colour has no significant effect on a seabird's decision to eat or leave bait, and all colours are ingested at the same frequency. (2) $H_{O2}$: bait colour has no significant effect on a seabird's order of preference for bait consumption.

Using R Studio (R 4.4.2), summary statistics were calculated, including the proportion of each colour eaten by species. To test $H_{O1}$, we used generalized linear mixed models (GLMMs). This tested whether there was a significant difference between the probability that any colours were (1) eaten or (2) left over any other colour, irrespective of the species or order of consumption. The response variable was a binomial indicating if a bait had been eaten (1) or not (0), with bait colour as the fixed effect, and each round was used as the random effect. After this, the GLMM was performed for each species with sufficient representation ($N_{trials} \geq 50$). If the null hypothesis was rejected, we further tested whether interspecific competition (the presence of more than one species in the trial) affected this result by adding competition as a binomial covariate to the GLMM.

To test $H_{O2}$, a one-way ordinal permutation test was used to determine whether the order that each colour was consumed differed significantly from random selection. Order effects were included in this study as another angle to test the colour preferences of seabirds, in addition to the approach of $H_{O1}$. This test was first conducted using all birds and all trials, then the test was conducted again on a species level (that is, those with sufficient sample sizes; $N_{trials} \geq 50$), excluding trials in which baits were left. This test was rerun in the same format to include baits that were left for comparison, with ‘left’ assigned the last order of preference. Post hoc testing of any significance used a pairwise permutation test to tease apart which groups differed from others. Benjamini and Hochberg's *P* value adjustment of controlling the false discovery rate was used for the post hoc testing.

## RESULTS

### Literature Review for Seabird Colour Preference

The GLOVE results showed that some groups of plastic colour were found in seabird necropsies at frequencies higher or lower than baseline availability (as established by Martí et al., 2020), but that these patterns differed by species (Fig. 3). Thirty-six species from the order Procellariiformes were reported, with representation from the albatross, fulmar, petrel, prion, shearwater and storm petrel groups. Broadly, for white-coloured plastics, petrels, shearwaters and storm petrels consumed these at rates higher than the baseline. Albatrosses consistently consumed white the least across all species, which was below the baseline (Fig. 3). All birds consumed reddish colours at or above the baseline, with albatrosses consuming up to 10 times more than the baseline. Prions, petrels and fulmars ate transparent/translucent plastics at the highest rates out of the six Procellariiformes groups, at or above the baseline. Grey was the only colour of plastic that all species were found to consume at rates approximately equal to the readily available quantities at sea. Most species consumed bluish-green plastics at or above the baseline, with albatrosses and petrels consistently ingesting these colours at rates higher than the baseline, up to five times higher for some species (e.g. Gould's and Cook's petrels and Chatham and southern royal albatrosses). Prions, shearwaters and storm petrels consumed black plastics at rates equal to, or higher than, the baseline availability. Albatrosses

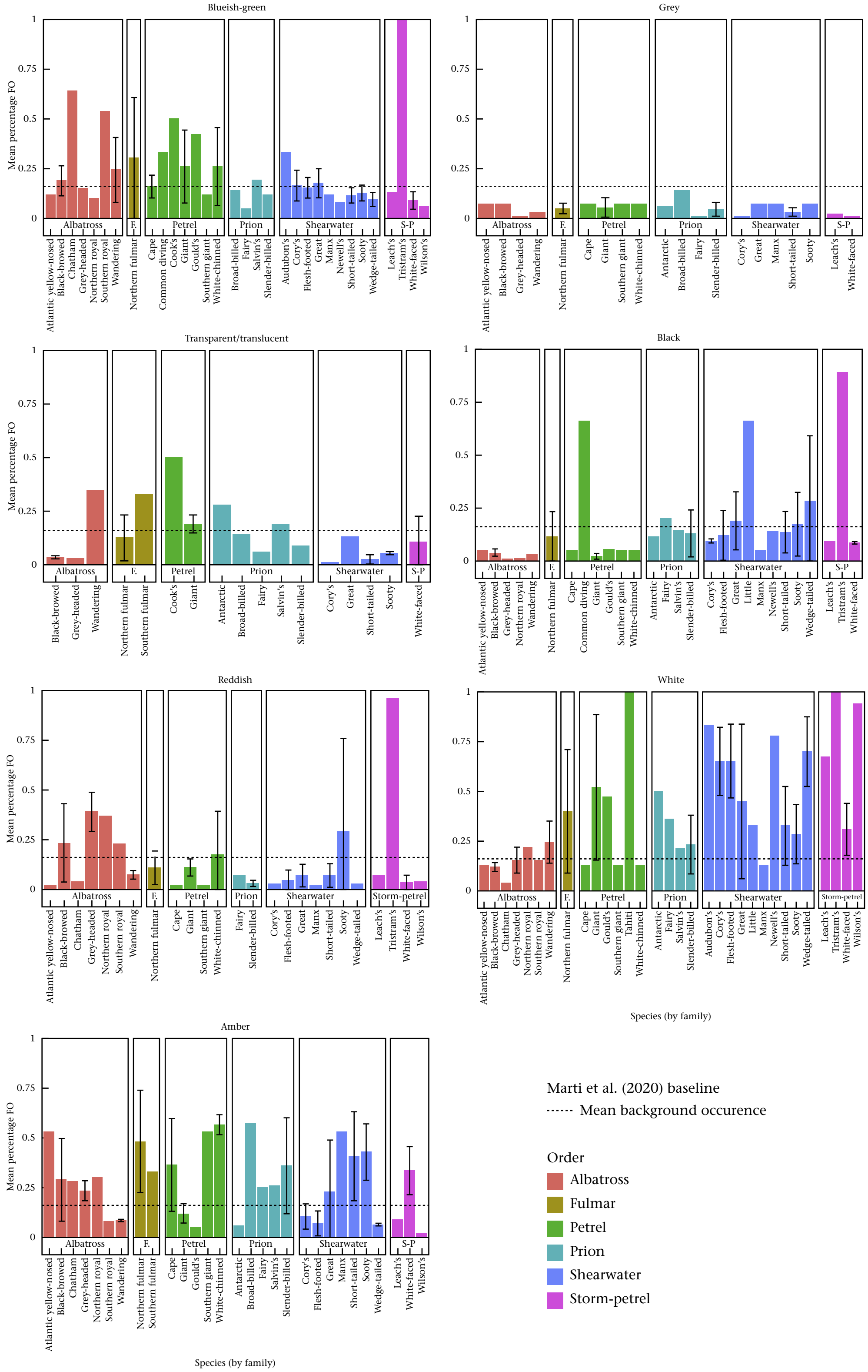

**Figure 3.** Bar plot of results of the GLOVE database seabird colour preference review for each colour category (bluish-green, grey, transparent/translucent, black, reddish, white, and amber) relating to the baseline availability of plastic floating at the sea surface, derived from Martí et al., 2020. The mean percentage frequency of occurrence was used to report these figures, with SD (see Text S1).

consumed black plastics the least of any of the groups, at rates consistently below the baseline. There was variance among each group for amber-coloured plastics, with albatross, prion and shearwater groups containing the most species that consumed amber at or above the baseline. Although some patterns, listed above, were observed, the overarching pattern was variability between taxonomic groups, and in some instances, between closely related species.

### Summary of Field Colour Preference Testing

In total, seven trips were undertaken for this study, during which 117 trials were conducted, deploying 702 baits (117 of each colour). A total of 562 (80.06%) baits were consumed by seabirds, and 140 baits (19.94%) were left (Table 1). Seven different seabird species consumed coloured baits during the experimental trials. In terms of trials consisting of a single species, there were 47 for the shy-type albatross, *T. cauta* and *T. steadii*, 16 for kelp gulls, *L. dominicanus*, and the remaining 54 were mixed species trials. The number of baits that each species consumed, in order of highest to lowest, were 270 for shy-type albatrosses (48.04%), 214 for kelp gulls (38.08%), 41 for white-chinned petrels, *Procellaria aequinoctialis* (7.3%), 28 for silver gulls, *Chroicocephalus novaehollandiae* (4.98%), five for Campbell albatross, *T. impavida* (0.89%), and two each for short-tailed shearwaters, *Puffinus tenuirostris* (0.36%) and black-browed albatrosses, *T. melanophris* (0.36%). Results from videoed rounds can be found in the Text S2 and Table S4.

### Which Colour Baits Were Eaten or Left ($H_{O1}$)

Combining all species across all trials, white baits were eaten most frequently in all but one trial. This was followed by, in order of decreasing frequency: yellow, eaten in 99 trials (84.62%), red in 96 trials (82.05%), green in 87 trials (74.36%), black in 86 trials (73.5%) and blue in 78 trials (66.66%; Fig. S2). The GLMM showed significant differences in the predicted probabilities of a bait being eaten by any seabird, contingent on bait colour; therefore, we rejected $H_{O1}$ that all colours are ingested at the same frequency. White baits had the highest probability of being eaten (10.9 ± SE 2.4, $Z = 4.6$, $P < 0.001$), followed by yellow, red, green, and black, and blue had the lowest probability of being eaten (Fig. 4, Table S5).

Although seven species consumed baits during this study, only the shy-type albatrosses and kelp gulls were analysed at the species level for $H_{O1}$, due to sample sizes. For shy-type albatrosses, the GLMM showed significant differences in the predicted probabilities of a bait being eaten (by colour); therefore, we also rejected the null hypothesis $H_{O1}$ that all colours are ingested at the same frequency for shy-type albatrosses. White baits had the highest probability of being eaten (4.50 ± 0.62, $Z = 7.32$, $P < 0.001$), followed by yellow, red, green, and black, and blue had the lowest probability of being eaten (Fig. 5, Table S6). When including the presence or absence of interspecific competition, a GLMM showed significant differences in the predicted probabilities of a bait being eaten (Fig. 5, Table S7). Shy-type albatrosses were significantly less likely to consume any bait colour if interspecific competition was present (−2.52 ± 0.60, $Z = 4.17$, $P < 0.001$). When rounds with interspecific competition were removed, a GLMM showed significant differences in the predicted probabilities of a bait being eaten ($P < 0.001$, Fig. S3; Table S8).

For kelp gulls, the GLMM showed significant differences in the predicted probabilities of a bait being eaten, contingent on bait colour ($P < 0.05$, Fig. 6, Table S9). When including the presence or absence of interspecific competition for kelp gulls, the GLMM showed significantly higher probabilities of baits of all colours being eaten when competition was not present (−3.06 ± 0.50,

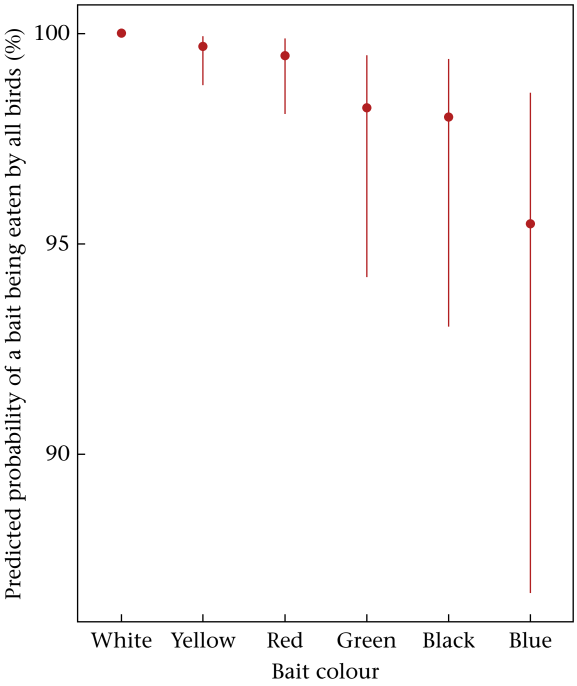

**Figure 4.** Generalized linear mixed model plot for all birds showing the predicted probabilities (95% CI) that a bird of any species will eat each coloured bait in any given trial.

**Table 1**
Number of baits eaten by each seabird species in the study

| Species | *N* Trials | Baits eaten or left, *n* (%) | | W | Y | R | G | Bla | Blu |
|---|---|---|---|---|---|---|---|---|---|
| All | 117 | Ate: | 562 (80.06%) | 116 | 99 | 96 | 87 | 86 | 78 |
| | | Left: | 140 (19.94%) | 1 | 18 | 21 | 30 | 31 | 39 |
| Shy-type albatross, *Thalassarche cauta* and *Thalassarche steadii* | 82 | Ate: | 270 (75.56%) | 82 | 46 | 48 | 38 | 27 | 28 |
| | | Left: | 88 (24.44%) | 1 | 12 | 13 | 19 | 20 | 23 |
| Kelp gull, *Larus dominicanus* | 55 | Ate: | 214 (64.84%) | 23 | 38 | 33 | 41 | 38 | 41 |
| | | Left: | 5 (1.51%) | 0 | 1 | 1 | 1 | 1 | 1 |
| Silver gull, *Chroicocephalus novaehollandiae* | 23 | Ate: | 28 (20.29%) | 10 | 8 | 3 | 1 | 6 | 0 |
| | | Left: | 9 (6.52%) | 0 | 2 | 2 | 2 | 1 | 2 |
| White-chinned petrel, *Procellaria aequinoctialis* | 15 | Ate: | 41 (45.56%) | 0 | 6 | 7 | 6 | 13 | 9 |
| | | Left: | 0 (0%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Campbell albatross, *Thalassarche impavida* | 4 | Ate: | 5 (20.83%) | 1 | 3 | 0 | 0 | 1 | 0 |
| | | Left: | 0 (0%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Black-browed albatross (*Thalassarche melanophris*) | 1 | Ate: | 2 (33.33%) | 0 | 1 | 0 | 1 | 0 | 0 |
| | | Left: | 0 (0%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Short-tailed shearwater, *Puffinus tenuirostris* | 1 | Ate: | 2 (33.33%) | 0 | 1 | 0 | 0 | 1 | 0 |
| | | Left: | 0 (0%) | 0 | 0 | 0 | 0 | 0 | 0 |

Number eaten is the number of baits eaten just by that species, the number left represents baits not eaten by any species. The percentage refers to the frequency of baits eaten or left by that species in each trial, with outstanding percentage representing baits taken by other species in the trial. Left baits were assigned to all species that had eaten a bait in a given round. Bla: black; Blu: blue; G: green; R: red; W: white; Y: yellow.

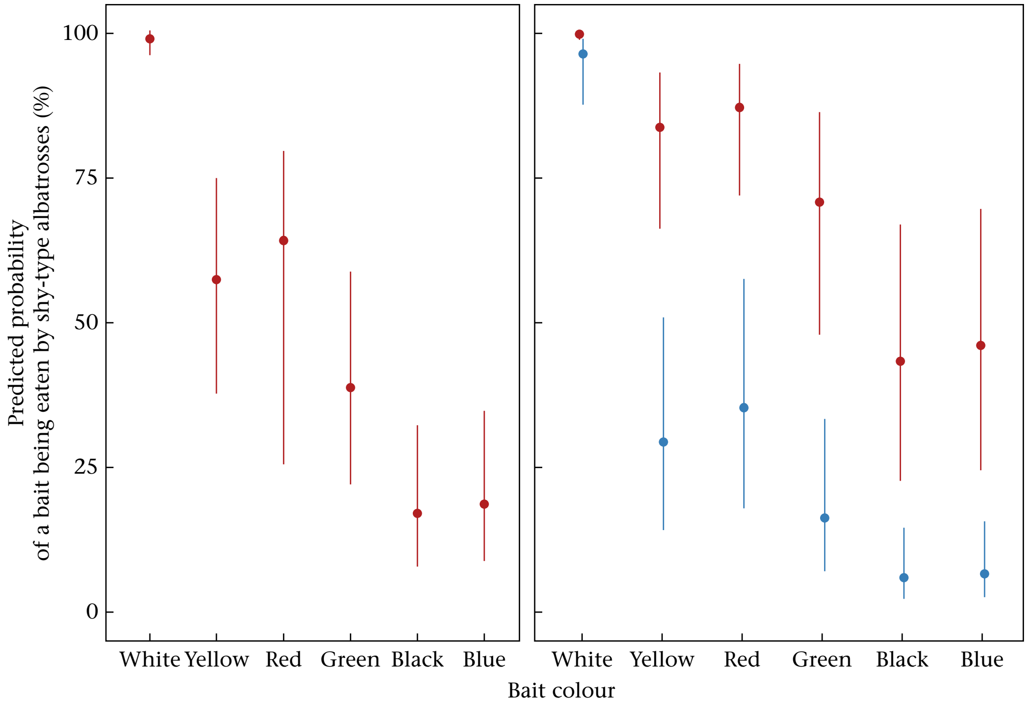

**Figure 5.** Generalized linear mixed model plot for shy-type albatrosses showing the predicted probabilities (95% CI) that a shy-type albatross will eat each coloured bait in any given trial (left), and with interspecific competition included as a variable (right).

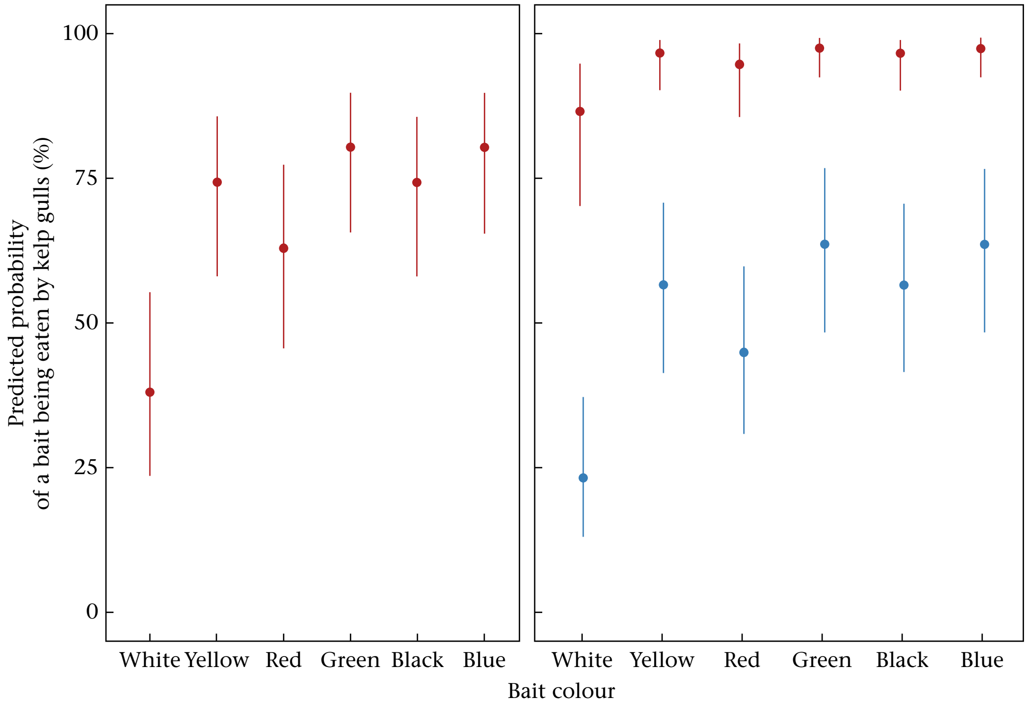

**Figure 6.** Generalized linear mixed model plot for kelp gulls showing the predicted probabilities (95% CI) that a kelp gull will eat each coloured bait in any given trial (left), and with interspecific competition included as a variable (right).

$Z = -6.16$, $P < 0.001$, Fig. 6, Table S10). When rounds with interspecific competition were removed, the GLMM showed that kelp gulls did not show significant differences in the probabilities that a bait of any colour was eaten ($P = 0.9$, Fig. S4; Table S11).

A supplementary statistical analysis for $H_{O1}$ using pairwise proportion tests can be found in Text S3.

### *Order of Preference of Bait Colours Eaten ($H_{O2}$)*

In the order of colour preference across all birds, white was eaten first 85.47% of the time. Yellow and red were commonly eaten second, 35.85% and 31.13% of the time, respectively, and, interchangeably, third at 31.96% and 23.71%, respectively. The fourth choice was typically green or black, at 27.17% and 28.26%, respectively. Red, yellow and blue ranged from 17.39% to 11.96% for fourth choice. The fifth choice was typically green, blue or black (26.51%, 25.31% and 25.31%, respectively), and blue was commonly the last bait to be eaten, at 52.24% of the time, followed by black at 28.87% of the time. Blue, black and green were the most often ignored, left 27.86%, 22.14% and 21.43% of the time, respectively, of a total of 140 coloured baits that were not consumed (Fig. 7).

A one-way ordinal permutation test indicated that there was statistical significance in the order in which the colours were consumed by all birds, which differed significantly from random chance ($\chi^2_5 = 190.04$, $df = 5$, $P < 0.05$). Using a post hoc pairwise permutation test, it was further revealed that the colour white was preferred first ($P < 0.05$), yellow and red were equally the second choice ($P < 0.05$), green and black were the third choice ($P < 0.05$) and blue was the least preferred ($P < 0.05$, Table 2).

### *Colour Preference by Species ($H_{O2}$—Individual Species)*

Although seven species consumed baits during this study, only the shy-type albatrosses, white-chinned petrels, kelp and silver gulls were analysed at the species level. Short-tailed shearwaters, black-browed albatrosses and Campbell albatrosses lacked sufficient representation (baits eaten $N = 2$, 2 and 5, respectively) to derive accurate or reliable statistical conclusions.

#### *Shy-type albatrosses*

Shy-type albatrosses had the largest sample size ($N = 270$), consuming white-coloured bait first 92.41% of the time (Table S12). Yellow and red were eaten second at 44.23% and 36.53% of the time, respectively. Blue and black were the least consumed colours, eaten 9.32% and 11.44% of the time of all the colours, compared with white, which was eaten 29.23% of the time (Fig. 8). Blue, black and green were also the most ignored colours, left at a rate of 26.53%, 24.29% and 22.45%, respectively, of the 88 baits that were left (Fig. S5).

**Table 2**
Colour preferences labelled by their statistically significant groups (A, B, etc.)

| | All | All (L) | SHAL | SHAL (L) | KEGU | KEGU (L) |
|---|---|---|---|---|---|---|
| White | A | A | A | A | A | A |
| Yellow | B | B | B | B | B | B |
| Red | B | B | B | B | BC | BC |
| Green | C | C | C | C | C | CD |
| Black | C | C | CD | D | C | D |
| Blue | D | D | D | D | D | E |

These are labelled in terms of their order of consumption (i.e. A = 1st, B = 2nd) for all birds combined, as well as shy-type albatrosses (SHAL) and kelp gulls (KEGU). The left column for each species represents only trials in which all baits were eaten, and the right column (labelled 'L') includes trials in which baits were left.

A one-way ordinal permutation test indicated that there was a significant difference between the order in which the colours were consumed by shy-type albatrosses and random chance ($\chi^2 = 88.19$, $df = 5$, $P < 0.05$). A post hoc pairwise permutation test revealed that the colour white was preferred first ($P < 0.05$), yellow and red were equal for the second choice ($P < 0.05$), green as the third choice ($P < 0.05$) and blue was generally the last colour eaten in a trial ($P < 0.05$). Black was preferred equal to both green and blue ($P < 0.05$, Table 2).

#### *Kelp gulls*

Kelp gulls had the second largest sample size ($N = 214$). White was eaten first 66.66% of the time. Red and green were eaten second at 30% and 26.66% of the time, respectively. Yellow was

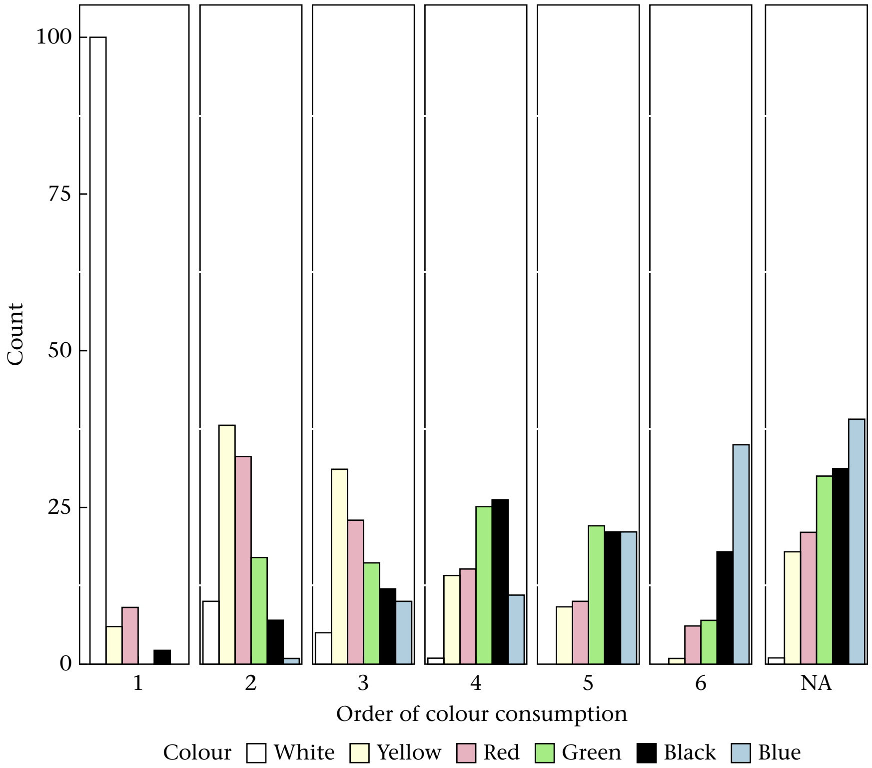

**Figure 7.** Count of each colour eaten across all species in order of their consumption. NA refers to colours that were left during a trial (i.e. the birds purposely chose to eat another colour).

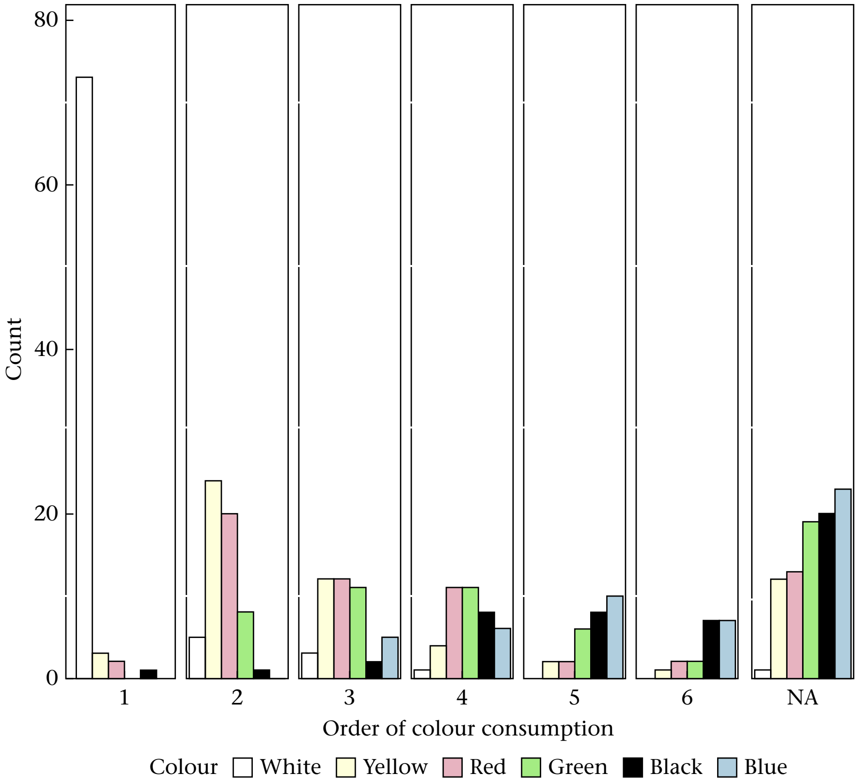

**Figure 8.** Shy-type albatross count of each colour eaten in order of their consumption. NA refers to colours that were left (i.e. not eaten by any seabird) during trials in which a shy-type albatross was involved. Note the negative (left) skewed distribution of white-, yellow-, and red-coloured baits.

eaten third the most at 38.34% of the time, before black, which was eaten third 20.59% of the time. Their fourth choice was out of black, green or yellow, consumed 30.77%, 28.21% and 20.51% of the time, respectively. Green was the most consumed fifth choice, at 31.81%, followed by black at 22.73%. Blue was consumed least often at 66.66% of the time (Fig. S6; Table S13). More baits were consumed at later orders (i.e. $N^{4th} = 39$, $N^{5th} = 44$ and $N^{6th} = 39$) than initial (i.e. $N^{1st} = 27$; Fig. 9). The kelp gulls rarely left any bait in the trials in which they were involved ($N = 5$; Fig. S6).

A one-way ordinal permutation test indicated that there was a significant difference between the order that the colours were consumed by kelp gulls and random chance ($\chi^2 = 75.62$, $df = 5$, $P < 0.05$). A post hoc pairwise permutation test revealed that the colour white was preferred first ($P < 0.05$), yellow was typically the second choice ($P < 0.05$), green and black equally as third choice ($P < 0.05$), and blue was the last colour eaten in a trial ($P < 0.05$). Red was preferred equally to both yellow and green ($P < 0.05$, Table 2).

Results and further data for silver gulls (Fig. S7; Table S14), white-chinned petrels (Fig. S8; Table S15), Campbell albatrosses (Table S16), black-browed albatrosses (Table S17) and short-tailed shearwaters (Table S18) can be found in the supplementary information.

## DISCUSSION

### *Seabird Bait Colour Preferences*

This study presents new evidence that, when consuming standardized, edible baits that vary by colour, seabirds exhibited preferences in both the colours and the order in which they consume them. This broadly supported the results of the literature review, which showed evidence that some colours of plastic were ingested more or less frequently than their baseline availability at the sea surface. Therefore, we rejected our null hypotheses that the seabirds studied do not exhibit selectivity when choosing which coloured bait they ingest or leave ($H_{O1}$), nor the order of preference ($H_{O2}$). We found that white baits were preferred over all colours when grouping all bird species, as well as when shy-type albatrosses were examined in isolation. We also found that the presence of competition affected the likelihood of baits being eaten by different species, and showed that unlike shy-type albatrosses, kelp gulls do not exhibit preferences about whether to eat bait of different colours. Shy-type albatrosses and kelp gulls both had statistically significant differences in their order of colour consumption, aside from the most (white) and least (blue) preferred. This is the first time that the colour preference of seabirds has been examined a priori, with the resulting clear significant order of preference having implications for seabirds in both fisheries and in a plastic ingestion context. Here, we explore the potential reasoning for certain colour choices in these species, as well as what implications this information will have.

The clearest distinction in preference between colours across all species is that of favouring white- and least preferring the blue-dyed baits. We posit that this preference for white baits over other colours may be explained by a combination of natural prey selection and the eyesight of the seabirds. White and associated hues (that is, silver, cream and even tan) are similar in colour to many seabird prey species, including cephalopods, small pelagic fish (e.g. Australian anchovy, *Engraulis australis*, Australian sardine, *Sardinops sagax*, and jack mackerel, *Trachurus declivis*) and zooplankton (e.g. coastal krill, *Nyctiphanes australis*). For the majority of the Southern Hemisphere's albatross and petrel species, cephalopods and fish dominate their diets, with some species also having a high dietary focus on Antarctic krill (*Euphausia superba*; Arnould &

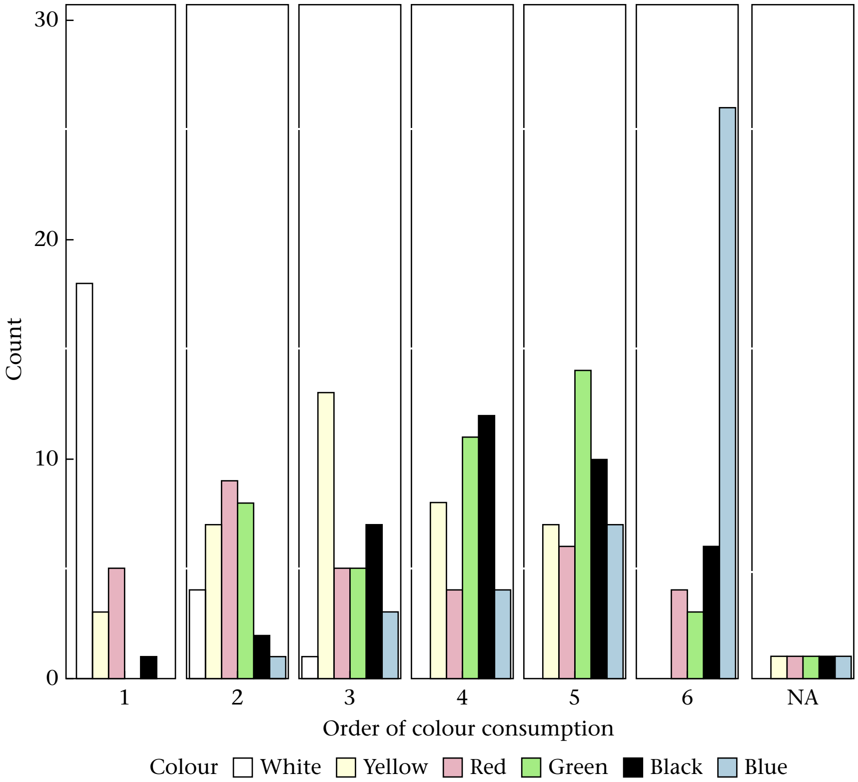

**Figure 9.** Kelp gull count of each colour eaten in order of preference. Note the positive (right) skewed distribution of white-coloured bait order of preference, the Poisson distribution of yellow and black baits order of preference and the negative (left) skewed distribution of blue-coloured baits.

Whitehead, 1991; Cherel & Klages, 1998; Quillfeldt et al., 2005). Antarctic krill and some squid species such as the Gould's squid, *Nototodarus gouldi*, and redbait, *Emmelichthys nitidus*, also found in Australian waters, have red-coloured pigmentation (although not as bright as the red-dyed baits) in addition to white (Tasmanian Government, 2024). This, as well as red being a ‘fleshy’ colour that would appeal to scavenging species, may help explain why red regularly featured as a second bait colour that was significantly preferred over blue by shy-type albatrosses. It is worth noting that these seabird diets vary, influenced by changes in prey type associated with monthly, yearly and decadal oceanic shifts due to natural and anthropogenic factors (Mills et al., 2020). This may explain their willingness to consume baits with colours brighter than typical prey.

A potential reason for the aversion of seabirds to the colour blue is its cryptic nature against the deep blue colouration of pelagic seas, as suggested by other authors (Cocking et al., 2008). Most seabirds, including Procellariiformes, are unable to see as far into the ultraviolet light spectrum as terrestrial birds, yet some gull species can (Machovsky Capuska et al., 2011). While this does not suggest that blue is invisible to the birds, it is possible that it is consumed last because there are more natural, bright or otherwise attractive colours available. This theory may also partially explain the lack of interest in black baits, as the same dark colour tends to blend in with the sea. Considering the natural camouflage of the seabirds' pelagic prey species (that is, typically dark colouration on the dorsal side and white/lighter on the ventral side), which helps them to be undetected from aerial predators, these findings align well with our understanding of natural prey camouflage functionality. However, the authors’ observations suggest the birds could see these blue-coloured baits but chose to eat them last (Text S4, Video S1, Fig. S10; Fig. S11).

### *Colour Preference Differences between Species from Experimental Trials*

The shy-type albatrosses showed a preference for white-, red- and yellow-coloured baits over the other options. Diet studies of shy albatrosses found that 89% of the birds' diet consisted of fish, dominated by jack mackerel and redbait, and 10% consisted of squid, especially Gould's squid (Hedd & Gales, 2001). These prey colours, white/silver and orange/red, are reflected as preferences in our study. Although albatrosses often ignored the remaining colours, it is possible that some individuals were less selective due to other external factors, such as hunger or body condition. Previous studies have found that seabirds make less selective food choices, including ingesting nonfood items, when they are in poor condition (Roman, Bryan, et al., 2021). When interspecific comparison was present, shy-type albatrosses ingested all bait colours, except white, less frequently. Based on our field observations, we propose they were likely outcompeted by less selective gulls for the less attractive bait colours. When there was no interspecific competition, the shy-type albatrosses were able to consume more baits.

Compared with shy-type albatrosses, kelp gulls were less selective, leaving baits only 2.3% of the time. Kelp gulls regularly forage on a broad swath of natural prey, such as fish, chitons and cephalopods, and also rely heavily on scavenging, consuming large quantities of human refuse (Coulson & Coulson, 1993; Wakefield et al., 2019). As blue baits were eaten in almost all trials that involved kelp gulls, albeit last, this likely reflects their plastic and scavenging foraging strategy. When testing for preference in the context of $H_{01}$, we found a significant difference in preference, which disappeared when rounds with interspecific competition were removed. In multispecies trials, we propose that these significant differences indicate that kelp gulls were often outcompeted by larger competitors (albatrosses) for the preferred white, red and yellow baits rather than showing a true preference for green, black and blue baits. This is also supported by the observation that when interspecific competition was not present, kelp gulls showed no statistically significant preference, eating baits of all colours. The foraging strategy of these gulls may have also played a part in why all baits were eaten in most trials. Kelp gulls typically used dipping as a foraging strategy (documented within trials that were videoed, $n = 71$; Fig. S9), giving them an overhead view of all baits. This contrasted with the typical foraging strategy of the albatrosses, which preferred surface seizing but also used dipping in some trials, and therefore may be less likely to see all bait options as they were mixed and dispersed by small surface waves (Fig. S9).

For white-chinned petrels, we acknowledge we cannot draw firm conclusions from the data due to low sample size, so the present discussion points are based on personal observation. White-chinned petrels are regarded as the species with the highest mortality rates in Southern Ocean longline fisheries (Phillips et al., 2006). The most recent mortality estimates from 1994–2008 are approximately 26 000 individual, white-chinned petrels annually (Ryan et al., 2012). While this is an older estimate, there have been no recent estimates at the time of this writing, but the overarching vulnerability of white-chinned petrels to fishery-related mortality is still conveyed. The species has been previously described to exhibit an aggressive approach to competing for fishing bait and discharge, which is reflected in their disproportionately high chances of becoming hooked on longlines, correlating with the number of individuals present (Phillips et al., 2006; Ryan et al., 2012). Our observations in the field support previous observations of aggressive foraging behaviour; and we highlight that all baits were consumed in each trial in which white-chinned petrels were involved. We also observed that the species did not show any clear colour preference, although more data would be required to lend quantitative support to this observation. We posit that the aggressive scavenging nature of white-chinned petrels and less selective approach to bait ingestion is likely linked to their vulnerability to fisheries mortality.

### *Seabird Colour Preference and Context from the Literature*

Our literature review suggests that some species ingest plastic colours at frequencies differing from their availability. However, we acknowledge this review is impacted by temporal and geographic mismatches (between seabird carcass and sea surface plastic sampling), unknowns in the seabirds' foraging ranges prior to death, methodological biases and small sample sizes. Here, we interpret the coarse patterns acknowledging these caveats. For albatrosses, the literature review shows that ‘reddish’ plastics were ingested more frequently than expected given sea surface abundance. Black plastics, however, were consumed less frequently than expected based on baseline availability. The literature review outcomes for these colours ingested by albatrosses broadly reflect the results of our experimental trials of relative colour preference of shy-type albatrosses. However, the literature review results also show albatrosses ingested white plastic less frequently than baseline availability, differing to our experimental results showing white was the most favoured colour. This difference may be due to a variety of factors, such as colour preference being influenced by other characteristics of the materials; for example, the texture of chicken skin differs substantially to that of hard plastics. It may also reflect spatial biases in the at-sea availability of different plastic colours. However, these outcomes may not conflict, as they address different questions. White may still be most preferred and, due to its abundance, ingested more overall.

Broadly, the coarse patterns shown through these plots support the theories of colour selectivity in seabird plastic ingestion based on necropsy findings, outlined in multiple publications focused on Procellariiformes (e.g. Lavers & Bond, 2016; Roman et al., 2016). The same rates of consumption did not hold for all species across each colour category, highlighting that some taxa may preferentially seek or encounter certain colours more than others. For example, albatrosses frequently ingested fewer pieces of white- and black-coloured plastic than the other taxa. However, some taxa ingested particular colours more frequently than the others. For example, the prions and shearwaters appeared to ingest the colour black more frequently than other taxa, and albatrosses ingested reddish colours more often.

The frequencies of colours ingested by seabirds in the GLOVE review, when viewed in the context of the global ocean surface plastic colours by Martí et al. (2020), provides evidence that plastic colour selectivity may be occurring broadly across the seabird taxa that ingest plastic. However, we note that this review assesses 31 separate studies that did not all use standardized methods of colour grouping. The review highlighted a mismatch between the colours floating at the sea surface and those ingested by seabirds. The apparent attraction to non-blue colours (i.e. red) suggests that seabirds may be contributing to a progressive enrichment of blue debris on the ocean surface as the other colours are removed (Martí et al., 2020; Roman et al., 2016). This may show early evidence that attraction differs by species, indicating a preference that could be influenced by many factors, including life-history strategies, yet very little is known about the colour selectivity of visual predators (Martí et al., 2020; Mitkus et al., 2016). Uncovering the colour preferences for heavily impacted species could help reduce the susceptibility and subsequent mortality of seabirds via fisheries and plastics.

## *Implications*

### *Colour preference in plastic ingestion*

This study provided empirical evidence that seabirds exhibit colour preference; therefore, we propose that colour likely also influences seabird plastic ingestion at sea. The distinct colour preferences observed largely corroborate with seabird plastic colour preferences suggested by studies focusing on surface-feeding seabirds (i.e. albatrosses and gulls). A study of plastic ingestion in surface-feeding seabirds in the Southern Ocean found that mainly white- (52.5%), brown- (not included in our colour selection; 21.3%) and yellow- (11.7%) coloured plastic dominated seabird stomach contents (Hidalgo-Ruz et al., 2021). In this same study, the colour of regurgitated plastics found in an albatross nesting site (i.e. northern, *Diomedea sanfordi*, and southern, *D. epomophora*, royal albatrosses and black-browed albatrosses) were found to be dominated by red- (32.7%), white- (20.9%) and yellow- (20.1%) coloured plastic, corresponding with the same top three colour preferences shown by shy-type albatrosses in our study (Agreement on the Conservation of Albatrosses and Petrels, 2009; Hidalgo-Ruz et al., 2021). The occurrence of white, red, and yellow colours in albatross diet samples, combined with our experimental evidence, suggests that these three colours are attractive to foraging albatrosses.

### *Fisheries*

The use of blue-dyed bait is employed as a seabird bycatch mitigation technique in some longline fisheries (Lydon & Starr, 2005), and our results support this evidence that blue-dyed baits were less preferred than other colours. Previous studies have documented a ‘confusion’ response among albatrosses when blue bait is deployed, including altered flight paths, brief landings and fewer birds following the vessel (Lydon & Starr, 2005). Numerous studies note that the efficacy of blue-dyed bait at reducing seabird bycatch was inconsistent and depended on weather, light conditions, sea surface colour, the amount of dye absorbed by the bait and the type of bait used (Gilman et al., 2003, 2016). For example, a previous study found that baiting hooks with blue-dyed squid led to a 68% reduction in seabird interactions compared to nondyed squid (Cocking et al., 2008). The authors of this study reported that blue-dyed squid is a more effective mitigator than blue-dyed fish baits but noted that the number of some species (e.g. wedge-tailed shearwaters, *Ardenna pacifica*) that ingested blue-dyed baits increased over time as they became accustomed to the colouration (Cocking et al., 2008). A 2011 study by Ochi et al. on a Japanese bluefin tuna longliner in the Southern Ocean found that blue-dyed bait was effective in reducing albatross and petrel bycatch, although the target species catch rate was also reduced (Ochi et al., 2011). Further research is needed on bait colour effects on target species before implementation. Ochi et al. (2011) speculated that dyed bait efficacy depends on the species of seabird, reflecting the findings of our study, given the lower frequency of blue baits consumed by shy-type albatrosses compared with kelp gulls. These studies consistently reaffirm that blue-dyed bait significantly reduces the risk of seabird capture compared to undyed bait, especially so when coupled with other countermeasures such as side-setting (Gilman et al., 2016; Minami & Kiyota, 2004).

Additionally, in a fisheries context, the reduction of baits eaten by shy-type albatrosses when interspecific competition was present in our study may illustrate further implications at sea. If there is a multispecies assemblage interacting with a vessel, then it is likely that the inherent nature of competition means a given species is less likely to interact with deployed longlines, as compared with only a single species being present when lines are set. A recent study on long-term, large-scale dedicated field observations in longline fisheries found that multispecies assemblages, alongside bird density, had a significant effect on the bait taking by superior competitors over inferior ones (Zhou & Brothers, 2021). Similarly, in our study, shy-type albatrosses would often be the first to interact with preferred white baits within a round, then kelp gulls would ‘clean up’ remaining baits. In rounds without competition, shy-type albatrosses were more likely to eat baits of less preferred colours. Despite being a superior competitor (based on size), shy-type albatrosses were still influenced by the presence of interspecific competition, which can be inferred and applied to scenarios associated with longline fisheries.

### *Caveats and considerations*

This study was conducted from a single small vessel off southern Australia in a seabird observation context. While informative, these conditions may not fully represent plastics at sea or typical fishery settings. Only one bait type and size were used, and different bait types, sizes, or colours might have influenced seabird preferences. Given that birds were attracted to and fed from a vessel, the experiment likely reflects a fishery context more than plastic pollution. While we cannot control which individual birds participated, the infrequent nature of trips and rare re-sightings of identifiable individuals suggest minimal bias from repeated exposure. Each trip likely involved a new cohort of birds. Future studies should expand the range of bait types, colours, sites and species to strengthen and generalize findings.

### *Future Directions*

Our study finds clear evidence of seabird colour preferences that can be used by industries to reduce the attractiveness of plastic items commonly lost at sea, reducing the risk of seabird ingestion. This can be achieved by changing the colour of items with a higher frequency of loss to colours less preferred by seabirds. A recent meta-analysis on debris items that were ingested and responsible for the deaths of 80 marine species found ‘disproportionately lethal items included plastic bags/sheets/packaging, rope/fishing nets, fishing tackle and balloons/latex’ (Roman, Schuyler, et al., 2020). Single high-risk items or industries offer opportunities for targeted reductions in items that might be ingested by seabirds. For example, changing the colour of high-risk latex items such as balloons (e.g. intentional balloon release, weather balloons; Roman, Schuyler, et al., 2020), to colours such as black and blue, may present a reduced risk of ingestion and, subsequently, death for seabirds (O'Shea et al., 2014; Roman, Schuyler, et al., 2020). In some regions, specific industries hold disproportionate responsibility for marine litter. For example, most floating plastics in the North Pacific subtropical gyre can be traced back to five industrialized fishing nations (Lebreton et al., 2022). Given that rope, fishing nets and tackle are recognized as high-risk items when ingested by seabirds (Roman, Schuyler, et al., 2020), colour changes of items commonly lost at sea in this single industry source of marine debris could potentially reduce seabird mortality.

## Author Contributions

**Elliot Styles:** Writing – original draft, Project administration, Formal analysis, Validation, Methodology, Visualization, Investigation, Data curation. **Karen Dick:** Investigation, Methodology, Conceptualization, Supervision, Data curation. **Lauren Roman:** Resources, Conceptualization, Supervision, Formal analysis, Writing – review & editing, Methodology.

## Data Availability

All data are available within the manuscript and attached supplementary information.

## Declaration of Interest

The authors declare that they have no known competing financial interests or personal interests that could have appeared to influence the work reported in this article.

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## Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123342.

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