

## Dominance interactions among New Zealand albatrosses and petrels at ecotourist boats

PAUL R. MARTIN\*

Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6

JAMES V. BRISKIE

School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

**Abstract:** Aggressive interactions among species competing for resources are common and usually asymmetric, leading to consistent dominance hierarchies. Here, we document aggressive interactions among six albatross and three petrel species off southern New Zealand, in response to supplemental food provided by ecotourism boats. For species with sufficient sampling, we found a consistent dominance hierarchy, with *Diomedea antipodensis gibsoni* > *D. epomophora* > *Macronectes halli* > *Thalassarche cauta* > *T. salvini* > *T. bulleri* > *Daption capense*. The heavier species was dominant in most species pairs. Dominant species monopolised the food provided by displacing subordinates. However, subordinate species appeared to gain access to some food through fast responses, greater manoeuvrability, and feeding on small pieces of food ignored by dominants. Similar congregations and interactions at natural food sources suggest that dominance hierarchies may play an important role in structuring the diverse seabird communities in the southern oceans.

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**Keywords:** dominance interactions, albatross, petrel, interference competition, behavioural dominance, aggressive interactions, seabird communities

### INTRODUCTION

Interference competition plays a central role in the structuring of ecological communities (Morse 1974; Persson 1985; Martin 2015; Grether *et al.* 2017), particularly among closely related species that share ecological traits, preferences, and resources (Martin & Ghalambor 2014). Aggressive, competitive interactions among species are usually asymmetric, leading to consistent selective pressures acting on species as a function of their position within a dominance hierarchy (Morse 1974; Freshwater *et al.* 2014; Martin *et al.* 2017). The extent to which

these dominance interactions influence the traits and distributions of species is poorly known, in part, because dominance relationships among most species are undescribed (Martin *et al.* 2020).

Here, we document dominance relationships among albatrosses and petrels in a diverse marine community in New Zealand. We first summarise the outcomes of aggressive contests among nine focal species, and use these data to test for consistent dominance relationships among pairs of species. We then qualitatively describe the behaviour and ecology of focal species in the context of their dominance and relative body mass. All data and observations came from albatrosses and petrels foraging on fish discards provided by ecotourism operators in southern New Zealand.

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\*Correspondence: pm45@queensu.ca

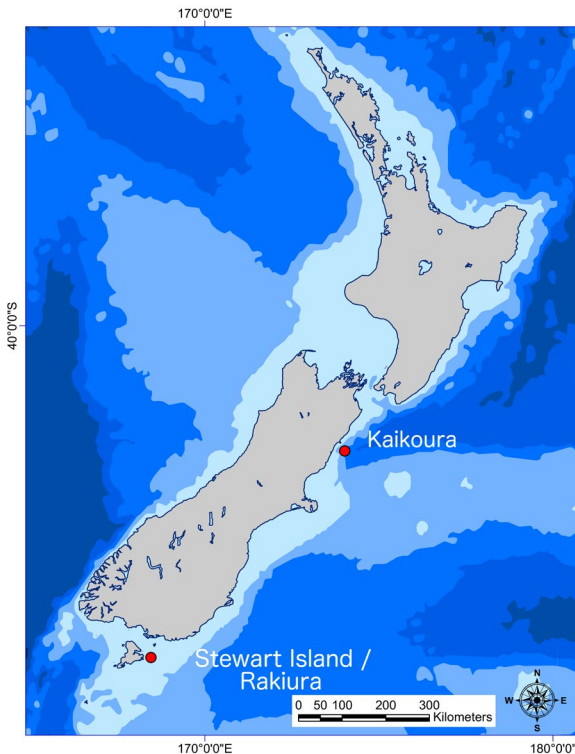
## METHODS

### Study area

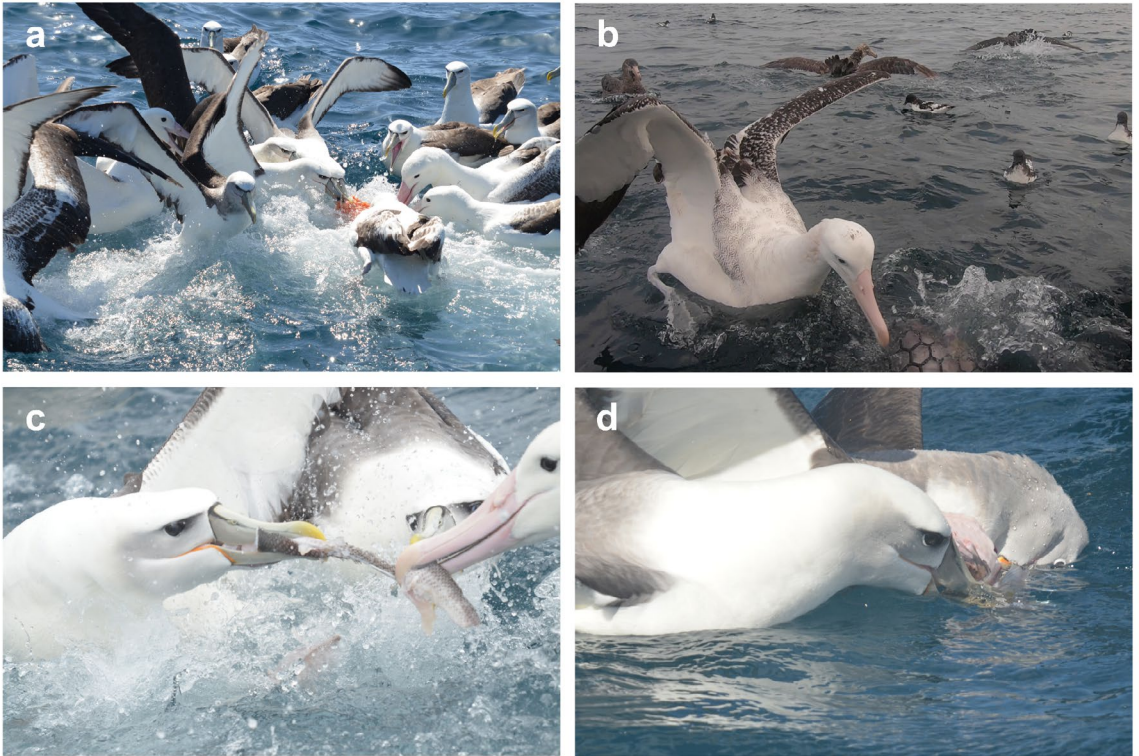
We recorded the outcomes of aggressive interactions among albatrosses and petrels that congregated behind ecotourism boats off Stewart Island/Rakiura, Southland (three trips, 24.5 hours total, 14–28 February 2020), and off Kaikoura, Canterbury (three trips, 6.5 hours total, 5–13 March 2020), New Zealand (Fig. 1). Stewart Island/Rakiura observations came from waters east of the island, from Halfmoon Bay (Oban) south to Wreck Reef and surrounding areas. Kaikoura observations came from areas offshore from South Bay to Goose Bay (The Sea Mount, The Royal, South Point, The Lump, The Outer Hole, and Trench off Barney's Rock). We obtained additional data from videos recorded by other observers and posted to YouTube (<https://www.youtube.com/>) or archived with the Macaulay Library (<https://www.macaulaylibrary.org/>), mostly recorded at Kaikoura, but with additional video recorded at Stewart Island/Rakiura and at an unspecified location in New Zealand.

### Focal species

We recorded the outcomes of aggressive interactions involving six species of albatross (Procellariiformes: Diomedidae): the Gibson's subspecies of Antipodean Albatross (*Diomedea antipodensis gibsoni*), Southern Royal Albatross (*Diomedea epomophora*), Black-browed Mollmawk (*Thalassarche melanophris*), Buller's Mollmawk (*Thalassarche bulleri*), White-capped Mollmawk (*Thalassarche cauta*), and Salvin's Mollmawk (*Thalassarche salvini*). We did not try to identify subspecies of *T. bulleri* or *T. cauta*; most or all *T. cauta* were likely *T. c. steadi* based on bill colouration and geographic location, while both *T. b. bulleri* and *T. b. platei* appeared to be present based on bill and head colouration and bill shape (Howell & Zufelt 2019), studied in photographs taken on the trips. We also recorded the outcomes of aggressive interactions involving three species of petrels (Procellariiformes: Procellariidae): Northern Giant Petrel (*Macronectes halli*), Cape Petrel (*Daption capense*), and White-chinned Petrel (*Procellaria aequinoctialis*). Focal species at Stewart Island/Rakiura were: *D. epomophora*, *T. bulleri*, *T. cauta*, *T. salvini*, and *D. capense*; focal species at Kaikoura were: *D. a. gibsoni*, *D. epomophora*, *T. cauta*, *T. salvini*, *M. halli*, *D. capense*, and *P. aequinoctialis*. Observations of aggressive contests involving *T. melanophris* came from online video exclusively. Birds were initially identified by expert tour leaders on the ecotourism trips (see Acknowledgements); birds and interactions recorded on video were identified using Howell & Zufelt (2019). It was not possible to estimate exact numbers of each focal species on each trip, but off Stewart Island/Rakiura, the minimum numbers of individuals recorded on each trip (range of minimum estimates across trips): *D. epomophora*: 10–30, *T. bulleri*: 5–10, *T. cauta*: 60–120, *T. salvini*: 6–20, *Daption capense*: 1–40. Other species of seabirds were observed during Stewart Island/Rakiura trips (e.g. Wandering/Antipodean Albatross [*Diomedea exulans/antipodensis*], Northern Royal Albatross [*Diomedea sanfordi*], *M. halli*, *P. aequinoctialis*); however, we did not observe these species engaging in aggressive contests for food around the boat. Off Kaikoura, the numbers of focal species per trip (range of estimates across trips) were: *D. antipodensis gibsoni*: 5–7, *D. epomophora*: 1–5, *T. cauta*: 2–4, *T. salvini*: 2–3, *M. halli*: 7–14, *Daption capense*: 20–40, *P. aequinoctialis*: 2–8. Again, other species were observed during Kaikoura trips (e.g. *T. melanophris*, *T. bulleri*, Westland Petrel [*Procellaria westlandica*]), but we did not observe these species engaging in aggressive contests. Numbers are minimum estimates because birds were not marked, and some birds followed the boat while others left and new birds arrived. Two other procellariids also fed on fish discards from our boats at Stewart



**Figure 1.** Map of New Zealand, showing the general locations of the two study sites (red dots). Boats moved around these sites, and thus dots show only the general locations. Shaded oceans show water depths of 0–200m, 200–1,000m, 1,000–2,000m, 2,000–3,000m, and 3,000–4,000m as progressively darker shades of blue. Map courtesy of Natural Earth ([naturalearthdata.com](http://naturalearthdata.com)).



**Figure 2.** Albatrosses and petrels compete for fish discards behind ecotourism boats in southern New Zealand. (a) *Diomedea epomophora*, *Thalassarche cauta*, and *T. salvini* (front, centre-left) compete for fish scraps off Stewart Island/Rakiura, February 2020. (b) *Diomedea antipodensis gibsoni* controls fish within a mesh container, with *Macronectes halli* and *Daption capense* in the background, off Kaikoura, March 2020. Photo from video. (c) *Thalassarche cauta* and *Diomedea epomophora* pull at scraps of fish off Stewart Island/Rakiura, February 2020. (d) *Thalassarche cauta* forces *T. salvini* under water as it attempts to take away its fish off Stewart Island/Rakiura, February 2020.

Island/Rakiura: Short-tailed Shearwater (*Puffinus tenuirostris*), and Sooty Shearwater (*Puffinus griseus*) (the latter on 21 February only). These species did not engage in aggressive interactions with other species; we discuss the behaviours that allowed them to feed without interacting directly with the other species.

### Food provisioning

All trips were commercial ecotourism excursions that used fish discards to attract seabirds to the boats. None of the trips were research driven; we simply joined pre-planned ecotourism excursions and recorded observations and video during the course of these trips. Off Stewart Island/Rakiura, tour leaders provided discards from commercial fishing, thrown individually from the back of the boat (Fig. 2a). Off Kaikoura, tour leaders provided fish discards within a mesh container attached by rope to the back of the boat (Fig. 2b).

### Dominance interactions

We recorded the outcomes of aggressive interactions between two individuals of different focal species, where there was a clear winner (dominant) and loser (subordinate). These interactions are referred to as 'dominance interactions'. Aggressive interactions incorporated, (1) chases, where one species actively pursued another in the air or on the water, (2) supplants/displacements, where one species flew, lunged, pushed, pecked, or bit at another species, causing the other species to leave its location, (3) fights, where two species pecked, bit, grabbed, grappled, or hit (e.g. with wings) each other, resulting in the losing species retreating from the interaction, and (4) kleptoparasitism, where one species aggressively engaged another species that was in possession of food, successfully taking the food away from the other species (Freshwater *et al.* 2014). We excluded observations that involved more than one individual of each species (following Freshwater *et al.* 2014) because larger groups

may have an advantage in aggressive contests, although we observed no evidence of individuals coordinating their aggression towards others. We also excluded cases where two (or more) birds had a hold on the same fish, pulling in different directions (Fig. 2c), because the fish often ripped apart, providing both individuals with some food. In these cases, dominance interactions typically did not occur – no one individual was in control of the fish, and any individual trying to displace, supplant, or fight directly with another individual would lose the fish to one or more of the many other competing individuals. To the categories of Freshwater *et al.* (2014), we added cases of active avoidance, where one individual quickly moved out of the way of another individual, even if the second individual did not use aggressive behaviours like lunging, biting, or bill clacking; all avoidance interactions were taken from video so that we could verify that the behaviour of the first (subordinate) individual occurred in response to the second. We included these avoidance behaviours in our study because they were common in some smaller species (*T. bulleri*, *Daption capense*) that actively avoided close proximity to larger species, and thus avoided pecking, biting, and other more overt interactions.

We obtained data on the outcomes of aggressive interactions among birds from both direct observations on the boats and from videos later transcribed. We recorded videos using a GoPro HERO7 Black video recorder (GoPro Inc., San Mateo, California, USA). For Stewart Island/Rakiura, we recorded the outcomes of 117 interactions from direct observations and 123 interactions from 123.5 minutes of recorded video. For Kaikoura, we recorded the outcomes of 73 interactions from direct observations and 182 interactions from 40.6 minutes of recorded video. We supplemented these data with data on the outcomes of 27 interactions from videos available online<sup>1</sup>.

### Mass

Larger mass provides an advantage in aggressive contests among birds (Morse 1974; Peters 1983; Robinson & Terborgh 1995), particularly among closely related species (Martin & Ghalambor 2014), and thus we compiled mass data for our focal species from Marchant & Higgins (1990) (Tables 1 & 2). We exclusively used masses of live and unemaciated adult birds. Average mass was used to test the hypothesis that larger species are typically dominant to smaller species in interactions.

### Statistical analyses

We tested for asymmetric dominance relationships among our focal species pairs using binomial tests (*binom.test*; R Core Team 2018). Binomial tests detect significant deviations from equality; we tested if the number of aggressive interactions between a species pair was greater than expected by chance (i.e.  $P < 0.05$ ), thus reflecting an asymmetry in dominance. We only conducted tests on species pairs with at least six recorded interactions, as this is the minimum sample required for a significant binomial test.

As the majority of our focal birds were not banded, we could not keep track of individuals involved in interspecific interactions. Thus, some of our interactions involved the same individuals, creating pseudoreplication in our data. We addressed this limitation by including three trips at each location, where different birds were likely to be involved in interactions on each trip. The tour boats visited a number of different sites on each trip, and although some birds followed the boat, each site clearly included new individuals. We also compiled information on as many interactions as possible, reducing the bias caused by one or a few oddly dominant or subordinate individuals.

## RESULTS

### Aggressive interactions

We recorded the outcomes of 522 aggressive interactions: 240 interactions from Stewart Island/Rakiura, 255 from Kaikoura, and 27 from published video from New Zealand (mostly from Kaikoura) (Tables 1 & 2). Aggressive interactions were common among species, but varied in frequency. Dominance interactions among species averaged 0.70/minute off Stewart Island/Rakiura (range 0–5.2/minute) and 4.0/minute off Kaikoura (range 0–10.0/minute) across all birds visible in the video frame (video clips ranged from 2–386 seconds, average = 71 seconds,  $n = 137$  video clips).

Aggressive interactions in Kaikoura were usually associated with control of food (either fish in the mesh container, or pieces of fish dislodged from the container). At Stewart Island/Rakiura, dominance interactions were common around the boat in the absence of food, as birds jockeyed for position in anticipation of fish being thrown. In response to fish thrown, most individuals focused on quickly obtaining and swallowing fish, with large scums of albatross pulling on pieces of fish in different directions; in these cases, dominance interactions were most evident in cases of kletoparasitism, where one individual pursued and took possession of fish initially controlled by another individual, usually by pursuing the individual in possession of the fish from the side and behind (e.g. Fig. 2d).

<sup>1</sup> <https://youtu.be/Ni0JsDzHv10> (Kaikoura); <https://www.youtube.com/watch?v=wt89NjgEe0s> (Kaikoura); <https://www.youtube.com/watch?v=QVsF-XaGfU> (Kaikoura); <https://www.youtube.com/watch?v=pMZGck4zyOM> (Kaikoura); [https://www.youtube.com/watch?v=8Wvf\\_FAIcZ0](https://www.youtube.com/watch?v=8Wvf_FAIcZ0) (unknown location, New Zealand); <https://www.youtube.com/watch?v=Z08HcAe4ck4> (unknown location, New Zealand); and Macaulay Library ML201457441 (Stewart Island/Rakiura)

Aggressive interactions among species usually involved displacements or supplants, often enabled by open or snapping bills or biting. For example, in video, displacements/supplants made up 101 of 123 interactions (82.1%; Stewart Island/Rakiura) and 146 of 182 interactions (80.2%; Kaikoura), while avoidance occurred 17 times (13.8%, Stewart Island/Rakiura) and 36 times (24.7%, Kaikoura), respectively. Prolonged chases were uncommon other than the pursuit of birds with fish (one time, 0.8%, Stewart Island/Rakiura; zero times, Kaikoura). Kleptoparasitism occurred only two times (1.6%, Stewart Island/Rakiura; zero times, Kaikoura) on video, but was more common when fish were thrown off the back of the moving boat (Stewart Island/Rakiura) because this situation was more likely to allow one individual to gain possession of a fish before others arrived (these were too distant to video using our camera). Prolonged fights (>2 seconds) only occurred in cases where *D. epomophora* attacked *T. cauta* (recorded on two occasions on our video [1.6%], four times overall, at Stewart Island/Rakiura).

**Dominance hierarchies**

We observed significant asymmetries in the outcomes of all pairwise interactions among species analysed with binomial tests. *Diomedea* spp. were dominant to all other seabirds, followed by

*Macronectes halli*, then *Thalassarche* spp., and finally *Daption capense* (Tables 1 & 2). Within *Diomedea*, *D. antipodensis gibsoni* was dominant to *D. epomophora*; within *Thalassarche*, *T. cauta* was dominant to both *T. bulleri* and *T. salvini*, while *T. salvini* was dominant to *T. bulleri* (Table 1). The outcomes of interactions between dominant and subordinate species were typically lopsided, with subordinates rarely winning aggressive interactions (Tables 1 & 2). An exception involved interactions between *T. cauta* and *T. salvini*, where the subordinate *salvini* won 15% of the aggressive contests with *cauta* (Table 1; Stewart Island). Overall, the outcomes of aggressive interactions suggest a consistent dominance hierarchy among our focal albatross and petrel species.

**Body mass and dominance**

The heavier species was dominant in aggressive contests in 12/13 species pairs (92.3%; Tables 1 & 2). The only case where the lighter species was dominant involved *Diomedea*, where *D. antipodensis gibsoni* was dominant to *D. epomophora* despite *epomophora* averaging 51.0% heavier than *antipodensis gibsoni* (Table 1; Fig. 3a,b).

**Behaviour and ecology of focal species**

*Diomedea antipodensis gibsoni* – *D. antipodensis gibsoni* was the behaviourally dominant species

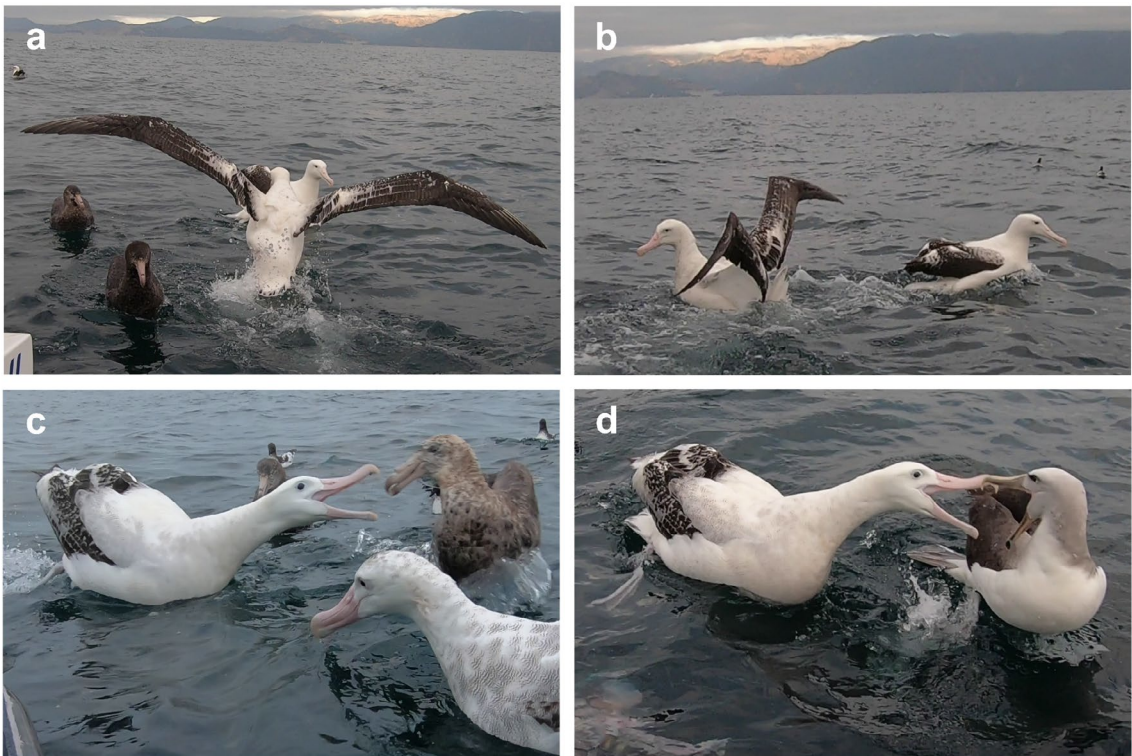
**Table 1.** Outcomes of aggressive interactions among albatross species observed off Stewart Island/Rakiura and Kaikoura, New Zealand (N=259), supplemented with observations from published video from New Zealand (N=10). ‘Species A wins’ and ‘Species B wins’ are the number of aggressive interactions won by Species A and Species B, respectively. *P* values are from binomial tests of asymmetries in the outcomes of aggressive interactions among each species pair. ‘Species A mass’ and ‘Species B mass’ provide the average mass in grams for Species A and Species B, respectively, with sample sizes in brackets, from Marchant & Higgins (1990).

| Species A                   | Species B                       | Species A wins | Species B wins | <i>P</i> | Species A mass | Species B mass | Location                          |
|-----------------------------|---------------------------------|----------------|----------------|----------|----------------|----------------|-----------------------------------|
| <i>Diomedea a. gibsoni</i>  | <i>Diomedea epomophora</i>      | 7              | 0              | 0.0156   | 5,960 (10)     | 9,000 (18)     | Kaikoura                          |
| <i>Diomedea a. gibsoni</i>  | <i>Thalassarche melanophris</i> | 1              | 0              | n/a      | 5,960 (10)     | 3,613 (98)     | Kaikoura                          |
| <i>Diomedea a. gibsoni</i>  | <i>Thalassarche cauta</i>       | 8              | 0              | 0.0078   | 5,960 (10)     | 3,983 (49)     | Kaikoura                          |
| <i>Diomedea a. gibsoni</i>  | <i>Thalassarche salvini</i>     | 7              | 0              | 0.0156   | 5,960 (10)     | 3,795 (29)     | Kaikoura                          |
| <i>Diomedea epomophora</i>  | <i>Thalassarche melanophris</i> | 2              | 0              | n/a      | 9,000 (18)     | 3,613 (98)     | unspecified                       |
| <i>Diomedea epomophora</i>  | <i>Thalassarche bulleri</i>     | 9              | 0              | 0.0039   | 9,000 (18)     | 2,793 (78)     | Stewart I.                        |
| <i>Diomedea epomophora</i>  | <i>Thalassarche cauta</i>       | 160            | 0              | 0.0000   | 9,000 (18)     | 3,983 (49)     | Stewart I.; unspecified           |
| <i>Diomedea epomophora</i>  | <i>Thalassarche salvini</i>     | 10             | 0              | 0.0020   | 9,000 (18)     | 3,795 (29)     | Stewart I.; Kaikoura; unspecified |
| <i>Thalassarche cauta</i>   | <i>Thalassarche bulleri</i>     | 32             | 1              | 0.0000   | 3,983 (49)     | 2,793 (78)     | Stewart I.                        |
| <i>Thalassarche cauta</i>   | <i>Thalassarche salvini</i>     | 22             | 4              | 0.0005   | 3,983 (49)     | 3,795 (29)     | Stewart I.                        |
| <i>Thalassarche salvini</i> | <i>Thalassarche bulleri</i>     | 6              | 0              | 0.0313   | 3,795 (29)     | 2,793 (78)     | Stewart I.                        |



**Table 2.** Outcomes of aggressive interactions involving petrel species observed off Stewart Island/Rakiura and Kaikoura, New Zealand ( $N=236$ ), supplemented with observations from published video from New Zealand ( $N=17$ ). ‘Species A wins’ and ‘Species B wins’ are the number of aggressive interactions won by Species A and Species B, respectively.  $P$  values are from binomial tests of asymmetries in the outcomes of aggressive interactions among each species pair. ‘Species A mass’ and ‘Species B mass’ provide the average mass in grams for Species A and Species B, respectively, with sample sizes in brackets, from Marchant & Higgins (1990).

| Species A                   | Species B                         | Species A wins | Species B wins | $P$    | Species A mass | Species B mass | Location              |
|-----------------------------|-----------------------------------|----------------|----------------|--------|----------------|----------------|-----------------------|
| <i>Diomedea a. gibsoni</i>  | <i>Macronectes halli</i>          | 203            | 0              | 0.0000 | 5,960 (10)     | 4,180 (235)    | Kaikoura              |
| <i>Diomedea a. gibsoni</i>  | <i>Daption capense</i>            | 8              | 0              | 0.0078 | 5,960 (10)     | 438 (179)      | Kaikoura              |
| <i>Diomedea epomophora</i>  | <i>Macronectes halli</i>          | 3              | 0              | n/a    | 9,000 (18)     | 4,180 (235)    | Kaikoura; unspecified |
| <i>Thalassarche cauta</i>   | <i>Daption capense</i>            | 1              | 0              | n/a    | 3,983 (49)     | 438 (179)      | Stewart I.            |
| <i>Thalassarche salvini</i> | <i>Daption capense</i>            | 2              | 0              | n/a    | 3,795 (29)     | 438 (179)      | Kaikoura              |
| <i>Thalassarche salvini</i> | <i>Procellaria aequinoctialis</i> | 1              | 0              | n/a    | 3,795 (29)     | 1,233 (80)     | Kaikoura              |
| <i>Macronectes halli</i>    | <i>Thalassarche cauta</i>         | 1              | 0              | n/a    | 4,180 (235)    | 3,983 (49)     | Kaikoura              |
| <i>Macronectes halli</i>    | <i>Thalassarche salvini</i>       | 6              | 0              | 0.0313 | 4,180 (235)    | 3,795 (29)     | Kaikoura              |
| <i>Macronectes halli</i>    | <i>Daption capense</i>            | 28             | 0              | 0.0000 | 4,180 (235)    | 438 (179)      | Kaikoura              |



**Figure 3.** (a, b) *Diomedea antipodensis gibsoni* charges at the larger *D. epomophora*, forcing the latter to turn and retreat, off Kaikoura, March 2020. (a) The initial charge, followed by (b), the same birds immediately after the interaction, with *D. antipodensis gibsoni* (left) turning to return to the food, and *D. epomophora* (right) retreating. *Diomedea antipodensis gibsoni* snaps at (c) *Macronectes halli* and (d) *Thalassarche salvini* off Kaikoura, March 2020. All photos from video.

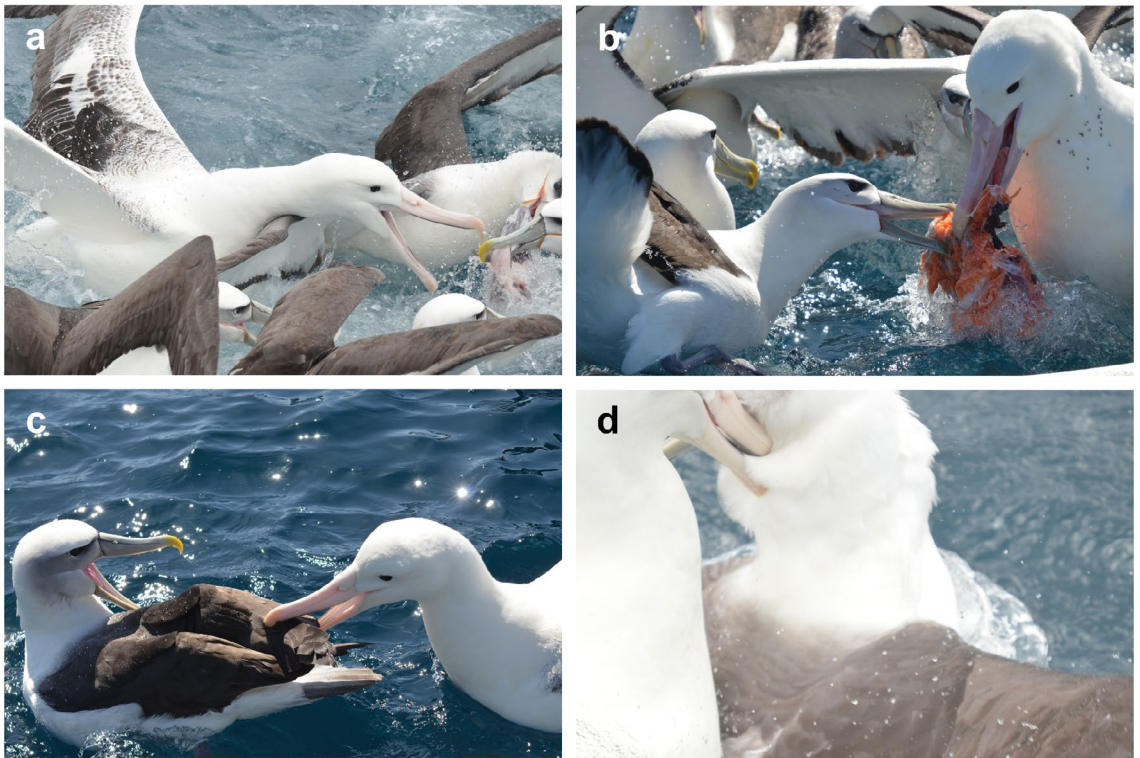
off Kaikoura. Typically, one or two individuals controlled and fed from the mesh container, snapping and sometimes chasing *M. halli* individuals that attempted to feed (Fig. 3c). The majority of interspecific aggressive interactions observed at Kaikoura involved *D. antipodensis gibsoni* snapping at *M. halli* near the fish (Table 2). *Thalassarche cauta* and *T. salvini* that attempted to feed on the fish were also chased off by *D. antipodensis gibsoni*, typically with bill snapping and a brief pursuit (Fig. 3d). *Daption capense* was occasionally displaced by *D. antipodensis gibsoni*, but more commonly ignored; *D. capense* avoided *D. antipodensis gibsoni* by scurrying out of their way. The most prolonged aggressive interactions involved conspecifics, where a dominant individual would displace the individual previously controlling the fish. Many of the behaviours used in conspecific interactions were also used in interactions with other species, including approaches with outstretched wings and upturned tail, lunges, bill clapping and chases with outstretched wings and open or snapping bills.

In contrast, *D. antipodensis gibsoni* was not observed to feed on fish off Stewart Island/Rakiura

(only two *D. exulans/antipodensis* were observed off Stewart Island/Rakiura, not identified to species; neither fed on fish near the boat).

*Diomedea epomophora* – *D. epomophora* was the behaviourally dominant albatross off Stewart Island/Rakiura. *Diomedea epomophora* typically responded more slowly to fish being thrown than the smaller albatrosses (*Thalassarche* spp.); even fish thrown in front of *epomophora* were typically first seized by *T. cauta*. Most *D. epomophora* waited until a piece of fish had been seized by multiple, tugging *Thalassarche*, and then muscled through to grab the fish (Fig. 4a). *Diomedea epomophora* that were able to grab onto fish were usually successful in obtaining some food, with fish often breaking apart so that multiple birds obtained parts.

*Diomedea epomophora*, however, often arrived too late to obtain fish, particularly when *Thalassarche* could swallow the fish quickly. Large pieces of fish that were occasionally thrown could not be quickly swallowed by *Thalassarche*, and eventually became controlled by *D. epomophora* (Fig. 4b), with



**Figure 4.** *Diomedea epomophora* (a) forces its way through other albatrosses to grab fish being contested by *Thalassarche cauta*, and (b) monopolises a larger piece of fish, off Stewart Island/Rakiura, February 2020. *Diomedea epomophora* bites *Thalassarche cauta* off Stewart Island/Rakiura, February 2020, (c) in the absence of fish, and (d) during contests for thrown fish.



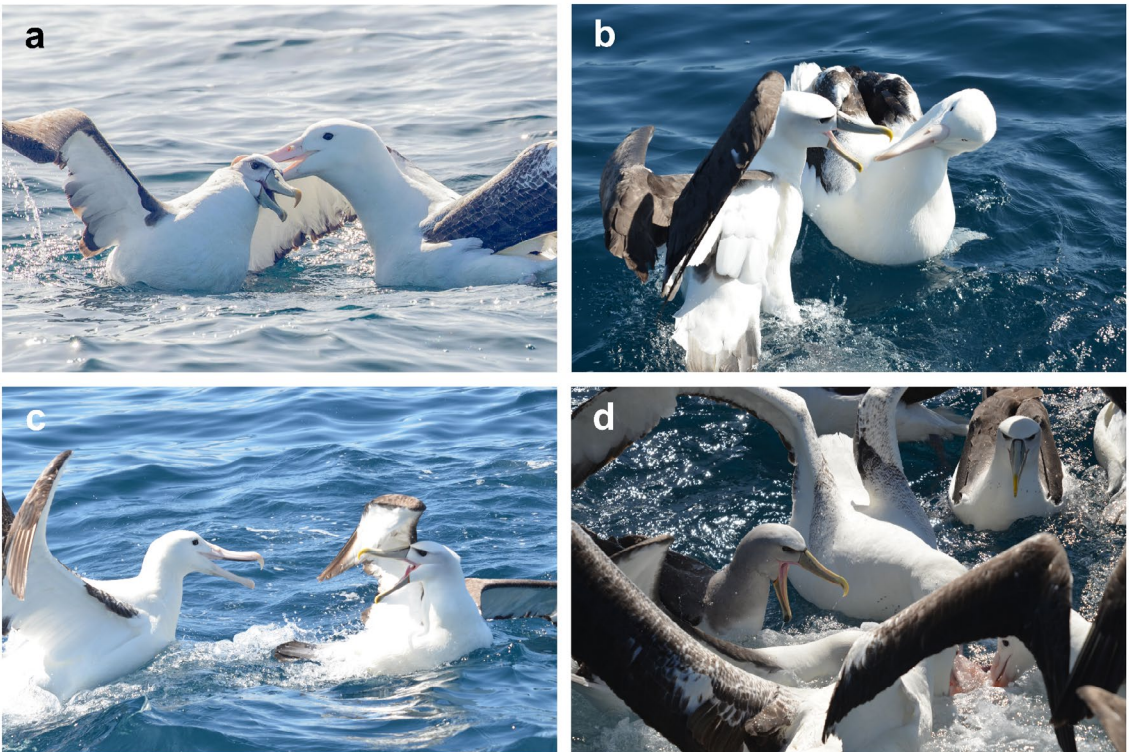
up to six individuals pulling in different directions. We did not observe *D. epomophora* dive for fish, despite *Thalassarche* spp. regularly diving.

Most dominance interactions at Stewart Island/Rakiura involving *D. epomophora* occurred in the absence of food, as birds jockeyed for position and displaced *Thalassarche* nearby. *Diomedea epomophora* commonly bit, bill clapped, snapped at, or pulled feathers of *T. cauta* (Fig. 4c) and *T. salvini*; most *T. bulleri* avoided *D. epomophora* and quickly moved out of the way of any *epomophora*. *Diomedea epomophora* also bit *T. cauta* during scrambles for fish, including deep bites on the neck (Fig. 4d). *Diomedea epomophora* directed aggressive displays towards other species, including approaching with outstretched wings and bill (Fig. 4a), lunges, and bill clapping; these displays were similar to those used in conspecific interactions (and similar to *D. antipodensis gibsoni* aggressive displays).

The most striking examples of dominance involved repeated cases of *D. epomophora* grabbing

a *T. cauta* by the neck or head, pulling them away, and repeatedly shaking them, holding on for >20 seconds and sometimes pushing their heads under water (Fig. 5a). This behaviour was observed on four occasions off Stewart Island/Rakiura and appeared violent enough to cause injury to *T. cauta*.

At Kaikoura, *D. epomophora* was subordinate to *D. antipodensis gibsoni* and was never observed to successfully feed on the fish discards. Individuals that approached *D. antipodensis gibsoni* in control of the fish retreated when *D. antipodensis* turned to face them, lunged at them, or chased them off (Fig. 3a,b). Even when *D. epomophora* occurred in numbers (three *epomophora*, with two *D. antipodensis gibsoni* near the food), they sat at the periphery, with individuals moving towards the fish, but then retreating each time. One bird appeared to challenge *D. antipodensis gibsoni* at the food, approaching, extending its bill forward, and giving a low guttural call; this bird was immediately chased off by the *D. antipodensis gibsoni* in control of the food (Fig. 3a,b). Kaikoura *D. epomophora* included some younger birds (including first cycles), but also adults (c.f.



**Figure 5.** (a) *Diomedea epomophora* holds *Thalassarche cauta* by the neck, intermittently shaking it, off Stewart Island/Rakiura, February 2020. Photo by Dan Barton. (b, c) *Thalassarche cauta* responds to being bitten by *Diomedea epomophora* off Stewart Island/Rakiura, February 2020. (d) *Thalassarche salvini* (centre left) calls after being pushed aside by *Diomedea epomophora* and *T. cauta* off Stewart Island/Rakiura, February 2020.



Howell & Zufelt 2019), and thus the dominance of *D. antipodensis gibsoni* (which included mostly adults) seems unlikely to simply reflect age class differences between the species; all *D. epomophora* were visibly larger than the *D. antipodensis gibsoni*. *Thalassarche bulleri* – *T. bulleri* was the most subordinate albatross studied, losing almost all dominance interactions with other *Thalassarche* and *D. epomophora*, and often avoiding larger albatrosses (especially *D. epomophora*) and intense scums of albatrosses competing for fish. *Thalassarche bulleri* was observed on all trips to Stewart Island/Rakiura and regularly came in to fish scraps; only one *T. bulleri* was observed off Kaikoura, and this individual did not land or engage with other birds at fish behind the boat.

*Thalassarche bulleri* were generally quicker than other albatrosses, and thus sometimes obtained fish or smaller fish pieces and swallowed them before other species. This approach was particularly successful on occasions where fish were tossed from a moving boat, and thus few albatrosses were able to respond. If *T. bulleri* was the first to reach the food and swallowed it before other species of albatross had settled, then they were successful; if other *Thalassarche* (usually *T. cauta*) reached them before they could swallow the fish, then they usually lost the fish to the dominant species (e.g. Macaulay Library video, ML201457441).

When fish was thrown behind a stationary boat (as was typical), *T. bulleri* stood out as one of the few species actively scurrying away from the fish in the opposite direction of most albatrosses, avoiding the large scums. Food thrown immediately in front of *T. bulleri* was sometimes passed up by *bulleri* if larger numbers of *T. cauta* were nearby. Even when food was not present, *T. bulleri* often remained at the periphery of waiting albatrosses, especially when large numbers of *T. cauta* and *D. epomophora* had congregated. *Thalassarche bulleri* also left the area during some periods when large numbers of *T. cauta* and *D. epomophora* were present.

Nonetheless, some *T. bulleri* engaged within the albatross scums, and even participated in pulling matches with *T. cauta*, with individuals of each species pulling a piece of fish in different directions. If this led to the fish breaking, *T. bulleri* obtained part or even most of the fish. *Thalassarche bulleri* also commonly moved actively about the edges of scums, eating smaller pieces of fish that had torn off, and diving under water to secure sinking pieces of fish. *Thalassarche bulleri* was most often displaced by *T. cauta* (Table 1), with *T. cauta* individuals lunging, charging, or bill snapping; *T. bulleri* regularly scurried out of the way of both *T. cauta* and especially *D. epomophora*, avoiding more direct interactions. *Thalassarche salvini* displaced *T. bulleri* through bill snaps and lunges.

*Thalassarche bulleri* was rarely an initiator of aggressive interactions (Tables 1 & 2). When attacked by other species, or retreating from scums of albatrosses, *T. bulleri* sometimes elevated its head, opened its bill wide, and called, moving its head side to side, highlighting the bill, gape, and mouth colouration, and the bright ridges of skin running posterior to the gape along the cheek. Similar displays were used in interactions with conspecifics.

*Thalassarche cauta* – *T. cauta* was the most abundant focal species off Stewart Island/Rakiura, with large numbers gathering at the boat in response to fish discards. *Thalassarche cauta* were quick, and thus usually the first species to grab fish, with each individual trying to swallow the fish before other albatrosses. Multiple individuals would grab a fish, leading to tugging and chaotic scums of albatrosses, all battling for pieces of fish (Fig. 2a,c). *Thalassarche cauta* sometimes dove underwater for sinking pieces of fish.

Dominance interactions involving *T. cauta* occurred as they waited for fish to be thrown, and involved *T. cauta* pulling at feathers on the back half of the recipient, often from the side or behind, biting, bill snapping or clacking, and lunging. *Thalassarche cauta* also placed their bills overtop the backs of *T. salvini* and lowered their bills to the water, with their lower mandible coming in contact with the primaries or rump of the other bird; this behaviour would result in the recipient scurrying away. Bill fighting, where two birds faced each other and knocked their partly open bills repeatedly, occurred regularly between *T. cauta* and *T. salvini*, and between *T. cauta* and *D. epomophora*; however, these interactions often did not produce a clear winner (and thus were not considered dominance interactions), but instead lead to both birds backing off. All aggressive interactions of *T. cauta* that were directed toward other species were also used towards conspecifics.

*Thalassarche cauta* kleptoparasitised *T. bulleri* and *T. salvini*, typically by approaching a bird with a fish from the side and behind, grabbing the fish, and then wrestling the fish away by pulling back and away. One individual appeared to force the head of *T. salvini* under water as they wrestled for the fish (Fig. 2d). *Thalassarche cauta* that engaged in tugging on opposite ends of a piece of fish (e.g. Fig. 2c) often failed to obtain all of the fish from the other species.

*Diomedea epomophora* was particularly aggressive towards *T. cauta* (Table 1), notably on the 28 February 2020 trip when multiple individuals continuously bit at any *Thalassarche* within biting distance (usually *T. cauta*; Fig. 4c,d), creating a ring of space around each *epomophora*. *Diomedea*

*epomophora* were also observed grabbing *T. cauta* by their head or neck after they swallowed fish, shaking them and sometimes holding their heads under water (Fig. 5a), presumably to force *T. cauta* to regurgitate food.

*Thalassarche cauta* that were attacked by other species, or involved in battles for fish, often responded by opening their bills to varying degrees and calling, highlighting their bill, gape, and mouth colouration, and the bright ridges of skin running posterior to the gape along the cheek (c.f. Marchant & Higgins 1990). These birds often pointed their bills at the other albatross(es), sometimes with wings partially open (Fig. 5b,c), but usually did not bite. In large groups of albatrosses, they often held their heads up, moving their bills side to side. Similar displays were used in interactions with conspecifics.

*Thalassarche cauta* was also present on all Kaikoura trips, albeit in small numbers. These individuals usually stayed peripheral to the fish controlled by *D. antipodensis gibsoni*, but occasionally approached in an attempt to feed. *Diomedea antipodensis gibsoni* responded to *T. cauta* by chasing them away while bill snapping.

*Thalassarche salvini* – Off Stewart Island/Rakiura, *T. salvini* was consistently present around the boat, but in smaller numbers than *T. cauta*. *Thalassarche salvini* behaved similarly to *T. cauta*, intermingling with *T. cauta* near the boat in anticipation of fish being thrown, and entering into scruns in pursuit of fish. Some *T. salvini* resisted moving into scruns, while others quickly moved away when large numbers of *T. cauta* wrestled for fish. *Thalassarche salvini* kleptoparasitised a fish from *T. cauta* on one occasion when fish was being thrown behind a moving boat, approaching *T. cauta* from behind and the side to secure the fish, and then wrestling it away. On at least three other occasions, however, *T. cauta* kleptoparasitised fish from *T. salvini*. Overall, *T. cauta* was dominant to *T. salvini*, although *T. salvini* occasionally displaced *T. cauta* by feather pulling/biting, bill snapping, and lunging. In contrast, *T. salvini* dominated *T. bulleri* in all observed interactions, displacing *T. bulleri* with bill snapping or lunging, sometimes with open wings. *Thalassarche salvini* usually avoided *D. epomophora*; when it approached *D. epomophora*, it was sometimes displaced by bill clacking, biting, and lunging. *Thalassarche salvini* also dove underwater for sinking pieces of fish.

*Thalassarche salvini* responded to attacks by other species, and battles for fish, in similar ways to other *Thalassarche* spp.: opening their bills wide and calling, highlighting bill, gape, mouth colouration, and the bright ridges of skin running posterior to

the gape along the cheek (Fig. 5d; c.f. Marchant & Higgins 1990). *Thalassarche salvini* also often pointed their bills at the other albatross(es), sometimes with wings partially open, and with heads held up, moving their bills side to side. As with the other *Thalassarche*, *T. salvini* used similar displays in interactions with conspecifics.

At Kaikoura, *T. salvini* was present in small numbers and behaved similarly to *T. cauta*. *Thalassarche salvini* usually stayed peripheral to the fish and *D. antipodensis gibsoni*; when they occasionally moved in to attempt to feed, *D. antipodensis gibsoni* responded by chasing them away while bill snapping (Fig. 3d). *Thalassarche salvini* was also displaced by *M. halli* off Kaikoura, and sometimes avoided them. On one occasion, *T. salvini* pursued *M. halli* in possession of fish, but was unable to take it from *halli*.

*Macronectes halli* – Off Kaikoura, *M. halli* was prominent at fish discards and commonly aggressive towards conspecifics, vocalising, displaying with bowed heads, spread wings, and upturned tails, and fighting. Aggressive displays were also directed towards *D. antipodensis gibsoni*, however, *M. halli* was consistently subordinate in aggressive interactions with *Diomedea*. Nonetheless, *M. halli* were persistent and the only other species consistently able to feed at the mesh containers of fish controlled by *D. antipodensis gibsoni*. Most *M. halli*, however, fed away from the mesh container, gathering pieces of fish that had dislodged and drifted away. While *M. halli* were subordinate to *Diomedea* in all interactions, they bit the tails of *D. antipodensis gibsoni* twice and *D. epomophora* once, always from behind. In response, *Diomedea* adjusted their positions slightly and wagged their tails side-to-side, but were not displaced and did not turn to retaliate. *Macronectes halli* displaced *Thalassarche* spp. (mainly *T. salvini*) by lunging and biting at their heads or tails. *Macronectes halli* occasionally displaced *D. capense*, but more often, *D. capense* scurried to get out of the way of (often fighting) *M. halli* that appeared to ignore *capense*.

*Daption capense* – *D. capense* was present around the boats at both sites, and came in to fish discards. At both sites, *D. capense* was subordinate, often energetically and erratically moving about the other seabirds, capturing small pieces of fish scattered about the water by pecking or dipping their heads and occasionally diving. When larger pieces of fish were available (e.g. when larger birds were engaged in a fight), *D. capense* would feed at the fish; however, they actively avoided larger species and showed aggression only towards conspecifics.

*Daption capense* were occasionally displaced or chased by larger birds; however, most larger species appeared to ignore them, with *capense* moving to keep out of the way.

*Puffinus tenuirostris* and *P. griseus* – At Stewart Island/Rakiura, *P. tenuirostris* (all trips), and *P. griseus* (on 21 February only), fed on fish discards at the back of the boat, but never engaged in aggressive interactions with other species. Instead, 1–4 individuals at a time sat at the periphery of the raft of albatrosses and petrels, diving and swimming underwater to collect sinking fish from underneath the other birds, and then returning underwater again to the periphery of the group. These species dove deeper than any of the albatrosses and petrels attracted to the fish discards, and appeared to actively avoid the other species, consistent with subordinate behaviour (*c.f.* similar avoidance behaviours of *P. tenuirostris* from the North Atlantic; Flood & Fisher 2020).

## DISCUSSION

The New Zealand albatross and petrel species studied here commonly interacted with each other and showed a consistent dominance hierarchy among species. These interactions, coupled with differences in behaviours and ecological strategies among the species, suggest that dominance hierarchies and interference competition play important roles within these seabird communities, at least when food sources are clustered and shared.

The larger albatrosses (*Diomedea*) were socially dominant and monopolised defendable food sources (Kaikoura; Fig. 2b), or obtained food in battles with other species for thrown fish (Stewart Island/Rakiura; Fig. 4a,b). Mid-sized albatrosses (*T. cauta*, *T. salvini*) were subordinate to *Diomedea*, but dominant to smaller albatross and petrel species. *Thalassarche cauta* and *salvini* were quicker to obtain thrown fish than *Diomedea*, and could out-compete larger species by obtaining and swallowing food quickly. The ability to obtain and swallow food quickly did not benefit these species when food was held within one mesh container (Kaikoura); in this case, the food source was monopolised and defended by larger *Diomedea* (and to a lesser extent, *M. halli*), suggesting that the outcome of competitive interactions depends on the distribution of the food source. The smallest and most subordinate albatross, *T. bulleri*, often fed on smaller pieces of fish, and was able to find, obtain, and swallow food quickly when fewer individuals of larger species were nearby. The smallest and most subordinate species was *Daption capense*. Individual *D. capense* moved about other seabirds, picking up small pieces of fish overlooked or passed over by larger species. The intermediate-

sized *M. halli* was aggressive and persistent at Kaikoura; some individuals were able to feed, even when the food was defended by dominant *Diomedea* (Kaikoura). In such cases, the costs of excluding persistent *M. halli* from the fish may have exceeded the benefits, as *Diomedea* in control of the fish often fed for extended periods of time, regardless of *M. halli*.

Overall, the behaviours and ecological strategies of albatrosses and petrels foraging on fish discards behind ecotourism boats matched their positions within the dominance hierarchy of species. Smaller species appeared to take advantage of peripheral resources in time (quicker to a resource), space (at the edges of large groups), and size (smaller pieces of fish), and often avoided direct competition with dominant species. Dominant species instead monopolised resources when present continuously (Kaikoura), or displaced other species from anticipated locations for acquiring fish (Stewart Island/Rakiura). The difference in food presentation at the two sites may mirror different food sources in nature, with Kaikoura (defendable food in mesh bag) more similar to a large, defendable carcass dominated by fewer, large species, and Stewart Island/Rakiura (individual fish thrown from boat) more similar to ephemeral schools of fish or squid approaching the surface that are more accessible to species with different ecological strategies (dominant and subordinate species).

The dominance hierarchies observed in this study are consistent with dominance hierarchies described in other seabird communities. For example, albatrosses and petrels off the Crozet Islands, southern Australia, and southeastern South America, and in Cook Strait, New Zealand, commonly fought over food, and showed evidence for consistent dominance hierarchies among species (Bartle 1974; Milledge 1977; Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Brothers 1991; Vaske 1991; Wood 1992; Olmos 1997; Jiménez *et al.* 2011). Similarly, Southern Giant Petrels (*Macronectes giganteus*), dominated *M. halli* in aggressive contests for seal carcasses, giving *giganteus* priority access to this food source on their shared breeding sites (Johnstone 1979; de Bruyn & Cooper 2005). *Macronectes* spp. generally dominate smaller petrels and albatrosses congregating at food (e.g. Harper 1987; Jiménez *et al.* 2011), sometimes even killing and eating smaller albatrosses and petrels (e.g. *Thalassarche carteri*, *D. capense*; Harper 1987; Marchant & Higgins 1990), but were excluded at food sources by larger albatrosses (Harper 1987; Jiménez *et al.* 2011). *Daption capense* feeding on larger prey had their prey usurped by larger *Macronectes* and albatrosses if they did not consume it quickly (Harper 1987). Interactions among other procellariid species that do not feed on carrion or



approach boats remain poorly known. However, Kermadec Petrels, (*Pterodroma neglecta*), regularly kleptoparasitise other procellariids in the eastern tropical Pacific, including Juan Fernandez Petrels (*Pterodroma externa*), and Wedge-tailed Shearwaters (*Puffinus pacificus*), appearing to mimic other kleptoparasitic species (jaegers [*Stercorarius* spp.], skuas [*Catharacta* spp.]) to improve success (Spear & Ainley 1993; Carboneras *et al.* 2016). Dominance interactions may be less common when food resources are not clustered, defensible, or easily stolen. In such cases, interference competition and dominance hierarchies may be more important for structuring communities through their influence on other resources, such as nesting burrows (e.g. Ramos *et al.* 1997; Spear & Ainley 2007).

### Body mass and dominance

Larger size usually confers an advantage in aggressive contests because heavier objects can displace lighter objects more easily (Peters 1983), and heavier species often have greater muscle mass and strength, thicker defensive coverings (like skin, feathers), and larger bills, wings, and feet used in fighting (Martin & Ghalambor 2014). In our study, the larger species were dominant to smaller species in 12 of 13 species pairs (92%). Previous studies of albatrosses consistently found larger species to dominate smaller species (Bartle 1974; Milledge 1977; Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Brothers 1991; Vaske 1991; Wood 1992; Olmos 1997; Jiménez *et al.* 2011), with similar results for procellariids (Johnstone 1979; Harper 1987; Spear & Ainley 1993; Ramos *et al.* 1997; de Bruyn & Cooper 2005; Jiménez *et al.* 2011). In other birds, larger species are usually dominant to smaller species (Robinson & Terborgh 1995; Freshwater *et al.* 2014), but the importance of large size for dominance declines with evolutionary distance: larger species were dominant in 93% of species pairs within the same genus, but only 71% of species pairs in different taxonomic families (Martin & Ghalambor 2014). The consistent importance of body size in interactions involving albatrosses and petrels – even among species in different taxonomic families – may reflect behavioural and ecological similarities among seabirds and the importance of size in their aggressive interactions, or the large differences in mass between the species (Tables 1 & 2), particularly compared with other groups of birds (e.g. small passerines).

The larger size-dominance exception in our study involved *Diomedea*, where the smaller *D. antipodensis gibsoni* were consistently dominant to *D. epomophora* (Kaikoura; Fig. 3a,b). We are not sure why the smaller *Diomedea* species was dominant; however, the smaller *D. antipodensis gibsoni* may

have exhibited greater aggression, speed and manoeuvrability, or risk-taking in aggressive contests, forcing the larger *epomophora* to retreat.

While the smaller, subordinate species were usually displaced or excluded from resources, small size may have provided other advantages. Smaller organisms require less food and energy to survive and reproduce, have faster response times, and are more manoeuvrable (Peters 1983). All of these benefits appeared to play an important role in New Zealand albatrosses and petrels, with smaller species taking advantage of their speed and agility to acquire food quickly (see also Milledge 1977; Harper 1987; Wood 1992), and some species focusing on gathering smaller pieces of fish that were likely profitable only to small-sized species. Some smaller species are also more likely to come closer to boats (Vaske 1991), perhaps reflecting a greater ability to take risks and evade threats, with faster response time, and greater manoeuvrability. The different benefits of larger size (behavioural dominance) versus smaller size (speed of response, manoeuvrability, etc.) illustrate an important trade-off in albatrosses and petrels that may help species of differing sizes to coexist, particularly when resources vary in space and time (e.g. Martin 2015).

### Dominance interactions and seabird community structure

While the results presented here suggest that dominance hierarchies and interference interactions among species are important selective pressures for New Zealand albatrosses and petrels, the question remains: Do interactions among species in response to fish discards behind boats tell us anything about natural communities? The interactions that we observed depended on resources being shared among species, clumped in their distribution, and limiting for our focal species. Many natural food sources used by our focal albatross and petrel species mirror these characteristics. For example, at natural food sources throughout the southern oceans, *Diomedea*, *Thalassarche*, *Macronectes*, and *Daption* feed at or near the ocean surface and regularly overlap in diet (particularly squid, fish, crustaceans, and carrion) (Barton 1979; Weimerskirch *et al.* 1986; Harper 1987; Cherel & Klages 1997). These species also congregate at food sources and interact aggressively for food under natural conditions (Weimerskirch *et al.* 1986; Harper 1987; Marchant & Higgins 1990; Harrison *et al.* 1991), similar to congregations that we observed behind ecotourism boats. While *D. capense* often forage on smaller prey ignored by our larger species (e.g. through filter feeding), they also feed on larger squid when opportunities occur (e.g. 109 g *Gonatus antarcticus*) (Harper 1987). Clustering of prey

(e.g. squid) feeding on schools of krill and other zooplankton (Harper 1987), carrion regurgitated by cetaceans (Clarke *et al.* 1981), or surface prey concentrated by predatory fish, mammals, and diving birds (e.g. penguins, Spheniscidae) (Barton 1979; Marchant & Higgins 1990; Harrison *et al.* 1991), could all lead to mixed-species congregations of feeding seabirds and competitive interactions similar to those described here (e.g. Barton 1979; Harrison *et al.* 1991).

Long-term studies of seabirds also suggest that dominance hierarchies and competitive interactions help to structure communities, even at broad spatial and temporal scales. Tropical Pacific seabird communities vary with ocean productivity: most productive regions are occupied by the largest, competitively dominant species (boobies [*Sula* spp.]), regions of mid-productivity are occupied by petrels of intermediate size and dominance (*Pterodroma externa*, *Puffinus pacificus*), and regions of low productivity are left to flocks of smaller, more energy-efficient, and subordinate species (dominated by Sooty Tern [*Onychoprion fuscatus*]) (Ballance *et al.* 1997; see also studies of seabirds in other regions, Anguita & Simeone 2016; Bellier 2019). Similarly, a long-term study of the dynamics of a recovering Mediterranean seabird community suggested that asymmetric, dominance interactions among species, mediated by differences in body size, played a central role in community assembly over time (mainly Laridae; Almaraz & Oro 2011). These previous studies suggest that the consequences of interference competition and dominance hierarchies for resource acquisition may extend to influence broad patterns of seabird distributions and community structure. How such interactions influence broader patterns of albatross and petrel distributions and community structure in the southern oceans (e.g. Phillips *et al.* 2005) remains to be discovered.

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