PATTERNS OF PIRACY IN THE SEABIRD COMMUNITIES OF THE GALAPAGOS ISLANDS AND SOUTHERN AFRICA

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Received 23 October 1982, accepted 7 December 1982

INTRODUCTION

Brockmann and Barnard (1979) reviewed the general conditions under which kleptoparasitism is likely to occur in birds. They did not attempt to predict patterns of kleptoparasitism among species of a community. Duffy (1980) showed that in the Humboldt Current, off the west coast of South America, seabird species with shallow depths of foraging were more likely to steal food from more deeply foraging species. This in turn appeared to be related to differential access to the anchoveta *Engraulis ringens* which is more abundant with increasing depth. The present paper examines the pattern of piracy in relation to the foraging depths of the species and to the depth distribution of prey in the marine environments of the Galapagos Islands and southern Africa.

METHODS

Data were collected in the course of other field work between January 1980 and August 1981 throughout the Galapagos Islands and between September 1981 and April 1982 off southern Africa between Ichaboe Island (25 43S, 14 50E) off South West Africa/Namibia and Dyer Island (34 41S, 19 15E), South Africa. Total time in the field was less than one month in the Galapagos and six weeks in southern Africa.

Success of piracies was not noted because of the difficulties of observing the fates of small prey items at long distances. Foraging methods (Table 1) were drawn from my own observations and follow the classification of Ashmole (1971). From these I estimated the maximum depth of foraging for each species. For surface feeding and shallowly diving species (0,0 - 2,0 m) I was able to estimate depth of penetration, if any, by direct observ- ation, often at close range, and by comparison of body size. The assignment of species to 2 - 15 m and > 15 m depths was more arbitrary. Surface diving species were assumed to be able to reach 15 m or more. Pursuit plungers and deep plungers were assumed to be able to reach depths between 2,0 and 15,0 m. The accuracy of the depths reached is less important than the accuracy of the relative depths of foraging for kleptoparasitic species and their victims. Masses were obtained from the literature (Murphy 1936; Sivertsen 1953; Rand 1956, 1960; Serventy *et al.* 1971; Cramp & Simmons 1977; Duffy 1980; Furness & Furness 1982; B.L. Furness, pers.comm.) and unpublished records of the Percy FitzPatrick Institute.

Masses, foraging methods, and depths are summarized in Table 1. The data on piracy are presented in Tables 2 and 3. Data were

TABLE 1

SPECIES INVOLVED IN PIRACIES, THEIR MASSES, ESTIMATED MAXIMUM DEPTHS FORAGED AND PRINCIPAL FEEDING METHODS

Maximum depth	Mass (kg)	Feeding methods
	GALAPAGOS ISLANDS	
0,0 m		
Skua spp. *Stercorarius* spp.	0,7	piracy, dipping
Pomarine Skua *S. pomarinus*	0,7	piracy, dipping
Magnificent Frigatebird *Fregata magnificens*	1,4	piracy, dipping
0,25 m		
Brown Noddy *Anous stolidus*	0,2	dipping
Swallowtailed Gull *Creagrus furcatus*	0,2	surface seizing
0,5 m		
Waved Albatross *Diomedea irrorata*	2,0	surface seizing, piracy
2,0 m		
Brown Pelican *Pelecanus occidentalis*	2,4	surface seizing, plunging
2-15 m		
Redbilled Tropicbird *Phaethon aethereus*	0,6	deep plunging
Bluefooted Booby *S. nebouxi*	1,5	deep plunging
Masked Booby *Sula dactylatra*	1,7	deep plunging
15 m or greater		
California Sealion *Zalophus californianus*	100-200	pursuit diving
	SOUTHERN AFRICA	
0,0 m		
Arctic Skua *Stercorarius parasiticus*	0,4	piracy
Pomarine Skua *S. pomarinus*	0,7	piracy
0,25 m		
Subantarctic Skua *Catharacta antarctica*	1,6	piracy, surface seizing

Maximum depth	Mass (kg)	Feeding methods
Pintado Petrel		
Daption capense	0,4	surface seizing
Hartlaub's Gull		
Larus hartlaubi	0,3	dipping, surface seizing
Kelp Gull		
L. dominicanus	1,0	surface seizing, piracy
Sabine's Gull		
L. sabini	0,2	dipping, surface seizing
0,5 m		
Comic Tern		
Sterna spp.	0,1	surface plunging, dipping
Swift Tern		
S. bergii	0,4	surface plunging, dipping
2,0 m		
Whitechinned Petrel		
Procellaria aequinoctialis	1,2	pursuit diving, surface seizing
2 - 15 m		
Great Shearwater		
Puffinus gravis	0,9	surface seizing, pursuit diving
Sooty Shearwater		
P. griseus	0,8	surface seizing, pursuit diving
15 m or greater		
Crowned Cormorant		
Phalacrocorax coronatus	0,7	pursuit diving
Blacknecked Grebe		
Podiceps nigricollis	0,3	pursuit diving
Cape Cormorant		
Phalacrocorax capensis	1,2	pursuit diving
Bank Cormorant		
P. neglectus	1,9	pursuit diving
Cape Fur Seal		
Arctocephalus pusillus	50-350	pursuit diving

analysed in two ways : by frequency of piracies and by species-pairs involved in piracies. The first analysis gives greatest weight to the most frequent piracies even if these were attempted by only one or two species. Analysis by species-pairs reduces this problem by treating all piracies between species-pairs equally, without regard to frequency. The second method also reduces potential sampling biases which might be the result of insufficient observations in areas where certain piracies were common.

Two hypotheses were tested because they appeared most relevant to the biologies of the species and since both had been invoked as explanations for community-wide piracy : pirating species have shallower foraging depths than their victim species (Duffy 1980); and heavier species steal from lighter ones (Kushlan 1978).

The data are also used to discuss the hypothesis that more agile species pirate from less agile species. I used one-tailed binomial tests (p = 0,5) because of the relatively small number of species-pairs (Siegel 1956).

RESULTS

Effect of depth

In the Galapagos Islands, 70 kleptoparasitic attacks were observed, involving seven pirate and seven victim species (Tables 1 & 2). Intraspecific piracies involving Magnificent Frigatebirds *Fregata magnificens* or Brown Pelicans *Pelecanus occidentalis* accounted for 16 % (n = 11) of these attacks. Of the 59 interspecific piracies, 98 % were by species which foraged less deeply than their victims and in only one instance (Bluefooted Booby *Sula nebouxi* on Brown Pelican) did the pirating species have a deeper foraging depth than its victim. Interspecific piracies involved 11 species-pairs, of which ten had pirates with shallower depths than their victims. This preponderance is significant (p = 0,006).

In southern Africa, 195 kleptoparasitic attacks were observed involving nine pirates and 13 victim species (Tables 1 & 3). Intraspecific piracies involving Kelp Gull *Larus dominicanus*, "Comic" Tern *Sterna* spp., Swift Tern *S. bergii* and Cape Cormorant *Phalacrocorax capensis* comprised 17 % (34) of all attacks. Of the 161 interspecific attempts, 98 % involved pirates with foraging ranges shallower than their victims and only 2 % involved pirates with deeper foraging ranges than their victims. Of the 22 species-pairs involved in interspecific piracy 91 % (20) had pirates with shallower foraging depths than their victims and none were deeper. This is significant at the 0,001 level.

The literature records several other interspecific piracies in both areas. In Galapagos waters, Great Frigatebirds *Fregata minor* are frequent pirates of Redfooted Boobies *Sula sula* (Nelson 1978); a Masked Booby (misidentified as a Peruvian Booby *S. variegata*) "attacked a wounded Bluefooted Booby and forced it to disgorge" (Gifford 1913: 92) and Dusky Shearwaters (presumably Audubon's Shearwaters *Puffinus lheminieri*) "pester" pelicans (Gifford 1913: 110). In southern Africa, Kelp Gulls have been observed stealing prey from Whitebreasted Cormorants *Phalacrocorax carbo* (A.M.

TABLE 2

DISTRIBUTION OF PIRACY ATTEMPTS AMONG SPECIES IN THE GALAPAGOS ISLANDS

Victims	Shallower Pirates					Deeper Pirates	
	Skua spp.	Pomarine Skua	Magnificent Frigatebird	Brown Noddy	Waved Albatross	Brown Pelican	Bluefooted Booby
Shallower							
Magnificent Frigatebird	-	-	9	-	-	-	-
Swallowtailed Gull	-	-	5	-	-	-	-
Brown Pelican	-	-	-	4	-	2	1
Redbilled Tropicbird	1	-	12	-	-	-	-
Bluefooted Booby	-	1	18	1	1	-	-
Masked Booby	-	-	14	-	-	-	-
Deeper							
Californian Sealion	-	-	-	-	-	-	1

TABLE 3

DISTRIBUTION OF PIRACY ATTEMPTS AMONG SPECIES OFF SOUTHERN AFRICA

	Shallower Pirates							Deeper Pirates	
Victims	Arctic Skua	Pomarine Skua	Subantarctic Skua	Pintado Petrel	Hartlaub's Gull	Kelp Gull	Comic Tern	Swift Tern	Cape Cormorant
Shallower									
Hartlaub's Gull	-	-	-	-	-	3	-	-	-
Kelp Gull	-	-	-	-	-	27	-	-	-
Sabine's Gull	12	1	-	-	-	1	-	-	-
Comic Tern	9	-	1	-	1	-	1	-	-
Swift Tern	-	-	-	-	1	-	-	4	-
Whitechinned Petrel	-	2	-	-	-	6	-	-	-
Great Shearwater	-	-	-	1	-	2	-	-	-
Sooty Shearwater	-	-	-	-	-	2	-	-	-
Crowned Cormorant	-	-	-	-	2	1	-	-	-
Blacknecked Grebe	-	-	-	-	-	-	-	1	-
Cape Cormorant	-	-	-	-	54	54	-	1	2
Bank Cormorant	-	-	-	-	3	1	-	-	-
Deeper									
Cape Fur Seal	-	-	-	-	-	2	-	-	-

Griffiths, pers.comm.). Furness (in press) recorded Arctic Skuas *Stercorarius parasiticus* pirating from Common Terns *Sterna hirundo*, Sandwich Terns *S. sandvicensis*, and Hartlaub's *Larus hartlaubii* and Kelp Gulls. Sinclair (1978, 1980) reported Subantarctic Skuas *Catharacta antarctica* stealing from Little Shearwaters *Puffinus assimilis*, Cory's Shearwaters *Calonectris diomedea*, Great Shearwaters *P. gravis* and Atlantic Petrels *Pterodroma incerta*; Black-browed Albatrosses *Diomedea melanophris* pirating from Cape Gannets *Sula capensis*; and Kelp Gulls from Subantarctic Skuas. Pirates with foraging depths deeper than their victims occurred in ten of these 14 cases and were significantly more frequent (p = 0,029).

Effect of mass

Of the 59 interspecific piracy attempts in the Galapagos Islands, 19 involved pirates heavier than their victims. Of the 11 interspecific pairs, four involved a heavier pirate and no pattern emerged (p = 0,274). In southern Africa, 34 of 161 interspecific piracies were by heavier pirates. Of the 22 interspecific pairs, 11 involved a heavier pirate, suggesting again no significant pattern (p = 0,584). These data do not support the hypothesis that heavier birds pirate from lighter birds (Kushlan 1978).

If one assumes that lighter birds are more agile than heavier birds (Hartman 1961), the frequency data presented above support the hypothesis that more agile birds pirate from less manoeuverable species. On the other hand, the data on species-pairs do not support this interpretation. Greater manoeuvrability may be a necessary condition for piracy but it is not sufficient to explain the pattern in the two communities. Alternatively, the assumption that lighter birds are more agile than heavier ones may not be correct.

DISCUSSION

This has not been a comprehensive coverage of kleptoparasitism in either area. Such coverage would be very hard to achieve while avoiding substantial sampling bias. Such coverage is also not necessary to test the hypotheses presented here.

Interspecific piracy among seabirds in the Humboldt Current involved mainly attacks by species with relatively shallow underwater foraging techniques on species able to forage at greater depths (Duffy 1980). Pirates presumably would benefit through greater access to the major prey species which become more available with increasing depth. The available literature on prey species of the Galapagos and southern African marine environments supports a similar interpretation of the patterns of piracy observed among seabirds in these regions.

In southern African waters, especially in the Benguela Current, most shoals of pilchards *Sardinops ocellata* occur within 8 m of the surface at night (Cram & Hampton 1976) but appear to be no closer than 20 m to the surface during the day (data from King & Macleod 1976). Pelagic Goby *Sufflogobius bibarbatus*, another important prey species for seabirds in the northern Benguela Current (Crawford & Shelton 1981), have a vertical distribution of larvae and juveniles from 6 - 90 m with most occurring between 10 and 20 m (D'Arcangues 1976).

Two prey species of Galapagos seabirds, the Peruvian Sardina *Sardinops sagax* and Japanese Mackerel *Scomber japonicus* (G.Robinson pers.comm.) have not been studied in Galapagos waters, but information on their depths is available from Peru. Sardines have the same shoaling behaviour as do anchoveta and cannot be distinguished from them by acoustic sampling gear (Johannesson & Vilchez 1980). Anchoveta were usually most abundant between 10 and 20 m depth, while echotraces between 40 and 100 m were believed to be of mackerel (Johannesson & Vilchez 1980). Smaller mackerel studied in South Africa occurred closer to the sea surface, at least at night (Baird 1974).

If prey in other marine environments becomes increasingly abundant with increasing depth, then we may expect a general pattern of piracy in communities of seabirds such that klepto-parasites tend to have shallower depths of foraging than their victims. A possible exception to this might occur in the "blue-water" tropics where many seabirds rely on tuna *Thunnus* spp. and other predators to drive prey to the surface. In such situations, interspecific variations in agility over patches of surfacing prey may be more important (e.g. Ashmole & Ashmole 1967) than depth foraging in determining access to prey. Differences in depth of foraging should then be poor indicators of interspecific piracy.

Patterns of piracy related to depth may be a special case of a more general relationship determining the distribution of kleptoparasitism within a community. In communities where a resource is differentially available to various species because of differences in foraging behaviour or morphology, species without access to the prey should pirate from those with access, assuming that the food can be handled by the pirate once obtained. As examples, one might predict that surface-feeding ducks will pirate from diving ducks; that short-billed shorebirds will steal food from longer-billed species which are able to take prey deeper in the substrate; and that vulture species capable of tearing meat will be parasitized by non-tearing small vultures, storks and kites (e.g. Kruuk 1967, Houston 1975, Pomeroy 1975). The other ecological constraints on piracy discussed by Brockmann and Barnard (1979) are also of importance and will modify this pattern but differential access to prey should be considered in discussions of community-wide patterns of piracy.

ACKNOWLEDGEMENTS

I thank B.L. Furness, A.M. Griffiths and G. Robinson for their observations. H.J. Brockmann, A. Cook, J. Cooper, R.W. Furness, M. Mohamed, J.B. Nelson, R. Prŷs-Jones and A.J. Williams all improved the manuscript with their comments. Field work in Galapagos was supported by a grant from the World Wildlife Fund to The Charles Darwin Research Station. Research conducted in southern Africa is part of the Benguela Ecology Programme, funded by The South African National Committee for Oceanographic Research (SANCOR). The Sea Fisheries Research Institute supplied transportation in southern Africa. I am grateful to these organizations for their support. This is contribution number 353 of the Charles Darwin Foundation.

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