Introduction

Giant petrels *Macronectes* spp. are aggressive predators and scavengers that feed on a wide range of prey, including other seabirds (Harper 1987, Marchant & Higgins 1990, Ridoux 1994). Studies at most breeding islands have found that adult penguins predominate in giant petrel diets (Warham 1962, Johnstone 1977, Marchant & Higgins 1990), comprising 50–80% of prey by mass (Hunter 1983, 1985, Ridoux 1994). Observations on land indicate that few healthy adult penguins are killed ashore, suggesting that most are eaten at sea, but it is unclear how many penguins are obtained. Warham (1962) assumed that they were killed directly, but mused that it was “strange that large and active species like shearwaters and penguins can be captured” (p. 157). Most subsequent authors have assumed that the penguin remains reported in diet studies are scavenged, either as carrion or by killing off birds.
already injured by other predators (e.g. Johnstone 1977, Hunter 1983, Ridoux 1994). This assumption is supported by observations of giant petrels taking penguins killed or injured by immature male Antarctic Fur Seals *Arctocephalus gazella* at Bird Island, South Georgia (Bonner & Hunter 1982). Similar behaviour has been observed among non-breeding giant petrels feeding in association with Cape Fur Seals *A. pusillus* off Dassen Island, South Africa (Shaughnessy & Voisin 1981).

Giant petrels occasionally tackle large avian prey such as albatrosses at sea (Cox 1978, Barton 1979), but penguins appear to be unlikely prey because of their much greater manoeuvrability (Warham 1962, Bonner & Hunter 1982). We were thus surprised to observe Northern Giant Petrels *M. halli* regularly killing Northern Rockhopper Penguins *Eudyptes moseleyi* off Nightingale Island, Tristan da Cunha. This note describes the strategies used by giant petrels to catch and subdue penguins at sea.

**Methods**

We visited Nightingale Island, Tristan da Cunha (37°25'S, 12°28'W), from 17 October to 4 November 2007. Some 25 000 pairs of Northern Rockhopper Penguins breed among tussock grass *Spartina arundinacea* in the north-eastern corner of the island (Richardson 1984). Most breeding penguins land at Penguin Rock, a sloping rock with a steep face 1–2 m high at water level. During our visit, the penguins were completing incubation, with the first chicks recorded on 20 October. Penguins arrived and departed the island throughout daylight hours, with departures peaking in the early morning, and returns in the late afternoon. Giant petrels are non-breeding visitors to the Tristan archipelago. Up to 30 gathered at Nightingale Island to roost each evening, mainly in the channel between Nightingale and Alex Island. Roughly two thirds were Northern Giant Petrels, and the remainder Southern Giant Petrels *M. giganteus*.

We recorded the behaviour of giant petrels that gathered off Penguin Rock from 18 October to 3 November. Hunting was defined as birds patrolling the waters off the rock, swimming back and forth to approach groups of penguins, and making attacks when penguins ventured close enough to strike. It was an active behaviour, readily distinguished from bouts of preening or roosting, or agonistic interactions with other giant petrels. Hunting usually took place in the area of open water within 30 m of the landing site, inshore from the main band of giant kelp *Macrocystis pyrifera* that occurs offshore around much of the island, whereas petrels usually moved offshore to roost amongst the kelp band where the water was relatively calm. While hunting, the petrels interspersed paddling around with occasional aerial forays in an attempt to ambush penguin groups. Only hunting bouts and the duration of feeding on carcasses was recorded. Petrels also flew to other parts of the island, and thus complete activity budgets could not be kept.

Observations were made all day on 28 and 29 October. Usually only one bird was present in the area. When there were 2–3 birds, it was often possible to recognise individuals by differences in primary moult and plumage colour (giant petrels gradually become paler with age; Marchant & Higgins 1990). Opportunistic observations were made on an additional 10 days, recording the number and type of attacks, and their success rate. Birds were observed through binoculars from the huts 60–80 m from the landing rock, because the petrels were quite wary and often ceased hunting if an observer walked out onto the landing rock. Attacks were photographed using a digital SLR camera with a 500 mm telephoto lens to ascertain additional details about the way penguins were handled.

**Results and discussion**

Giant petrels hunted off the penguin landing area on at least 11 of the 12 days when observations were made. They were most active in the afternoon, when large numbers of penguins returned to the island, but hunting took place from just after sunrise until after sunset. On 3 November a bird finally gave up at 19:50 (local sunset 19:26), and one was already patrolling off the rock by 5:50 the following morning (sunrise 5:42). Most of the time when hunting was observed, only one petrel
was present (89% of hunting observations). If another petrel arrived, the bird already present typically swam over to the intruder, and exhibited some level of aggression (calling with hackles raised, or charging). In 7 of 11 cases the intruder flew away or swam off. Birds in pale, adult plumage usually dominated dark-plumaged immature birds. However, on three occasions two or more birds hunted at the same time. On one evening, up to five petrels patrolled the landing area. That evening 14 petrels were present in the vicinity (most roosting offshore), but only 2–3 birds were seen to lunge at passing penguins.

Hunting petrels were observed for 14.8 h (16.6 h of bird effort, including observations when two or more birds were hunting at the same time). Six kills were observed, at an average rate of 0.36 per hour of hunting. All six kills were made by Northern Giant Petrels. Based on subtle variations in plumage and differences in primary moult, at least three birds killed penguins, and judging by their pale grey plumage and large size, all were adult males. Several immature Northern Giant Petrels and at least one immature Southern Giant Petrel also attempted to catch penguins, but were unsuccessful. On the two days when continuous observations were made, petrels hunted for 2.8 h and 3.5 h, killing 1 and 2 penguins, respectively. Three additional penguins were observed being eaten when the actual kill was not observed. Penguins were killed throughout the day, between 7:45 and 19:00, with most kills in the afternoon (6 of 9 kills took place between 13:00 and 19:00).

Hunting birds patrolled the waters off the landing rock, in an arc up to 50 m from the landing area. They used four strategies to attempt to catch penguins (Table 1). Most time was spent swimming in pursuit of groups of penguins, and attempting to grab any penguin that approached too closely, either surfacing next to the petrel, or swimming close to the surface next to the petrel. Such incautious birds were grabbed by a swift downward lunge of the head, sometimes half submerging. Petrels also flew or pattered over the water to intercept penguin groups, dropping onto them from the air. This was the most common attack method (Table 1), and was especially frequent during high winds, when it was easy for the petrels to take off. Some birds attempted to catch birds as they landed on the rock, either grabbing them directly from the rock face, or taking birds that fell or were washed off while attempting to land (Fig. 1A). This technique was used mainly when there was a large swash over the landing rock, and involved birds either swimming close to the rock, or pattering over to the rock as penguins were coming ashore. Finally, some petrels attempted to sneak up on penguins bathing or resting on the surface, by swimming up to them while lying flat on the water (‘stealth’ attacks, Fig. 1B).

Overall, 17% of attempts resulted in a capture, and 18% of penguins captured were killed, thus 3% of attacks resulted in a kill. Surface lunging was the most successful technique, accounting for 4 of the 6 penguins observed killed (Table 1). Attacking at the landing rock resulted in a high proportion of captures, but almost all were dropped within a few seconds, apparently because they were not grabbed correctly. Most attacks at the landing rock were made by a single petrel that

<table>
<thead>
<tr>
<th></th>
<th>Lunge</th>
<th>Patter</th>
<th>Off rock</th>
<th>Stealth</th>
<th>Total</th>
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<tr>
<td>Number of attacks</td>
<td>50</td>
<td>88</td>
<td>42</td>
<td>20</td>
<td>200</td>
</tr>
<tr>
<td>- of which caught</td>
<td>11 (22%)</td>
<td>7 (8%)</td>
<td>16 (38%)</td>
<td>0 (0%)</td>
<td>34 (17%)</td>
</tr>
<tr>
<td>- of which killed</td>
<td>4 (36%)</td>
<td>1 (14%)</td>
<td>1 (6%)</td>
<td>0 (0%)</td>
<td>6 (18%)</td>
</tr>
<tr>
<td>Success (kills/attack)</td>
<td>8%</td>
<td>1%</td>
<td>2%</td>
<td>0%</td>
<td>3%</td>
</tr>
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Figure 1. Northern Giant Petrels attacking Northern Rockhopper Penguins at Nightingale Island: A) attempting to catch birds at the landing rock; B) ‘stealth’ approach, lying prone on the water; C) subduing a penguin after capture.
grabbed 12 birds in 1 h. This bird even attempted to take birds queuing up to leave the rock. Aerial ‘patter’ attacks were the most common type of attack, but they resulted in relatively few captures, and only one kill (Table 1). However, this is somewhat misleading, as only a few patters led to a serious attack; in most instances the penguins dived before the petrel reached them, and it merely landed again. Stealth attacks were rather infrequent, and were not seen to result in a capture (Table 1).

Only penguins caught by the back of the neck were killed. Photographic evidence suggests that penguins grasped elsewhere on their body were able to twist their heads round to threaten the petrel, whereupon they were released. One penguin grasped by the bill was held for several minutes, but eventually broke free. Once a petrel had caught a penguin, it would hold it underwater, actively paddling its feet to keep its head down, and usually raising its wings (Fig. 1C). The entwined birds slowly rotated, apparently driven by the penguin's frantic efforts to break free. All penguins killed were held in this position for 5–6 min, before eventually ceasing to struggle. Towards the end of this time, the petrel could be seen to bite at the penguin's neck. In one case, a penguin broke free after 4 min, but was recaptured when the petrel pattered 10 m across the surface after the submerged penguin and plunged in to regain its grip on the hapless bird. It was subsequently killed (this case was treated as a single attack in Table 1).

Once a penguin had ceased to struggle it was eaten by the petrel, entering the body cavity either via the front of the neck or belly. Meals lasted 30–50 minutes, and often involved several petrels competing for access to the carcass. Competition was most intense between adult male Northern Giant Petrels, with the killer sometimes abandoning his carcass to immature giant petrels in order to pursue a protracted bout of posturing and fighting with another intruding adult male. When several petrels were present at the same time, they would usually fly over to another petrel as soon as it had caught a penguin, but did not interfere, or attempt to compete for the prey until the penguin had been subdued. Subtropical Fur Seals Arctocephalus tropicalis also frequented the waters around Nightingale Island, and often swam close to the penguin landing rock. They were never seen to harass or attack penguins, or attempt to take penguins from giant petrels. However, petrels struggling with penguins twice were scared off by a fur seal surfacing next to them. Once a carcass had been opened up, it was often fed on by large (30–40 cm) Five-fingers Acantholatris monodactylus (Cheilodactylidae), a marine fish. These appeared to discomfort some giant petrels, but were ignored by others. Up to four Antarctic Terns Sterna vittata also gathered over feeding petrels, dipping down to take scraps.

The penguins appeared to be aware of the giant petrels’ intentions. When a petrel was patrolling within 10–15 m of the landing rock, parties of penguins circled offshore rather than attempting to land. Even if they were inshore of a petrel, they would porpoise offshore as long as the petrel was within 10–15 m of the landing site. If a petrel swam or flew towards a group of penguins, they would all dive once the petrel got within a few metres of the group. Little bathing or surface resting took place while a petrel was present, and was largely confined to >50 m from the landing rock. The penguins’ behaviour changed noticeably once a penguin had been caught, however, with a marked increase in comfort behaviours, and some birds even swimming up to the petrel to investigate it.

The petrels did not attempt to attack penguins on land, despite coming right up to the landing rock, and even pulling birds off the rock into the water. Only one giant petrel was observed ashore. An immature Northern Giant Petrel clambered up the landing site at Penguin Rock and was seen roosting at an adjacent landing site, but did not exhibit any interest in the penguins. The penguins were initially wary of the petrel ashore, running away when it first landed, but soon started walking around it once it appeared to offer no threat. After a while it was approached to within 1 m by a large group of penguins, which caused the petrel to shuffle away.
This is the first record of systematic hunting of penguins at sea by giant petrels (Marchant & Higgins 1990). The technique used to subdue penguins was remarkably similar to that used by a Southern Giant Petrel to catch and kill a sleeping Black-browed Albatross Thalassarche melanophris (Cox 1978), suggesting it may be a widespread technique. Although their success rate was low, petrels that exhibited patience usually were able to capture a penguin, which represents a significant meal for these non-breeding birds. Our observations challenge the widespread assumption that adult penguins eaten by giant petrels are scavenged (Bonner & Hunter 1982, Hunter 1983, Ridoux 1994). However, it must be noted that the petrels struggled to subdue the Northern Rockhopper Penguins, which are appreciably smaller than the Macaroni Penguins Eudyptes chrysolophus that predominate in the diets of giant petrels at most sub-antarctic breeding islands (Marchant & Higgins 1990, Ridoux 1994). It remains to be determined what proportion of adult penguins eaten by breeding giant petrels are killed directly at sea.

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REFERENCES


SAMENVATTING

Reuzenstormvogels Macronectes spp. staan bekend als agressieve jagers en aaseters die zich voeden met allerhande dierlijk materiaal, veelal in de buurt van kolonies zeevogels en zeezoogdieren. Het is bekend dat een belangrijk deel van hun voedsel bestaat uit pinguïns. Over het algemeen wordt aangenomen dat het hierbij gaat om de resten van pinguïns die op de een of andere manier aan hun einde waren gekomen. Uit de hier beschreven waarnemingen blijkt echter dat reuzenstormvogels wel degelijk actief op pinguïns jagen. De auteurs deden waarne-eming aan Noordelijke Reuzenstormvogels Macronectes halli die het gemunt hadden op Noordelijke Rotspringers Eudyptes moseleyi bij Tristan da Cunha in de zuidelijke Atlantische Oceaan. Er werden in totaal 200 aanvallen genoteerd, verspreid over 12 dagen. Dit resul-teerde in zes gedode pinguïns en drie waarvan de aanval niet werd geobserveerd. Er werden vier jachtstrategieën onderscheiden. De stormvogels haalden uit naar zwemmende pinguïns, lieten zich uit de lucht op zwemmende pinguïns vallen en sleurden pinguïns die aan land proberden te komen van de rotsen. Verder probeerden ze pinguïns te ‘besluipen’ door met hun hoofd laag over het water op ze af te zwemmen. Geen van deze methodes was erg succesvol, maar een eenmaal buitgemaakte pin- guïn zal waarschijnlijk genoeg voedsel opleveren om een hoop uren vrucheloos jagen te rechtvaardigen. (KK)

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