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KLEPTOPARASITISM BY KERMADEC PETRELS, JAEGERS, AND SKUAS IN THE EASTERN TROPICAL PACIFIC: EVIDENCE OF MIMICRY BY TWO SPECIES OF *PTERODROMA*

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ABSTRACT.—We studied the ecology and behavior of pelagic seabirds in the Eastern Tropical Pacific (1984–1992). We hypothesize that the absence of kleptoparasitism (hereafter "parasitism") by jaegers and skuas (subfamily Stercorariinae, hereafter "skuas") on Kermadec Petrels (*Pterodroma neglecta*) and Herald Petrels (*P. arminjoniana*) observed in this study, compared to regular attack on procellariids of similar size, resulted from Batesian mimicry by the former of skuas. As mimics of skuas, Kermadec and Herald petrels avoided being kleptoparasitized because skuas do not parasitize conspecifics. We also document regular parasitism by Kermadec Petrels on other large procellariids, and further hypothesize that this petrel is successful as a parasite because it is a foraging mimic of the subadults of the larger skuas (Pomarine Jaegers [*Stercorarius pomarinus*] and South Polar Skuas [*Catharacta maccormicki*]) through its similarity of color pattern, flight profile, and behavior when initiating an attack, and because the large skuas (its models) are very effective as parasites. This petrel's incidence of attack and frequent use of alternate feeding methods suggests that it is a less specialized parasite than are the skuas. Kermadec Petrels prefer the same hosts and use a similar method of attack as do the large skuas, which achieve a very high rate of success in the Eastern Tropical Pacific because of their ability to threaten hosts through size-mediated aggressiveness. The Kermadec Petrel is smaller or similar in size to its preferred hosts and is not as aggressive as large skuas, but its rate of success as a parasite is higher than expected. *Received 1 September 1991, accepted 22 June 1992.*

KLEPTOPARASITISM (hereafter termed "parasitism") is a well-known feeding method of seabirds, particularly for skuas (*Catharacta* spp.) and jaegers (*Stercorarius* spp.; subfamily Stercorariinae, hereafter referred to collectively as "skuas"), frigatebirds (*Fregata* spp.), gulls (*Larus* spp.) and, to a lesser extent, terns (*Sterna* spp.), boobies (*Sula* spp.), pelicans (*Pelecanus* spp.), cormorants (*Phalacrocorax* spp.), and members of the Procellariiformes (reviewed by Furness 1987a, b, Duffy 1980, 1982, 1989). In procellariiforms, the use of parasitism as a regular means of feeding has been described only in the Waved Albatross (*Diomedea irrorata;* Duffy 1980), and no procellariiform parasite has been known to tenaciously pursue hosts as do skuas, the most highly evolved of avian parasites. Herein, we describe skualike parasitism by a procellariid, the Kermadec Petrel (*Pterodroma neglecta*).

Parasitism by Parasitic Jaegers (*S. parasiticus*), Great Skuas (*C. skua*), and South Polar Skuas (*C. maccormicki*) has been studied extensively on the breeding grounds (reviewed *in* Furness 1987a, b) and at a coastal estuary on the migratory route (Parasitic Jaeger; Taylor 1979). However, few studies have documented the foraging behavior of skuas away from the breeding grounds, other than species parasitized at given locations (but see Duffy 1980, Sinclair 1980, Furness 1983).

Skuas possess a distinct and highly conspicuous white patch in the inner primary region of their otherwise dark-colored wings (Harrison 1987, Olsen 1989). In flight, this mark can be seen at a great distance at any angle except when the birds are flying directly toward, or away from, the observer. As a result of this distinctive feature, and the tenacious, aggressive, and highly skilled qualities of skuas as parasites, they qualify as aposematic species. Aposematism is a condition used by more dangerous/noxious species to advertise their particular qualities and, thus, ensure the desired response from animals with whom they interact (usually avoidance by predators; reviewed in Pough 1988, Malcolm 1990). In skuas, aposematism may serve as an affective, long-distance signal between conspecifics, which do not parasitize one another (Furness 1987a), thereby preventing less-rewarding interactions between individuals of equal ability, or between kin (see Malcolm 1990). Aposematism might also benefit skuas as a quickly perceived signal to their hosts of their identity. Thus, experienced hosts may be more easily overwhelmed in an attack, resulting in less-energy-demanding chases and possibly a higher success rate among skuas than they could achieve if they were not aposematic.

Species most often mimicked are the more aposematic, dangerous ones (reviewed in Pough 1988). Our initial observations in the Eastern Tropical Pacific (ETP) of the Kermadec Petrel and Herald Petrel (*P. arminjoniana*), which are two of three species of seabirds other than skuas that possess conspicuous white inner primaries (see Harrison 1987), led us to formulate two hypotheses. First (H1), these petrels mimic skuas to avoid being parasitized by the latter, which do not parasitize conspecifics. Second (H2), Kermadec Petrels use their mimicry to behave as parasites with higher success than they could achieve if they were not confused with skuas.

The mimic in H1 would be Batesian "defensive," which resembles a dangerous/noxious species (the model) to gain protection from a predator or parasite. This form of mimicry is selected by the behavior of a predator/parasite (Malcolm 1990). The H2 mimic would be "foraging" (also known as "aggressive"), which resembles a nondangerous model to deceive prey or hosts (i.e. the selective agents), thereby gaining access to them or their resources (Owen 1980, Endler 1981, Pough 1988, Malcolm 1990). This being so, the foraging mimic we suspect would be different from those previously described because this mimic would, like Batesian mimics, resemble a dangerous model rather than a nondangerous one. Few examples of mimicry are known in birds (Owen 1980, Pough 1988). The best documented examples are parasitic species that mimic the eggs and young of their hosts (reviewed in Pough 1988) and the Zone-tailed Hawk (*Buteo albonotatus*), which is thought to gain better access to its prey by resembling the nonpredatory Turkey Vulture (*Cathartes aura*; Willis 1963).

Properties typical of most mimics of the type hypothesized in H1 and H2 (Owen 1980, which includes exceptions; Huheey 1988) are: (1) the mimic's range overlaps with that of the model; (2) the mimic is less abundant than the model; (3) the appearance and behavior of the mimic resemble a dangerous and conspicuously marked model; and (4) the mimic is less dangerous than the model or, in H2, the petrel should be less threatening to its hosts than are skuas. Therefore, to examine H1 and H2, we studied the range, relative numbers, and color phases of the color-polymorphic Kermadec Petrel, Herald Petrel, and skuas in the ETP during spring and autumn. To further examine H1, we tested the null hypothesis that Kermadec and Herald petrels are parasitized less often by skuas than are other large procellariids. To further examine H2, we studied incidence of parasitism, attack method, selection of hosts, success rate, and related factors of the Kermadec Petrel and four species of skuas.

Methods

We made 4,303 h of observations during 18 cruises in the ETP between 25°N and 25°S, and from 175°W to beyond 185 km of the American coasts. Most observations were made between 110°W and 155°W. Cruises included 10 during spring and 8 during autumn (1984–1992). Census methodology is described in Ainley and Boekelheide (1984), except that we were able to extend the transect width to 600 m due to the height of our observation platform (16 m). Due to the paucity of seabirds in the ETP, extending the transect width beyond the standard 300-m width (see Tasker et al. 1984) was necessary to obtain an adequate sample of observations. Identification of birds in the outer section of the transect zone was not a problem because we had easy access to 25 × 150 mm binoculars mounted on the flying bridge of each vessel. During regular observations, two or three persons observed simultaneously with hand-held binoculars, and recorded all birds and all feeding attempts (by species) seen in the transect zone.

We usually noted the color phase of Kermadec Petrels, Herald Petrels, and jaegers, considering birds as "light" if they had white breasts and bellies, and "dark" if they did not. We also noted the age of skuas as adult or subadult (for description of jaeger plumages, see Olsen 1989); subadult South Polar Skuas are especially dark and lack the adults' glossy sheen on the neck (see Ainley et al. 1985).

During five cruises (1989–1991), we also recorded the presence and behavior of Kermadec Petrels and skuas seen within 600 to 2,500 m of the ship using the 25 × 150 mm mounted binocular. Increasing the range of observation was necessary to increase the sample size of observations on parasitism, but could only be done if we had additional personnel. It is unlikely that inclusion of data from the outer transect (600–2,500 m) biased comparisons of relative frequency that different species of hosts were attacked (i.e. the number of hosts attacked per number seen). We cued only on parasites, and proportions of hosts of different species appeared similar in inner (<600 m) and outer transect zones. Note, however, that analyses of relative attack frequency compare the number of potential hosts seen within the inner zone with the number of attacks summed for both the inner and outer zones in some years. Therefore, our data overestimate absolute frequency that hosts were attacked.

We considered an attempted parasitism to have occurred if a parasite suddenly accelerated towards another bird, thereby causing the latter to alter its flight behavior or give up its prey. We usually noted chase success, where success was scored when the host dropped or regurgitated prey, which then was retrieved by the parasite. We compared attack behavior of Kermadec Petrels with species of skua by noting (1) whether host was member of multispecies bird flock feeding over predatory fish (where flock is defined as group of three or more birds), or was alone. Also, following Furness (1978) and Caldow and Furness (1991), with some modification, we noted: (2) aspect of attack relative to the flight direction of the host, scored as from behind, the side, or from front (i.e. grouped into 90° segments, with one segment from either side, one from the front, and one from behind); (3) mean altitude of parasite during the final 50 m of approach to intended host, scored as low (altitude 1 m or less), medium (>1 and <5 m), and high (5 m or more); (4) flight plane of parasite when making contact with host, scored as lateral (flight plane horizontal with sea surface ± 10°), ascending, and descending; (5) element of surprise attained by parasite when attacking host as estimated by distance between host and approaching parasite when host first reacted (i.e. host dropped its prey, regurgitated, or began accelerated and/or aerobatic flight) and scored as high (host did not react until parasite was within 1-2 m), moderate (reaction distance 3-10 m), low (reaction distance >10 m); (6) chase durations scored as short (duration <5 s), medium (5-10 s), and long (>10 s). Chase duration was considered as the interval beginning when a host first responded and ending when the host gave up its prey or the parasite discontinued the chase. Chase duration also was considered as short when a host released its prey upon initial contact with the parasite (i.e. no chase involved).

We grouped Parasitic Jaegers and Long-tailed Jaegers (*S. longicaudus*) as "small skuas" in the following analyses because for subadults we could not always distinguish species, and because they had similar attack behaviors. Pomarine Jaegers (*S. pomarinus*) and South Polar Skuas also had similar attack behavior. We usually grouped them as "large skuas." Exceptions included analyses of variables for which significant differences ($P < 0.050$) existed between the two species.

We examined the proportion of feeding attempts involving parasitism versus feeding attempts using other methods, and examined incidence of attacks to delineate the relative importance of parasitism as a feeding method of the different species. Because we did not record "other feeding attempts" that occurred beyond 600 m, comparisons of feeding methods used includes only parasitic attempts that occurred within the 600-m zone. We define incidence of attack as the number of attacks divided by the observed number of parasites of a given species. In order to examine the possibility that species of parasites were selective towards different species of hosts, we grouped hosts into three categories: (1) large procellariids including large *Pterodroma* (mass >250 g) and large shearwaters (*Puffinus* spp.); (2) hydrobatids and small procellariids; and (3) larids. Three attacks on Red-billed Tropicbirds (*Phaethon aethereus*), one by a Kermadec Petrel and two by Pomarine Jaegers, were excluded from analyses on host selection by different species of parasites due to the small number of occurrences.

We compared masses of Kermadec Petrels, skuas, and their preferred hosts using data from fresh specimens collected in the ETP and Southern Ocean. Mass does not include the mass of food in the stomach.

G-tests were used (Zar 1974). We also employed analyses of variance (ANOVA) followed by Sidak tests (Anonymous 1990). All comparisons were of numbers, not percentages or proportions.

RESULTS

Relative abundance and color-phase frequencies of petrels and skuas.—We observed Kermadec Petrels, Herald Petrels, and four species of skua throughout most of the study area during both spring and autumn (see also King 1967, Pitman 1986, Spear et al. 1992). Skuas were mostly subadults (Table 1). Kermadec and Herald petrels never were abundant. The ratio of Kermadec Petrels to skuas (species grouped) was 1:3.7 (n = 585) in the spring and 1:4.7 (n = 652) in the autumn. Combining Kermadec and Herald petrels, the ratio of petrels to skuas was 1:2.2 (n = 333) in the spring and 1:1.8 (n = 518) in the autumn (only birds counted within the 600-m transect zone were included in latter comparison). If only Kermadec Petrels and large skuas are considered, the overall ratio (seasons grouped) was 1:2.3 (n = 782).

Kermadec and Herald petrels were predominantly dark phase, and jaegers were predominantly light phase (Table 1). Color-phase frequencies varied little between the two species of petrels (G = 1.75, df = 1), or between small skuas and Pomarine Jaegers (G = 0.32, df = 1). Differences in color-phase frequencies were significant, however, when compared between the petrels (grouped) and jaegers (grouped; G = 151.79, df = 1, $P < 0.001$). South Polar Skuas do not exhibit plumage polymorphism of the same type found in jaegers; all are dark-phase

TABLE 1. Numbers observed, age-class and color-phase composition, proportion of feeding attempts that were parasitic, and incidence of parasitic attempts for Kermadec Petrels and skuas in Eastern Tropical Pacific from 1984–1992. Values in parentheses are total numbers of observations.

	No. seen	Proportion[a]		Parasitism as proportion of all feeding attempts[b]	Incidence of parasitic attempts[c]
		Subadults	Light phase		
Kermadec Petrel	239	—	0.26 (205)	0.50 (8)	0.06 (15)
Small skuas	455	0.86 (165)	0.76 (303)	0.86 (35)	0.24 (110)
Pomarine Jaeger	502	0.82 (248)	0.79 (314)	0.95 (22)	0.19 (96)
South Polar Skua	41	0.91 (35)	—	0.83 (12)	0.56 (23)

[a] Proportions of subadults vs. adults, and light vs. dark phase. Proportion of light-phase Herald Petrels was 0.33 (n = 110).

[b] Calculated from observations of feeding attempts occurring only within 600-m transect zone.

[c] Number of parasitic attempts divided by number of parasites seen.

types under the criterion we used. Including South Polar Skuas with dark-phase Pomarine Jaegers resulted in little effect on color-phase frequencies of large skuas (72% light phase vs. 28% dark phase) because of relatively low numbers of South Polar Skuas. The ratio of dark-phase Kermadec Petrels to large, dark-phase skuas in the overall sample was 1.2:1 (n = 323 dark birds).

Use of feeding methods other than parasitism, and incidence of attempted parasitism.—Kermadec Petrels fed more often by methods other than parasitism compared to skuas (skuas grouped; G = 6.04, df = 1, P = 0.016; Table 1). Incidence of attempted parasitism by Kermadec Petrels was lower than that by small skuas, Pomarine Jaegers, and South Polar Skuas (G-tests, $P < 0.001$). Attacks by Pomarine Jaegers included three in which one individual made two separate attacks, each on different hosts. Attacks by South Polar Skuas included eight by two skuas during two episodes: one skua attacked five hosts, and the other attacked three hosts. Attacks by two skuas on the same host were observed twice. The first occurred when two South Polar Skuas simultaneously attacked a Long-tailed Jaeger, and the second when two Pomarine Jaegers simultaneously attacked a Sooty Tern (*Sterna fuscata*).

Selection of hosts.—We assumed that parasites were selecting species of hosts if the number of attacks on a given species was greater than expected ($P < 0.050$), given the numerical proportion of the respective species within the entire population of potential hosts (as determined on 600-m transects). We excluded 1 of 16 attacks by Kermadec Petrels (reported above) from these comparisons because we observed the attack when we were not conducting censuses. We also excluded from these comparisons species that feed little while migrating across the ETP (Point Reyes Bird Observatory unpubl. data; Table 2).

Comparisons of the relative frequency that parasites attacked different species of hosts indicated that Kermadec Petrels and large skuas preferred large procellariids rather than small procellariids/hydrobatids, and larids (frequency of attack compared between groups of host species; G = 25.43, df = 2, $P < 0.001$, and G = 124.81, df = 2, $P < 0.001$; Tables 2 and 3; small skuas included in larid category), and that small skuas preferred larids (G = 101.20, df = 2, $P <$ 0.001; small skuas excluded from larid category). Relative frequency that different host species were attacked by Kermadec Petrels differed markedly from that of the small skuas (G = 61.06, df = 2, $P < 0.001$), but marginally from the large skuas (G = 6.02, df = 2, $P < 0.050$). In both cases, differences were mostly due to attacks on larids by skuas. Note that total number of hosts seen pertains only to those counted within the 600-m transect zone. Therefore, values for frequency of attack (which includes attacks seen within 2,500 m in some years) are overestimates (see Methods).

None of 352 Kermadec and Herald petrels observed were attacked by large skuas, a significantly lower attack frequency than the frequency that other large procellariids were attacked by large skuas (91 attacks/14,506 birds observed; G = 4.38, df = 1, P = 0.037; Tables 2 and 3).

Mass of Kermadec Petrels, skuas, and their preferred hosts.—Mass of Kermadec Petrels was similar to, or greater, than that of small skuas, and was 1.7 and 3.4 times less than that of Pomarine Jaegers and South Polar Skuas, respec-

TABLE 2. Total number of potential hosts and number of attacks by different parasites seen during 600-m transects (1984–1992), including number of attacks observed in a 2,500 m zone (1989–1991).[a] Observations in Eastern Tropical Pacific (ETP) between 25°N and 25°S latitude, and at distances greater than 185 km from nearest land. Asterisks denote species that fed infrequently in ETP (Point Reyes Bird Observatory unpubl. data).

Species attacked	Total no.	Parasitic attempts[b]				
		KE	LP	PO	SK	Total
Large procellariids						
Dark-rumped Petrel (*Pterodroma phaeopygia*)	156			2		2
Juan Fernandez Petrel (*P. externa*)	6,247	5	1	33	7	46
White-necked Petrel (*P. cervicalis*)	244			1		1
Tahiti Petrel (*P. rostrata*)	847	2				2
Wedge-tailed Shearwater (*Puffinus pacificus*)	5,838	7	2	36	10	55
*Sooty Shearwater (*Pu. griseus*)	1,017			1		1
Newell's Shearwater (*Pu. auricularis newelli*)	664		2	2		4
Small procellariids and hydrobatids						
Black-winged Petrel (*P. nigripennis*)	1,822			1		1
White-winged Petrel (*P. leucoptera*)	1,314			1		1
Stejneger's Petrel (*P. longirostris*)	566		1			1
Ringed Storm-Petrel (*Oceanodroma hornbyi*)	236	1				1
Leach's Storm-Petrel (*O. leucorhoa*)	8,141		20	1		21
Band-rumped Storm-Petrel (*O. castro*)	297		2			2
Wedge-rumped Storm-Petrel (*O. tethys*)	3,128		1			1
Markham's Storm-Petrel (*O. markhami*)	671		4			4
White-throated Storm-Petrel (*Nesofregetta fuliginosa*)	56		1			1
Phaethontids						
Red-billed Tropicbird (*Phaethon aethereus*)	62	1		2		3
Larids						
Small skuas	455				3	3
Franklin's Gull (*Larus pipixcan*)	46			1		1
Sabine's Gull (*Xema sabini*)	16		2			2
Swallow-tailed Gull (*Creagrus furcatus*)	56			2		2
Arctic Tern (*Sterna paradisaea*)	97		4			4
Sooty Tern (*S. fuscata*)	11,048		67	12	3	82
Black Noddy (*Anous minutus*)	47		1			1
White Tern (*Gygis alba*)	641		2			2

[a] Species observed but that were not attacked included following groups of birds. (1) **Large procellariids:** White-chinned Petrel (*Procellaria aequinoctialis*), 13; Parkinson's Petrel (*P. parkinsoni*), 5; Kermadec Petrel, 239; Phoenix Petrel (*P. alba*), 191; *Solander's Petrel (*P. solandri*), 7; *Murphy's Petrel (*P. ultima*), 103; *Mottled Petrel (*P. inexpecta*), 88; Herald Petrel (*P. a. heraldica*), 113; *Flesh-footed Shearwater (*Puffinus carneipes*), 13; *Pink-footed Shearwater (*Pu. creatopus*), 42; Buller's Shearwater (*Pu. bulleri*), 91; *Short-tailed Shearwater (*Pu. tenuirostris*), 5; Christmas Shearwater (*Pu. nativitatis*), 169; Townsend's Shearwater (*Pu. auricularis auricularis*), 41. (2) **Small procellariids and hydrobatids:** Cook's Petrel (*P. cookii*), 110; Defilippe's Petrel (*P. defilippiana*), 331; Pycroft's Petrel (*P. pycrofti*), 100; Bulwer's Petrel (*Bulweria bulwerii*), 462; Audubon's Shearwater (*Pu. lherminieri*), 19; Wilson's Storm-Petrel (*Oceanites oceanicus*), 22; White-faced Storm-Petrel (*Pelagodroma marina*), 274; White-bellied Storm-Petrel (*Fregetta grallaria*), 71. (3) **Larids:** Laughing Gull (*Larus atricilla*), 4; Gray-backed Tern (*Sterna lunata*), 37; Black Tern (*Chlidonias niger*), 12; Brown Noddy (*Anous stolidus*), 28; Blue-gray Noddy (*Procelsterna cerulea*), 6. Other species that were not attacked included: Waved Albatross (*Diomedea irrorata*), 28; Laysan Albatross (*Diomedea immutabilis*), 4; White-tailed Tropicbird (*Phaethon lepturus*), 30; Red-tailed Tropicbird (*Ph. rubricauda*), 192; Masked Booby (*Sula dactylatra*), 364; Blue-footed Booby (*S. nebouxii*), 15; Brown Booby (*S. leucogaster*), 12; Red-footed Booby (*S. sula*), 277; frigatebirds (*Fregata* spp.), 123; Red-necked Phalarope (*Phalaropus lobatus*), 4; Red Phalarope (*P. fulicaria*), 910. Species of which three or fewer individuals were seen are not reported. Totals reported for Kermadec Petrels and small skuas include those observed within 2,500 m in 1989–1991 because, during these observations, they were at risk of being parasitized by large skuas.

[b] KE, Kermadec Petrel; LP, Long-tailed Jaeger and Parasitic Jaeger; PO, Pomarine Jaeger; SK, South Polar Skua.

tively (Fig. 1). Mass of Kermadec Petrels was significantly less than that of two preferred hosts (Sidak test, $P < 0.01$), the Juan Fernandez Petrel (1.2 times) and Tahiti Petrel (1.1 times); it was similar ($P > 0.5$) to the mass of Wedge-tailed Shearwaters. Mass of skuas was 1.5 to 3.4 times greater, depending on species, than their preferred hosts, the Sooty Tern (preferred by small skuas), Wedge-tailed Shearwater and Juan Fernandez Petrel (preferred by large skuas).

Attack behavior of parasites.—Except where noted, small procellariids/hydrobatids were ex-

TABLE 3. Total number of hosts seen on 600-m transects in Eastern Tropical Pacific (1984–1992), and number of attacks by parasites seen on 600-m transects (1984–1992), plus number of attacks observed between 600 and 2,500 m (1989–1991). Values in parentheses are number of parasitic attacks divided by total number of hosts with the result multiplied by 100.

		No. parasitic attacks by		
Host	Total no. seen[a]	Kermadec Petrel	Small skuas	Large skuas
Large procellariids	14,858[b]	14 (0.09)	5 (0.03)	91 (0.61)
Small procellariids/ hydrobatids	17,620	1 (<0.01)	29 (0.16)	3 (0.02)
Larids	12,493[c]	0 (0.00)	76 (0.63)[d]	21 (0.17)

[a] Total number of individuals seen includes all species observed (see Table 2) except for species that fed little in ETP.
[b] Includes 352 Kermadec and Herald petrels as potential hosts.
[c] Includes 455 small skuas; these species were potential hosts of large skuas.
[d] Calculated after excluding 455 small skuas from total for larids seen. Species of skuas do not attack conspecifics (Furness 1987a).

cluded from the following analyses because they were not preferred hosts. Parasites usually attacked hosts that were associated with multispecies flocks feeding on prey forced to the surface by predatory fish (Table 4). Kermadec Petrels attacked hosts associated with flocks at a similar rate as did large skuas ($G = 1.47$, df = 1), but significantly less often than did small skuas ($G = 4.51$, df = 1, $P = 0.037$).

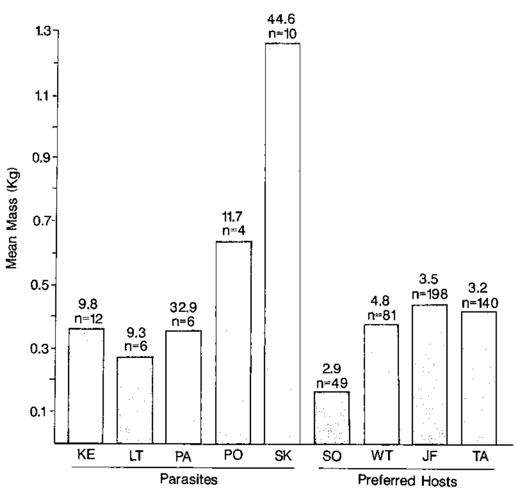

Fig. 1. Mean mass of parasites and their preferred hosts, with standard error and sample size given above each mean: (KE) Kermadec Petrel; (LT) Long-tailed Jaeger; (PA) Parasitic Jaeger; (PO) Pomarine Jaeger; (SK) South Polar Skua; (SO) Sooty Tern; (WT) Wedge-tailed Shearwater; (JF) Juan Fernandez Petrel; and (TA) Tahiti Petrel. Sooty Terns were preferred hosts of small skuas. Wedge-tailed Shearwaters and Juan Fernandez Petrels were preferred hosts of Kermadec Petrels, Pomarine Jaegers, and South Polar Skuas. Tahiti Petrels were attacked only by Kermadec Petrels (see Table 2).

Parasites usually initiated attacks from behind their hosts (Table 4). The differences in aspect of attack varied little between the Kermadec Petrel and small skuas ($G = 1.43$, df = 1; ratios compared were of attacks from the rear vs. attacks not from the rear), or between the petrel and large skuas ($G = 0.33$, df = 1).

Kermadec Petrels flew at a low altitude when initiating attacks (Table 4). This altitude differed significantly from that used by small skuas ($G = 31.79$, df = 2, $P < 0.001$), which approached hosts from various altitudes. Approach altitude of Kermadec Petrels also differed significantly

TABLE 4. Aspects of behavior of Kermadec Petrels and skuas when attempting to parasitize other seabirds in Eastern Tropical Pacific. Number of observations in parentheses. Sample size for "host association" is total number of attacks in which we noted whether or not a host was associated with a flock.

	Parasite		
	Kermadec Petrel	Small skuas	Large skuas
Host associated with feeding flock	0.67 (15)	0.90 (69)	0.81 (90)
Aspect of attack			
Behind	0.87 (13)	0.73 (62)	0.92 (76)
Side	0.07 (1)	0.09 (8)	0.06 (5)
Front	0.07 (1)	0.06 (5)	0.02 (2)
Altitude of approach			
Low	1.00 (16)	0.28 (15)	0.53 (31)
Medium	0.00 (0)	0.26 (14)	0.26 (15)
High	0.00 (0)	0.45 (24)	0.21 (12)
Plane of attack on preferred hosts			
Lateral	1.00 (14)	0.53 (34)	0.65 (48)
Ascending	0.00 (0)	0.47 (30)	0.08 (6)
Descending	0.00 (0)	0.00 (0)	0.27 (20)

from that of large skuas ($G = 16.98$, df $= 2$, $P < 0.001$). Although the majority of approaches by the latter were made at low altitudes, large skuas often approached at medium and high altitudes. Approach altitude also differed significantly between large and small skuas ($G = 9.57$, df $= 2$, $P = 0.008$).

Kermadec Petrels attacked preferred hosts (large procellarids) from a lateral plane (Table 4). Plane of attack by small skuas on larids was nearly equally divided between lateral and ascending. Attacks on large procellariids were descending ($n = 4$) or lateral ($n = 1$), a finding generally dissimilar from that obtained for Kermadec Petrels. Although most attacks on large procellariids by large skuas were lateral (i.e. the same plane of attack used by Kermadec Petrels), plane of attack differed significantly between these skuas and Kermadec Petrels ($G = 11.58$, df $= 1$, $P < 0.001$; ratios compared were frequencies of lateral vs. nonlateral attack), mostly because of regular descending attacks by the skuas.

In each case, Kermadec Petrels initiated attack by accelerating suddenly with continuous flapping to quickly attain a speed faster than the host. A continuous flapping mode of flight is unusual for petrels, which typically glide in wheeling arcs interspersed with infrequent flapping. We have also observed continuous flapping in Juan Fernandez Petrels when attempting to intercept volant flying fish (Exocoetidae) and in other procellariids attempting to elude a parasite. Only Juan Fernandez Petrels appeared capable of attaining speeds similar to those of Kermadec Petrels when flapping continuously; however, we did not see Juan Fernandez Petrels sustain a high-speed, flapping mode for distances as great as did Kermadec Petrels (up to 0.5 km).

Parasitic attempts by Kermadec Petrels did not involve the aerobatics typical of small skuas (see below). Physical contact between Kermadec Petrels and their preferred hosts occurred in 2 of 14 (14%) attempts, but we did not consider these encounters as intentional physical attacks. In the first, a Kermadec Petrel was about 1.5 m behind a Tahiti Petrel when the latter splashed to a landing. The aggressor then tumbled onto the host's back, but did not bite it. In the second, a Kermadec Petrel was 1 m behind a Wedge-tailed Shearwater when the latter landed abruptly, followed by the petrel, which slid into it.

Although small skuas usually attained high initial speeds, all of their attacks on larids involved aerobatics. Small skuas attacked larids (terns) physically in 2 of 76 (3%) attempts when they seized the bill or prey being held in it. Large skuas usually attained very high initial speeds in an attack. Although large skuas were not as maneuverable as small skuas, they made physical attacks on preferred hosts more often ($G = 4.71$, df $= 1$, $P = 0.032$; see below), and they were more aggressive. In 10 of 92 attempts (11%) by large skuas on large procellariids (8 by Pomarine Jaegers and 2 by South Polar Skuas), hosts were bitten (9 cases), repeatedly shaken by the head or neck (6), pulled from the air to the water by the wing or tail (4), held underwater by the head or neck (2), and struck from the air to the water in a body to body collision (1 by a South Polar Skua).

Success rate.—The success rate of parasitic attacks by Kermadec Petrels was similar to that of small skuas ($G = 1.09$, df $= 1$; Table 5), and marginally similar to that of large skuas ($G = 3.08$, df $= 1$, $P = 0.083$; attacks on small procellariids, hydrobatids, and phaethontids included). Lack of significance may have been due to the small sample of attacks by Kermadec Petrels ($n = 16$); their success rate was 1.5, 1.7, and 2.9 times lower than that of small skuas, Pomarine Jaegers, and South Polar Skuas, respectively. Successful attempts by each parasite mostly were the result of hosts regurgitating prey rather than dropping it from their bill, or having prey stolen from their bill.

Attacks by Kermadec Petrels included 6 (37%) by light-phase and 10 (63%) by dark-phase birds. Incidence of attack by birds of different color phases was proportional to respective color-phase ratios observed during censuses ($n = 205$; $G = 0.96$, df $= 1$; Table 1). The four successful attacks by Kermadec Petrels were divided evenly among dark- and light-phase birds. Success rate was not compared between color phases due to the small sample of successful attacks.

Small skuas experienced higher success when attacking larids versus large procellariids ($G = 4.45$, df $= 1$, $P < 0.037$; Fig. 2), but not when attacking small procellariids/hydrobatids ($G = 0.53$, df $= 1$). Large skuas had higher success when attacking large procellariids versus larids, small procellariids, hydrobatids, and phaethontids grouped ($G = 5.49$, df $= 1$, $P = 0.029$). We could not compare success rates of Kermadec Petrels when attacking different species be-

TABLE 5. Success rate, method of release of prey by hosts, element of surprise, and chase duration of Kermadec Petrels and skuas when attempting to parasitize hosts in Eastern Tropical Pacific (1984–1992). Values in parentheses are number of attacks observed.

	Parasite			
	Kermadec Petrel	Small skuas	Pomarine Jaeger	South Polar Skua
Success rate	0.25 (16)	0.38 (78)	0.43 (80)	0.72 (18)
Method of release of prey by host				
Regurgitated	0.75 (3)	0.65 (13)	0.87 (21)	1.00 (9)
Prey dropped/stolen from host's bill	0.25 (1)	0.35 (7)	0.13 (3)	0.00 (0)
Element of surprise				
High	0.67 (10)	0.55 (32)	0.56 (42)	0.25 (4)
Moderate	0.20 (3)	0.19 (11)	0.24 (18)	0.44 (7)
Low	0.13 (2)	0.26 (15)	0.20 (15)	0.31 (5)
Chase duration				
Short	0.69 (9)	0.23 (15)	0.44 (37)	0.63 (10)
Medium	0.31 (4)	0.41 (27)	0.32 (25)	0.31 (5)
Long	0.00 (0)	0.36 (24)	0.19 (15)	0.06 (1)
Host released prey upon initial contact with parasite[a]	0.50 (4)	0.00 (30)	0.29 (34)	0.46 (13)

[a] Includes data from successful attempts only.

cause we observed only two attacks by them on species other than large procellariids; both were unsuccessful.

Factors affecting success rates.—Element of surprise (ES) attained by Kermadec Petrels varied little from that of small skuas and Pomarine Jaegers ($G = 1.78$, df $= 4$; Table 5); however, South Polar Skuas attained a lower ES than did other species as a group ($G = 6.30$, df $= 2$, $P < 0.044$).

We grouped data for low and moderate ES in the following analyses to increase sample sizes and because success rates differed little between the two categories for any of the four species/groups of parasites (G-tests, $P > 0.5$; Fig. 3). The

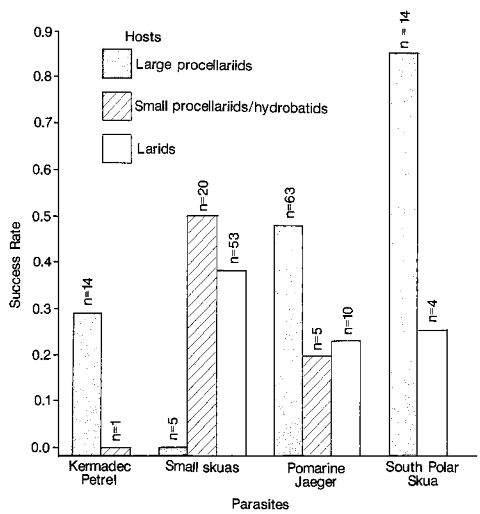

Fig. 2. Success rates of parasites when attacking different species of hosts. We observed no attacks by Kermadec Petrels on larids, or by South Polar Skuas on small procellariids or hydrobatids. Attacks not shown include three attacks on Red-billed Tropicbirds, one unsuccessful by a Kermadec Petrel and two by Pomarine Jaegers (one successful and one unsuccessful).

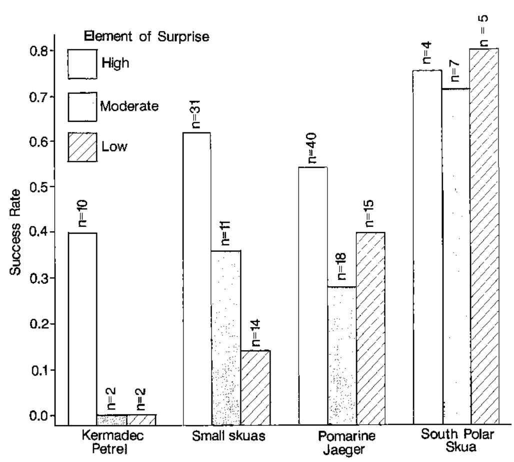

Fig. 3. Success rates of parasites and element of surprise attained when initiating attack on hosts.

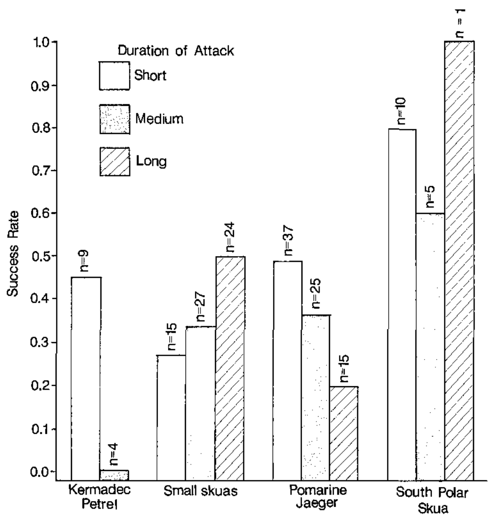

Fig. 4. Success rates of parasites and duration of attack on hosts. We observed no attacks of long duration by Kermadec Petrels.

success rate of Kermadec Petrels and small skuas increased significantly with increase in ES ($G = 3.94$, df = 1, $P = 0.048$, and $G = 8.05$, df = 1, $P = 0.005$). A similar tendency among Pomarine Jaegers was not significant ($G = 2.73$, df = 1, $P = 0.099$), and no relationship between success rate and ES was apparent in South Polar Skuas ($G = 0.00$, df = 1).

When ES was high, success rates differed little among Kermadec Petrels, small skuas, and large skuas ($G = 1.41$, df = 2). At low/moderate ES, however, success rate of Kermadec Petrels was significantly lower than that of small skuas/Pomarine Jaegers (grouped; $G = 13.40$, df = 1, $P < 0.001$). South Polar Skuas had a higher success rate with low/moderate ES than did Kermadec Petrels ($G = 10.01$, df = 1, $P = 0.002$), or small skuas/Pomarine Jaegers (grouped; $G = 8.70$, df = 1, $P = 0.004$).

Kermadec Petrels exhibited a higher proportion of attacks of short duration compared to small skuas ($G = 15.05$, df = 2, $P < 0.001$; Table 5), and large skuas ($G = 6.08$, df = 2, $P = 0.048$). Large skuas also had a higher proportion of short attacks compared to small skuas ($G = 12.96$, df = 2, $P = 0.002$).

The success rate of Kermadec Petrels tended to be higher when chase duration was short versus medium ($G = 3.68$, df = 1, $P < 0.057$; no chases of long duration observed; Fig. 4). Success rates of small skuas and Pomarine Jaegers differed insignificantly with respect to chase duration ($G = 2.54$, df = 2, $P = 0.29$, and $G = 4.01$, df = 2, $P = 0.15$, respectively) although, as duration increased, success rate of small skuas tended to increase and that of Pomarine Jaegers tended to decrease. Success rates of South Polar Skuas were high regardless of chase duration. Small samples were problematic in these comparisons.

The proportion of successful attacks in which hosts released prey upon initial contact (i.e. no chase involved) varied little between the Kermadec Petrel and large skuas ($G = 0.38$, df = 1; Table 5). We observed no attacks by small jaegers that were successful upon initial contact with hosts.

Discussion

Species of skuas do not parasitize conspecifics (Furness 1987a). Therefore, absence of parasitic attempts by large skuas on Kermadec Petrels and Herald Petrels, compared to the frequency of attempts against other procellariids of equivalent size, indicates that Kermadec and Herald petrels may have evolved avoidance features. We suggest that they have become Batesian mimics of the aposematic skuas to reduce the incidence of parasitism. Indeed, these petrels exhibit the properties typical of Batesian mimics. In addition to skualike appearance, the petrels were less aggressive (i.e. less dangerous; see also Warham 1990), have extensive range overlap with skuas (Pitman 1986, Harrison 1987) and, within the ETP, were present in lower numbers than skuas.

Other than a strikingly similar wing pattern (with few exceptions; see Murphy and Pennoyer 1952, Spear et al. 1992), the flight profile of the Kermadec Petrel, with its bulky body, short, square-shaped tail, and wide extended-wing profile (references above; see also Harrison 1987), is also very similar to subadult skuas, which comprised the majority (82–91% by species) of skuas we observed in the ETP. Usually, the latter also lack the distinct pattern on the head (jaegers) and extended tail projection characteristic of adults. The flight profile of the Herald Petrel, however, is less similar to that of skuas than that of Kermadec Petrels because of a slighter body and longer, more slender wings and tail. In addition, the wing pattern shows a less precise resemblance to skuas and, in fact, the white inner-primary patch is absent in the dark phase of the Pacific race of Herald Petrel.

Both petrel species were also opposite in color-phase frequencies compared to skuas.

Although imprecision, including geographic variation, in resemblance of mimics to their models is common (Owen 1980, Pough 1988; see below), the dissimilarities noted above raise questions as to the functional significance of plumage coloration in these petrels with respect to Batesian mimicry. The Solander's Petrel and to some extent the Murphy's Petrel also have skualike plumage coloration and overlapping ranges. Further study is needed on the behavioral interaction of each of the four skualike *Pterodroma* with skuas, taking into account the difficulty in testing the functional significance of plumage coloration and pattern (e.g. Caldow and Furness 1991). Behavioral observations and a better understanding of petrel phylogenetic relationships (see reviews in Warham 1990:83–90, Duffy 1991) could provide a more thorough evaluation of the possibility that these birds, or a common ancestor, evolved coloration patterns as Batesian mimic(s) of skuas.

We believe that a strong case exists that the Kermadec Petrel is a foraging mimic of skuas (i.e. that these petrels use their resemblance to skuas in such a way that they are able to parasitize other seabirds with greater success than they could attain otherwise). The possibility that foraging mimicry would not have evolved secondarily to Batesian mimicry (i.e. that another selective agent was responsible for evolution of plumage characteristics) does not preclude the foraging-mimicry hypothesis. To develop the evidence regarding foraging mimicry by Kermadec Petrels, we begin by comparing parasitic behavior of the petrel with that of skuas.

No species of bird is an obligate parasite (Furness 1987a, b). We were not surprised, therefore, to see each of the five parasites feeding by methods other than parasitism (for South Polar Skua feeding behavior at sea in the Antarctic, see Ainley et al. 1984). However, the more frequent use of alternate feeding methods and the lower incidence of attempted parasitism by the Kermadec Petrel compared to skuas indicate that the petrel is a less specialized parasite. In the ETP, the success rate of Kermadec Petrels (0.25) was similar to, and that of skuas (0.38 to 0.72) was higher than, success rates observed in studies of Parasitic Jaegers, and Great and South Polar skuas ($\bar{x}$ = 0.24, 95% confidence interval ± 0.05, n = 33; and $\bar{x}$ = 0.20, 95% confidence interval ± 0.09, n = 10, respectively; Furness 1987b:table 5.1) feeding at higher latitudes. Whatever the factors involved, this finding indicates that parasitism should be adaptive for the petrel despite the fact that its success rate tended to be lower than that of skuas in the ETP.

Interestingly, we sometimes saw combinations of skuas, Kermadec Petrels, other large procellariids, and other larids closely associated in multispecies flocks, either flying together or sitting together on the water. Sometimes they were within pecking distance of one another, but we saw no aggressiveness on the part of the parasites or the appearance of concern by the hosts (for similar observations, see Furness 1983). This behavior suggests that close proximity of a parasite to its host, per se, may be of secondary importance as a means of threatening the latter compared to intent communicated through threatening behavior depending on experience of the host. Along these lines, attack behavior of Kermadec Petrels was most similar to that of large skuas. In fact, when in the continuous-flapping mode of flight (i.e. as when initiating attack), the Kermadec Petrel appeared to us at first to be a small, subadult Pomarine Jaeger.

Compared to attacks by small skuas, which relied on maneuverability for success (for similar observations, see Furness 1978, Taylor 1979, Caldow 1988), attacks by Kermadec Petrels and large skuas were less aerobatic and of shorter duration, indicating that they relied primarily on frightening hosts upon initial contact. The element of surprise also was an important determinant of success for Kermadec Petrels and small skuas (for similar observations on Parasitic Jaegers and Great Skuas, see Furness 1978, Caldow 1988). This probably enabled small skuas to approach within a range close enough to be sufficiently threatening in the ensuing chase (see also Furness 1987a), whereas Kermadec Petrels were probably more threatening the closer they were upon initial contact. In contrast, the element of surprise attained by Pomarine Jaegers, and especially South Polar Skuas, did not appear as important a factor in their success rate (for dissimilar observations on Great Skuas, see Furness 1978, Caldow 1988). A possible factor involved, and one that we could not quantify, was the very high flight speed of large skuas when initiating attack. We suspect that hosts sensed that the chance of escape by increasing flight speed was small, even if the element of surprise was not high. Thus, the element of surprise attained by large skuas when attacking procellariids may be sufficient at greater distances from hosts than that achieved by Kermadec Petrels or small skuas detected at similar distances.

The main difference in attack behavior between the Kermadec Petrel and large skuas was the higher level of aggressiveness in the latter (for similar observations on large skuas, see Andersson 1976, Divoky et al. 1979, Sinclair 1980), a behavior facilitated by the larger size of large skuas compared to their hosts. This is interesting because Kermadec Petrels preferred the same large procellariid hosts as did large skuas, even though these hosts were similar or larger in size than the petrel. If aggressiveness and the resultant threat factor is as important as it appeared to be in the attack strategy of large skuas, then we find the success rate of Kermadec Petrels quite surprising, unless another factor is involved. We suspect that this petrel is a foraging mimic of large skuas (subadults) through its close resemblance in color pattern, flight profile, and (in particular) its behavior when initiating an attack; also, its model is a highly effective parasite.

In conclusion, although Kermadec Petrels effectively exhibit the properties of a foraging mimic, they might qualify as an imprecise mimic of large skuas because of smaller size and possibly the reversal in color-phase frequencies of the petrel compared to large skuas, which was opposite to our expectation in a mimetic relationship (for other selective factors that could be involved, see Caldow and Furness 1991). We suspect that any disadvantages resulting from the imprecision noted above are minimal because of the petrels close resemblance of key features of large skuas. Of equal importance would be the very high success rate observed in the model. Pough (1988) noted that the mimic's resemblance of an especially noxious/dangerous model can be imprecise; exact likeness is not required for effective results. We suspect that large skuas, in fact, are perceived as being highly dangerous by their hosts in the ETP because of the regularity and severity of attack. High threat intensity is consistent with both the high success rate of attacks, and the frequency of success upon initial contact. Similar responses to large skuas have been noted elsewhere (Ainley et al. 1984; reviewed in Furness 1987a, b, Caldow 1988).

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