

PREDATION AND KLEPTOPARASITISM BY MIGRATING PARASITIC JAEGERS¹

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Abstract. Parasitic Jaegers (*Stercorarius parasiticus*) are thought to rely exclusively on kleptoparasitism of seabirds to obtain their food while on migration. We investigated this dependence of fall migrating birds at a stopover located on the shore of the St. Lawrence River, Québec. We found that in addition to kleptoparasitism, jaegers also preyed upon invertebrates (*Gammarus* spp.), ducks, and shorebirds. Small *Calidris* sandpipers were chased more often than expected according to their availability whereas Black-bellied Plovers (*Pluvialis squatarola*) were chased less often. The capture rate was independent of the type of shorebird chased. Capture rate was not influenced by the number of jaegers (one to five) participating in a chase. The number of jaegers, however, significantly affected the per capita hunting yield through prey defense against gulls; pair members obtained the highest yield. Predation of shorebirds was mainly performed by territorial jaegers which restrained other jaegers from the main hunting area. Kleptoparasitic interactions were mostly aimed at Common Terns (*Sterna hirundo*), which were chased more often than expected considering their availability, whereas Black-legged Kittiwakes (*Rissa tridactyla*) and Ring-billed Gulls (*Larus delawarensis*) were chased less often. Terns were more likely to drop food than kittiwakes. The success rate at inducing a tern to drop a fish increased with jaegers' group size (one to seven), whereas the per capita feeding yield decreased. No such trend was observed when jaegers chased kittiwakes. Occurrence of predation and kleptoparasitic events was influenced by tide and time of day.

Key words: Parasitic Jaeger; *Stercorarius parasiticus*; predation; kleptoparasitism; shorebirds; kittiwake; tern.

INTRODUCTION

The foraging behavior and diet of breeding Parasitic Jaegers (*Stercorarius parasiticus*) are relatively well known (Furness 1987a). Birds nesting in the North Atlantic primarily kleptoparasitize fish from alcids and larids breeding in large colonies (Grant 1971, Andersson 1976, Arnason and Grant 1978, Furness 1978), whereas jaegers nesting in the tundra primarily prey upon shorebirds, passerines, bird eggs, and small rodents (Bent 1921, Maher 1974, Eisenhauer and Paniyak 1977, Martin and Barry 1978, Pruett-Jones 1980, Enquist 1983). Kleptoparasitism in the tundra is infrequent, although some individuals are known to rely on both predation and kleptoparasitism when visiting coastal areas (Belopol'skii 1961, Andersson and Götmark 1980).

In contrast, the feeding behavior of migrating

and wintering jaegers has received much less attention (Furness 1987a). Foraging studies have mostly focused on kleptoparasitic behavior, with emphasis on the factors influencing the outcome of kleptoparasitic events (Taylor 1979, Furness 1983, Paterson 1986, Birt and Cairns 1987, Wuorinen 1992, Spear and Ainley 1993). Moreover, almost all anecdotal observations of non-breeding jaegers report acts of kleptoparasitism against seabirds (e.g., Jones 1957). This leads us to believe that this species relies almost solely on kleptoparasitism during migration and winter (e.g., Furness 1987a, 1987b; Wuorinen 1992).

To document the extent to which fall migrating jaegers rely on kleptoparasitism, we studied their foraging behavior at a migratory stopover located on the north shore of the St. Lawrence River, in Québec. This site offers a large array of potential hosts and prey. In this paper, we first describe the relative use of different species of hosts and prey in relation to their availability. We then investigate the effect of tide and time of day on the occurrence of the different foraging activities. Finally, we examine several factors that may affect the feeding success of jaegers. These include

¹ Received 2 February 1995. Accepted 25 April 1995.

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the type of host or prey species, the number of jaegers involved in a kleptoparasitic or predation event, the escape behavior of the prey, and the presence of a visible food item in the bill of the host. The occurrence of interference caused by other bird species (some of which are potential competitors for food) during a kleptoparasitic or predation event is also documented.

STUDY AREA AND METHODS

Field work was conducted from a 4 km sandbar at the mouth of the Portneuf River (48°38'N, 69°06'W), a tributary of the St. Lawrence River in Québec. The sandbar runs upstream parallel to the shore and forms a bay which is drained at low tide. The upper portion of the bay is covered by a saltmarsh dominated by *Spartina alterniflora* and the remainder by mudflats. Observations were made from 20 August to 2 September 1991 and from 17 August to 6 September 1992, when the highest numbers of shorebirds and jaegers visit the sandbar. Daily observations lasted approximately 10 hr for a total of 341 hr over the two years, and were made with binoculars and a telescope from elevated sites. Larid abundance was determined each day at roosting sites whereas shorebirds were counted while foraging on small mudflats during flood tide. The minimum number of jaegers was determined by using the largest number of jaegers seen together on a given day, and by referring to age and individual plumage characteristics (e.g., color morph, width of breast band, relative length of central tail-feathers).

A chase was defined as any pursuit occurring between members of a given dyad; i.e., a jaeger or group of jaegers against a specific individual or flock of potential hosts or prey. For each chase, the following details were noted on a tape recorder: time of day, number and age of jaegers, species and age of host or prey, the activity of jaegers and pursued individuals were engaged in before the chase was initiated, and the outcome of the chase. The latter was considered successful if the jaegers caught and subdued a prey or if they induced a host to release food. When a chase was given up, the possible cause of the abandon was attributed to the interference made by other birds or the escape behavior of the host or prey. For kleptoparasitic interactions, we also noted the occurrence of physical contacts, the presence of a visible food item in the bill of the host, whether or not the dropped food was secured,

and the position in the line of pursuit of the jaeger that secured it.

The utilization of the different species of hosts and prey was compared to their availability using the Neu et al. (1974) method. We assumed that a species relative abundance represented its availability and we only considered species known to be kleptoparasitized or preyed upon by Parasitic Jaegers (Whitherby et al. 1941; Maher 1974; Martin and Barry 1978; Pruett-Jones 1980; Furness 1987a, 1987b; MB, pers. observ.). Sanderlings (*Calidris alba*), Semipalmated (*C. pusilla*), White-rumped (*C. fuscicollis*), and Least Sandpipers (*C. minutilla*) were grouped in a single category referred to as small *Calidris* since they have similar sizes and behavior.

The frequency distribution of predation and kleptoparasitic interactions in relation to tide and time of day was also analyzed according to Neu et al. (1974). The expected frequency of predation or kleptoparasitic events for a given tide and time of day was determined by the proportion of observation time devoted to this category. Tides were mixed and semidiurnal with two daily complete oscillations unequal in height and duration. Tidal stage was categorized as low, flood, high, or ebb, and was determined from tide tables. It was assumed that low and high tides lasted 90 min on each side of their respective slack, thus making these periods 3 hr long. Flood and ebb stages were consequently of similar duration. Daytime was divided into two periods of 6 hr: 07:00 to 13:00 and 13:00 to 19:00 (EST). Independence between variables was investigated with contingency table tests (Zar 1984) pooling data for both years. The significance level for all tests was set at 0.05.

RESULTS

The mean daily abundance of Parasitic Jaegers was 3.9 ± 1.1 ($\bar{x} \pm SD$, $n = 14$) in 1991 and 6.3 ± 3.9 in 1992 ($n = 19$). At least 18 and 29 different individuals visited the sandbar in 1991 and 1992, respectively. Only three of all the birds seen in both years were immatures. In 1991, two jaegers identified as a pair by their courtship feeding behavior (Perdeck 1963), defended the entire bay. In 1992, the bay was defended by only one individual. Defense was both intra (45%) and interspecific (55%) ($n = 229$; Table 1). Most interspecific interactions were aimed at gulls and raptors. *Aggressive Uprights*, *Long Calls*, *Swoops*, and *Pursuit Flights* (sensu Perdeck 1963) dis-

TABLE 1. Species involved in agonistic interactions with territorial Parasitic Jaegers at the Portneuf Sandbar, 1991 and 1992 ($n = 229$).

Species	%
Parasitic Jaeger (<i>Stercorarius parasiticus</i>)	45.0
Herring Gull (<i>Larus argentatus</i>)	18.3
Ring-billed gull (<i>Larus delawarensis</i>)	14.0
American Crow (<i>Corvus brachyrhynchos</i>)	6.1
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	3.5
Great Black-backed Gull (<i>Larus marinus</i>)	3.5
Northern Harrier (<i>Circus cyaneus</i>)	3.1
Merlin (<i>Falco columbarius</i>)	2.6
Osprey (<i>Pandion haliaetus</i>)	2.2
Peregrine Falcon (<i>Falco peregrinus</i>)	0.9
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	0.4
Pomarine Jaeger (<i>Stercorarius pomarinus</i>)	0.4

played by the territorial individuals prevented other jaegers from moving freely or entering the bay. *Long Calls* were also displayed against raptors, gulls, and crows that crossed the flight path of the jaegers.

PREDATION

Predation by jaegers took two very different forms according to the types of prey. Jaegers fed upon invertebrates at low tide when mudflats were available ($n = 92$ feeding bouts). They presumably consumed *Gammarus* spp. (Amphipoda) which was the only organism found in samples taken at foraging sites immediately after the feeding bouts (MB, unpubl. data). Jaegers made 206 predation attempts against birds. Five were aimed at female or juvenile Northern Pintails (*Anas*

acuta). Each time, one duck was isolated from a flock but eventually escaped by reaching water and diving as the jaegers swooped down on it, or by gaining speed and altitude. Of the remaining 201 predation attempts, territorial jaegers within the bay performed 79.1% of the attacks against shorebirds, whereas the remaining 20.9% were made by nonterritorial jaegers at the tip of the sandbar.

Seven species of shorebirds were chased by Parasitic Jaegers (Table 2). Each year, this group of species made up 99% of the shorebird mean daily total abundance which was $3,960 \pm 762$ in 1991 ($n = 14$) and $1,714 \pm 205$ in 1992 ($n = 19$). In both years, Black-bellied Plovers (*Pluvialis squatarola*) were chased less often and small *Calidris* more often than expected (1991: $\chi^2 = 20.391$, $df = 3$, $P < 0.001$; 1992: $\chi^2 = 20.536$, $df = 3$, $P < 0.001$; Table 2). Furthermore, the utilization and availability of Black-bellied Plovers increased in 1992 as the utilization and availability of small *Calidris* decreased. Ruddy Turnstones (*Arenaria interpres*) and Red Knots (*Calidris canutus*) were chased in proportion to their availability. Other shorebird species observed in the study area but not chased by jaegers included the American Golden Plover (*Pluvialis apricaria*), Semipalmated Plover (*Charadrius semipalmatus*), Killdeer (*Ch. vociferus*), Greater (*Tringa melanoleuca*) and Lesser Yellowleg (*T. flavipes*), Spotted Sandpiper (*Actitis macularia*), Whimbrel (*Numenius phaeopus*), Hudsonian (*Limosa haemastica*) and Marbled Godwit (*L. fedoa*), Baird's (*Calidris bairdii*), Pectoral (*C. melanotos*), and Stilt Sandpiper (*C. himantopus*), Dunlin

TABLE 2. Utilization of the different shorebird species hunted by Parasitic Jaegers at the Portneuf Sandbar, 1991 and 1992.

Year	Prey*	Prey total abundance	Prey relative abundance	Expected number of chases	Number of chases observed	Proportion of chases observed (P)	Bonferroni 95% confidence interval
1991	Black-bellied Plover	5,950	0.11	12	0	0.00	$0.00 \leq P \leq 0.00$
	Ruddy Turnstone	2,185	0.04	5	2	0.02	$0.00 \leq P \leq 0.05$
	Red Knot	2,740	0.05	6	2	0.02	$0.00 \leq P \leq 0.05$
	Small <i>Calidris</i>	44,343	0.80	92	111	0.97	$0.92 \leq P \leq 1.00$
	Total	55,218	1.00	115	115	1.00	
1992	Black-bellied Plover	9,235	0.29	25	8	0.09	$0.01 \leq P \leq 0.18$
	Ruddy Turnstone	1,250	0.04	3	1	0.01	$0.00 \leq P \leq 0.04$
	Red Knot	908	0.03	2	1	0.01	$0.00 \leq P \leq 0.04$
	Small <i>Calidris</i>	20,790	0.65	56	76	0.88	$0.79 \leq P \leq 0.98$
	Total	32,183	1.00	86	86	1.00	

* Small *Calidris* included Sanderling, Semipalmated Sandpiper, White-rumped Sandpiper, and Least Sandpiper.

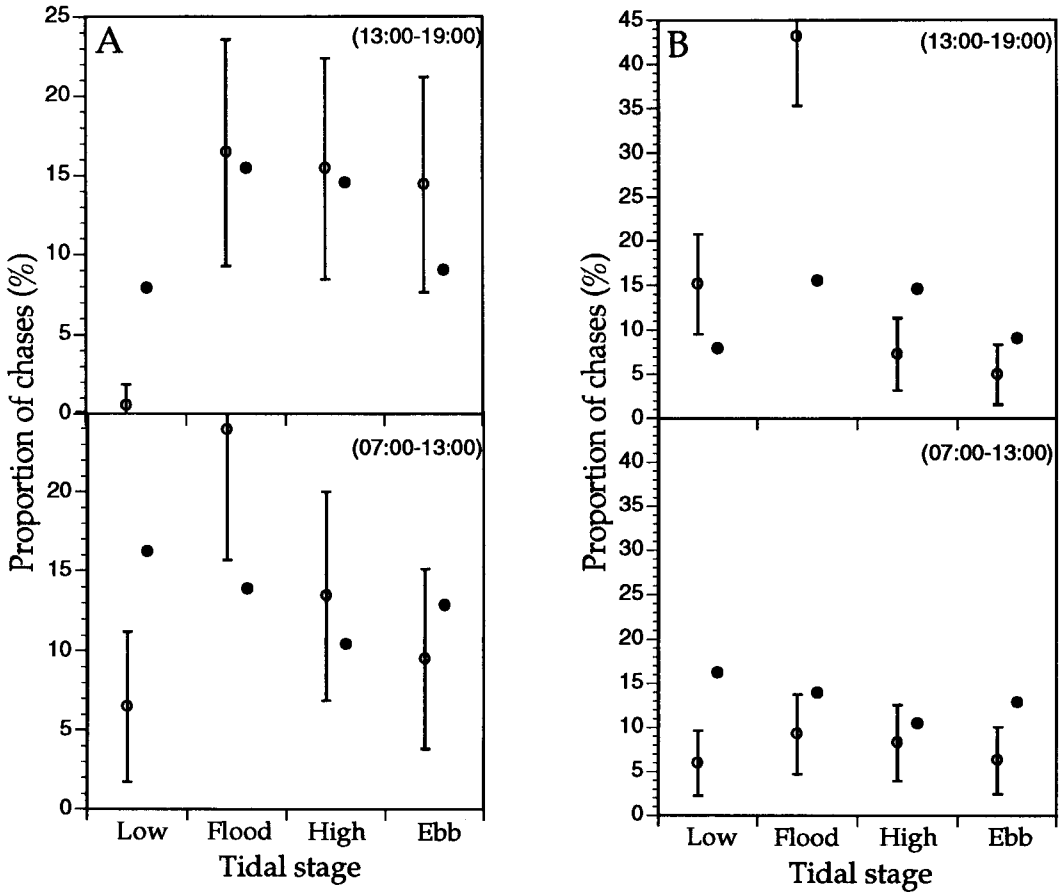


FIGURE 1. Relative frequency distribution of predation attempts aimed at shorebirds (A, $n = 201$) and of kleptoparasitic attempts aimed at larids (B, $n = 304$) by Parasitic Jaegers in relation to tide and time of day at the Portneuf Sandbar, 1991 and 1992. Open circles represent observed proportions of chases with 95% Bonferroni proportion confidence intervals. Filled circles represent expected proportions of chases determined by the proportion of observation time devoted in each tide and time of day category.

(*C. alpina*), and Short-billed Dowitcher (*Limnodromus griseus*). Taking into account the length of the study periods and the total number of jaeger-days observed in each of these, jaegers chased shorebirds 4.2 times more often in 1991 than in 1992 (0.149 vs. 0.036 chases jaeger $^{-1}$ 10 hr $^{-1}$).

Shorebirds were not chased randomly in relation to tide and time of day ($\chi^2 = 50.639$, $df = 7$, $P < 0.001$; Fig. 1A). Chases occurred more often than expected by chance during flood tide between 07:00 and 13:00 and less often at low tide in both time periods (07:00–13:00 and 13:00–19:00). Observed frequencies in the other tide and time of day categories matched the expected frequencies.

Jaegers patrolled the bay solitarily or in groups, flying, soaring, or hovering at 3–10 m above the ground or water. Among the 201 chases, 52.7% were executed by solitary jaegers, 42.3% by two jaegers, and 5.0% by three to five jaegers. The flight path of an individual seemed erratic and rarely intersected the path of another jaeger although the members of the territorial pair frequently patrolled together. All the chases were initiated by solitary individuals, of which 71.6% ($n = 194$) were already in flight. If other jaegers were present when a chase was initiated, they joined in immediately and placed themselves in line behind the initiator. Jaegers chased shorebirds silently by following them as closely as possible, and while hunting in groups often ex-

changed the leading position as the prey made turns too quickly for the leader to follow. The position exchange occurred as the second jaeger in line took the lead by short-cutting the turn and the ex-leader re-entered at the back of the line. Groups of jaegers chased small *Calidris* more often than solitary jaegers (1: 89.6% of 106; 2+: 96.8% of 95; Fisher's exact test, $P = 0.054$).

Shorebirds were either flying in flocks (76.4%), flying alone (18.5%), or found in dense vegetation patches (5.1%) when attacked ($n = 195$). The number of jaegers involved in a chase and the behavior/situation of the shorebirds at the start of a chase were not related (1 vs. 2+: $\chi^2 = 0.269$, $df = 2$, $P = 0.874$). When flocks of shorebirds were chased, their members always reacted in cohesion and gained altitude by spiraling up. Groups of jaegers were more efficient at inducing a shorebird to isolate itself from a flock than solitary jaegers (1: 77.8% of 81; 2+: 91.2% of 68; Fisher's exact test, $P = 0.042$). Shorebirds usually tried to escape by diving vertically, straightening out horizontally just a few m above the mudflats or water, and then starting to fly erratically.

The success rate at catching shorebirds was not influenced by the number of jaegers involved in a chase although only solitary individuals and the territorial pair were successful (1 vs. 2 vs. 3+: $\chi^2 = 3.947$, $df = 2$, $P = 0.139$); the overall success rate being 17.4%. Hunting success was not related to the type of shorebird pursued (small *Calidris* vs. other species lumped: Fisher's exact test, $P = 0.472$). Success rate decreased as the shorebirds were hiding in vegetation, flying solitarily, or flying in flocks (40.0% of 10; 25.0% of 36; 14.7% of 149; $\chi^2 = 5.543$, $df = 2$, $P = 0.063$). Jaegers were more successful against birds that flew erratically at low altitude than against birds that gained altitude (21.3% of 141 vs. 3.7% of 27; Fisher's exact test, $P = 0.031$). Success rate was independent of tidal stage ($\chi^2 = 0.378$, $df = 3$, $P = 0.945$, $n = 201$).

Jaegers captured shorebirds either by grasping or striking them with their bill (68.6%), by stunning them with a wing stroke (5.7%), or by forcing them to lose altitude until they hit the ground or water (25.7%, $n = 35$). Jaegers performed the latter technique by using their body, wings, and legs to cover the shorebirds. The territorial pair shared their prey by repeatedly pulling it in opposite directions. Only small *Calidris* were eaten;

the only Red Knot that was caught escaped while the jaeger that captured it mobbed a gull.

Jaegers that caught a shorebird were always subject to kleptoparasitism by either Herring (91.4%) or Great Black-backed Gulls (8.6%) ($n = 35$). Gulls acted solitarily, attempting to secure the shorebird before the jaegers or, if too late, trying to aggressively displace the jaegers. When gulls had access to a prey, they swallowed it entirely and instantly. Solitary jaegers apparently tried to prevent kleptoparasitism by pursuing the gulls and striking them with their feet or bill. However, when gulls tried to kleptoparasitize the territorial pair, only one jaeger mobbed the gull as the other remained with the prey. Solitary jaegers were kleptoparasitized nearly twice as much as the pair (1: 75.0% of 16; 2: 42.1% of 19; Fisher's exact test, $P = 0.087$) and their hunting yield (prey consumed/chase) was 2.8% (3/106) compared to 12.9% (11/85) for the pair (Fisher's exact test, $P = 0.011$). Since the pair members shared their prey, their individual hunting yield was twice that of solitary jaegers (6.5% vs. 2.8%).

Jaegers gave up chases when facing the escape behavior of shorebirds (79.5%), or the interference made by other jaegers, raptors, or gulls joining the chase or crossing their path (20.5%) ($n = 166$). Interference was mainly caused by Parasitic Jaegers (20.6%) and Herring Gulls (70.6%); Ring-billed Gulls, Northern Harriers, and Sharp-shinned Hawks were equally involved in the remaining instances ($n = 34$). Groups of jaegers were subjected to interference more than solitary individuals (1: 11.3% of 106; 2: 23.5% of 85; 3+: 20.0% of 10; $\chi^2 = 5.074$, $df = 2$, $P = 0.079$). The capture rate of shorebirds in the absence of interference was 17.0% (16/94) for one, 29.2% (19/65) for two, and 0.0% (0/8) for three or more jaegers ($\chi^2 = 5.686$, $df = 2$, $P = 0.058$). Interference had no effect on other success rate analyses; i.e., neither the success rates nor the statistical conclusions varied. The success rate at inducing a shorebird to isolate itself from a flock was not affected by interference because the latter happened after the isolation.

KLEPTOPARASITISM

All 304 kleptoparasitic interactions were directed against larids and performed outside the bay. Three species served as hosts: Ring-billed Gull, Black-legged Kittiwake (*Rissa tridactyla*), and Common Tern (*Sterna hirundo*) (Table 3). All

TABLE 3. Utilization of the different species subject to kleptoparasitism by Parasitic Jaegers at the Portneuf Sandbar, 1991 and 1992.

Year	Host	Host total abundance	Host relative abundance	Expected number of chases	Number of chases observed	Proportion of chases observed (P)	Bonferroni 95% confidence interval
1991	Ring-billed Gull	6,050	0.45	15	0	0.00	$0.00 \leq P \leq 0.00$
	Black-legged Kittiwake	5,525	0.41	14	7	0.21	$0.04 \leq P \leq 0.38$
	Common Tern	1,780	0.13	4	26	0.79	$0.62 \leq P \leq 0.96$
	Total	13,355	1.00	33	33	1.00	
1992	Ring-billed Gull	18,705	0.33	90	5	0.02	$0.00 \leq P \leq 0.04$
	Black-legged Kittiwake	36,750	0.65	176	73	0.27	$0.20 \leq P \leq 0.33$
	Common Tern	951	0.02	5	193	0.71	$0.65 \leq P \leq 0.78$
	Total	56,406	1.00	271	271	1.00	

hosts were adults except for one immature gull. These species made up 82% and 92% of the mean daily total abundance of larids in 1991 and 1992, respectively (1991: $1,165 \pm 245$, $n = 14$; 1992: $3,239 \pm 1,739$, $n = 19$). In both years, gulls and kittiwakes were chased less often, and terns more often than expected on the basis of their availability (1991: $\chi^2 = 139.500$, $df = 2$, $P < 0.001$; 1992: $\chi^2 = 7209.356$, $df = 2$, $P < 0.001$; Table 3). Although species utilization was similar in both years, kittiwake's availability increased while it decreased for gulls and terns. Other larids observed on the study area but not chased by jaegers included the Pomarine Jaeger, Long-tailed Jaeger (*Stercorarius longicaudus*), Little Gull (*Larus minutus*), Bonaparte's Gull (*L. philadelphia*), Herring Gull, and Great Black-backed Gull. Herring Gulls made up 16% and 8% of the mean daily total abundance of larids in 1991 and 1992, respectively. Considering the length of the study periods and the total number of jaeger-days observed in each of these, kleptoparasitism was used 2.6 times more often in 1992 than in 1991 (0.112 vs. 0.043 chases jaeger⁻¹ 10 hr⁻¹).

Kleptoparasitic interactions were not randomly distributed in relation to tide and time of day ($\chi^2 = 223.592$, $df = 7$, $P < 0.001$; Fig. 1B). They occurred more often than expected at low and flood tides between 13:00 and 19:00. They were, however, less frequent than expected during ebb and low tides between 07:00 and 13:00, and during high and ebb tides between 13:00 and 19:00. Observed frequencies in the other tide and time of day categories matched the expected frequencies. Both kittiwakes and terns were chased more frequently between 13:00 and 19:00 (70.0%) than between 07:00 and 13:00 ($\chi^2 = 2.842$, $df = 1$, $P = 0.092$, $n = 299$).

Chases were always directed against flying hosts and were usually initiated by already flying jaegers (85.9%; $n = 304$). Although chases were initiated by solitary individuals, other jaegers could subsequently join in. In the latter case, jaegers exchanged the leading position as when pursuing shorebirds. Group size ranged from one to four when chasing kittiwakes (1: 86.3%; 2: 10.0%; 3+: 3.8%; $n = 80$) and from one to seven when chasing terns (1: 71.2%; 2: 19.2%; 3+: 9.6%; $n = 219$). Terns were chased more often by groups than kittiwakes ($\chi^2 = 7.197$, $df = 2$, $P = 0.027$). Gulls were chased by solitary jaegers ($n = 5$). While none of the observed kittiwakes carried fish dangling from their bill, 48.1% of the chased terns did carry one ($n = 81$). This proportion did not vary across chasing group sizes (1 vs. 2 vs. 3+: $\chi^2 = 0.131$, $df = 2$, $P = 0.937$). Physical contacts only occurred against kittiwakes, and did so in 20.0% of the chases ($n = 80$). Kittiwakes were usually grabbed by a wing or the tail, and consequently lost altitude. Occurrence of physical contacts was independent of the chasing group size (1 vs. 2+: Fisher's exact test, $P > 0.999$).

Of the five chases directed toward gulls, only one was successful and was aimed at a gull carrying a large dead fish (ca. 25 cm; Table 4). Jaegers were twice as successful against terns than against kittiwakes ($\chi^2 = 16.782$, $df = 1$, $P < 0.0001$; Table 4). Success rate did not vary with group size when chasing kittiwakes (1 vs. 2+: Fisher's exact test, $P = 0.448$), but increased when chasing terns ($\chi^2 = 17.566$, $df = 2$, $P = 0.0002$; Table 4). Physically harassing kittiwakes did not alter the success rate (Fisher's exact test, $P > 0.999$). Nevertheless, jaegers chasing terns carrying a visible fish in their bill doubled their success rate (89.7% of 39 vs. 45.2% of 42; Fish-

TABLE 4. Outcome of kleptoparasitic interactions directed at Ring-billed Gulls, Black-legged Kittiwakes, and Common Terns by Parasitic Jaegers at the Portneuf Sandbar, 1991 and 1992.

Host	Number of jaegers	Number of chases	Success rate (%)	Dropped fish secured (%)	Feeding yield (% fish secured chase ⁻¹)	
					Group	Individual ^a
Gull	1	5	20.0	100.0	20.0	20.0
Kittiwake	1	69	21.7	80.0	17.4	17.4
	2	8	12.5	100.0	12.5	6.3
	3+	3	0.0	—	0.0	0.0
	Total	80	20.0	81.3	16.3	13.7
Tern	1	156	37.2	96.6	35.9	35.9
	2	42	66.7	96.4	64.3	32.1
	3+	21	71.4	100.0	71.4	20.3
	Total	219	46.1	97.0	44.7	31.2

^a Individual feeding yield was computed for weighted mean group sizes.

er's exact test, $P < 0.0001$). Hosts released only one fish which was not shared among chase participants.

Jaegers were quite efficient at securing the fish dropped by their hosts, usually securing it while still in the air. They were more efficient at securing fish dropped by terns than by kittiwakes (Fisher's exact test, $P = 0.033$; Table 4). Efficiency did not change with the chasing group size (for both kittiwakes and terns, 1 vs. 2+: Fisher's exact test, $P > 0.999$; Table 4). Of six fish not retrieved by jaegers, four were kleptoparasitized by Herring Gulls once they reached water and two were lost in water.

Jaegers experienced a feeding yield (fish/chase) nearly three times higher when chasing terns than when chasing kittiwakes ($\chi^2 = 20.388$, $df = 1$, $P < 0.0001$; Table 4). Although the feeding yield when chasing kittiwakes did not vary significantly with group size (1 vs. 2+: Fisher's exact test, $P = 0.682$; Table 4), it did increase when chasing terns ($\chi^2 = 17.473$, $df = 2$, $P = 0.0002$; Table 4). The feeding yield was equivalent to the chase success rate when chasing gulls (Table 4). The per capita feeding yield decreased with group size when either chasing kittiwakes or terns (Table 4). Furthermore, it varied with the position that an individual occupied in the line when chasing terns. The best positions were first in pairs and second in groups of three or more jaegers; no jaegers were able to secure a fish above the third position (Table 5).

Jaegers abandoned their chases as the hosts outmaneuvered them (97.3%) or as Herring Gulls interfered by joining the pursuits (2.7%) ($n = 186$). Gulls only joined chases executed by sol-

itary jaegers. The proportion of abandoned chases attributed to either causes was similar for both kittiwakes and terns (Fisher's exact test, $P > 0.999$, $n = 182$). Herring Gulls joined chases directed toward kittiwakes or terns at the same rate (kittiwakes: 2.5% of 80; terns: 1.4% of 219; Fisher's exact test, $P = 0.613$). Interference never occurred in chases directed toward gulls. Even if interference instantly led to the giving up of chases, it had no effect on success rates nor statistical conclusions.

DISCUSSION

MIGRATING PARASITIC JAEGERS AS OPPORTUNISTIC FORAGERS

Hitherto perceived as exclusive kleptoparasites upon seabirds, it is now clear that migrating Parasitic Jaegers can use different foraging methods opportunistically. Indeed, the foraging behaviors used by the jaegers in this study are likely to be related to the diversity of potential prey and host species found in the sandbar area. Anecdotal ob-

TABLE 5. Feeding yield (% fish secured chase⁻¹) as a function of the position in the chasing line for different group sizes of Parasitic Jaegers chasing Common Terns at the Portneuf Sandbar, 1991 and 1992.

Number of jaegers	Number of chases	Position in the chasing line ^a			
		1th	2nd	3rd	4th+
1	156	35.9	—	—	—
2	42	40.5	23.8	—	—
3	15	20.0	53.3	0.0	—
4+	6	0.0	50.0	16.7	0.0

^a Feeding yield was computed for weighted mean group sizes.

servations of jaegers fishing for themselves by dipping to surface (Whitherby et al. 1941, Belopol'skii 1961), and exploiting fish offal and galle refuse from ships (Watson et al. 1971 in Furness 1983, Boswall 1977) also support the idea that migrating Parasitic Jaegers exploit different food sources opportunistically.

The opportunity and decision to use different foraging strategies depend on both environmental (e.g., tide) and ecological factors (e.g., densities of competitors, kleptoparasites, hosts and prey) (Brockmann and Barnard 1979; Goss-Custard et al. 1982; Furness 1987a, 1987b; Vickery et al. 1991). The small proportion of predation attempts that were observed against shorebirds during low tide could be associated with their wide scattering on mudflats and to their low propensity to fly around (see Bijlsma 1990). On the contrary, during flood tide when a large proportion of the chases occurred, shorebirds formed flocks and performed long erratic flights before gathering at roosting sites during high tide. At ebb tide, they flew directly from roosting to feeding sites and were then probably less exposed to predation. Most of the chases (95%) were initiated toward flying shorebirds although the success rate did not vary with tidal stage. Kleptoparasitic events mainly took place between 13:00 and 19:00. This may coincide with the massive afternoon arrival of hosts in the sandbar area as kittiwakes returned to their roosting sites after feeding offshore and migrating terns stopped at the tip of the sandbar (see Wuorinen 1992).

We suspect that the yearly variation in the utilization of different foraging behaviors could be related to changes in abundance of prey and hosts. In fact, we observed a decrease in the predation rate upon shorebirds as their mean daily total abundance declined from 1991 to 1992, and inversely, an increase in kleptoparasitism rate against larids as their mean daily total abundance rose during these two years. Whether jaegers invested more effort in one type of foraging behavior is difficult to establish because one cannot ascertain that the jaegers are searching for feeding opportunities when they are alert and because jaegers probably search for potential hosts and prey at the same time.

Species of shorebirds that were chased consisted of almost the entire population of shorebirds present on the study site. Nevertheless, small *Calidris* were chased more often and Black-bellied Plovers less often than expected. The ab-

solute abundance of prey species was probably not a major determinant of prey selection since it was high enough for not being considered as a limiting factor, at least for small *Calidris* and Black-bellied Plovers. Chase success rate may have played an insignificant role since it did not vary among prey types. Hunting yield, however, was probably a main determinant of prey selection since it was highly influenced by the kleptoparasitism made by gulls. We suspect that jaegers selected small *Calidris* and did not select plovers in order to limit their loss to gulls. The frequency and success of kleptoparasitic attempts is likely to increase with prey size because larger prey are difficult to manipulate, increase handling time and visibility. They are also easier for the parasite to collect and represent a higher energetic value to the parasite (e.g., Brockmann and Barnard 1979; Furness 1987b). That knots and turnstones, two rather large shorebirds, were used in proportion to their availability is difficult to explain. Our results, however, reflect individual foraging preferences and hunting skills.

Host species comprised the core of the larid population if we consider that the Herring Gull never served as a host species. The low utilization of Ring-billed Gulls is probably related to them feeding mainly on polychaetes worms, amphipods, and insects (MB, pers. obs.); i.e., prey that would have been regurgitated as a bolus and hence difficult to collect (Brockmann and Barnard 1979, Furness 1987b). Alternatively, terns and kittiwakes dropped fish that were easily collected by the parasite. Still, terns were selected over kittiwakes. This could be explained by the high success rate of obtaining food from the former. In addition, terns were more predictable and reliable as hosts since they often flew with a fish in their bill. Likewise, terns fished near the sandbar, ensuring the jaegers that they were likely to have a fish inside their throat or bill. Kittiwakes usually passed by in large flocks and were never observed feeding near the sandbar.

TERRITORIALITY IN MIGRATING PARASITIC JAEGERES

Parasitic Jaegers defend territories during the breeding season and exhibit agonistic behavior mainly toward other jaegers and birds of prey (e.g., Bent 1921; Perdeck 1963; Maher 1974; Martin and Barry 1978; Andersson and Götmark 1980; Furness 1987a). The same kind of birds were harassed by territorial jaegers in this study.

However, it is only the second time that territoriality is reported outside the breeding season. Barton (1982) in Furness (1987a) suspected the presence of territorial behavior in local sedentary groups of Parasitic Jaegers wintering in the Western Tasmanian Sea and suggested that it may serve the purpose of limiting group density. In this study, territorial behavior was restricted to the bay where shorebirds were concentrated and was never observed in areas where jaegers fed by kleptoparasitism. Consequently, territoriality only affected the number of jaegers that could have access to the bay and potentially prey upon shorebirds. Indeed, predation on shorebirds was mostly performed by territorial jaegers and the number of participants in chases rarely exceeded two. Since the resource, shorebirds, was abundant and probably not limited, territoriality could have served the purpose of preventing interference and scrounging by other jaegers. The reason why jaegers do not defend territories when they kleptoparasitize seabirds will remain unexplained until we understand the economics of grouping and the ecological determinant of foraging group size of this species.

SHOREBIRD PREDATION

Success rate at catching shorebirds tended to be higher for jaegers that chased in pairs when interference was not considered. This improvement could be related to an increase in efficiency at inducing birds to isolate themselves from flocks and to cooperation at preventing the escape of the pursued shorebird. We suspect that cooperation in catching and defending prey is restricted to mated pairs which show cohesion and share their prey (see Pruett-Jones 1980). Chases composed of more than two jaegers had less cohesion, aborted early, and consequently had no success. The absence of cohesion and of prey sharing likely leads to costs through interference and scrambling and thus reduce the advantage of group foraging (e.g., Packer and Ruttan 1988).

Jaegers were never observed trying to enter a flock of flying shorebirds and physically isolate an individual as falcons often do (e.g., Buchanan et al. 1988; Bijlsma 1990). Flocking was thus unlikely to reduce the success rate of jaegers via some vigilance or confusion effects (e.g., Kenward 1978; Cresswell 1994a). Chasing already flying birds in an open area with high visibility level and not closely interacting with the flocking individuals as they had chosen their prey rule

out these possibilities. We suggest that the success rate against flocking birds was thus likely to depend on their perseverance at following flocks and on the decision of one particular bird to leave the flock. The decision of a shorebird to isolate itself could possibly be driven by its physical condition. A bird in poor physical condition at the edge of the rear-flock and having difficulty keeping up could possibly decide or be forced to drop out. Empirical evidence has started to accumulate on the selective pressure that predatory birds may exert on low condition prey individuals (e.g., Kenward 1978; Temple 1987; Bijlsma 1990; Cresswell 1994b).

LARID KLEPTOPARASITISM

When jaegers chased terns, their success rate at inducing the host to drop a fish increased and their feeding yield per capita decreased with the number of individuals participating in the chase, supporting the results of Andersson (1976), Arnason and Grant (1978), Furness (1978), Taylor (1979), and Birt and Cairns (1987). These trends probably derive from the small amount of food that is dropped by the hosts, the absence of food sharing, the interference between jaegers at large group sizes, and from the proportion of hosts that can potentially drop food. Nevertheless, Taylor (1979) who looked at jaeger-tern interactions obtained a bell shape relationship between the feeding yield per capita and group size. Still, these trends show a lot of temporal and dyadic variation and are often based on small samples, especially at large group sizes. This considered altogether may partly explain why we did not find this relationship with kittiwakes.

Food visibility has been proposed to increase the success rate of parasites at inducing a host to drop food (Furness 1987a, 1987b). Although we were not always able to confirm the possession of a fish by the hosts, we did find a radical increase in success rate against terns carrying a fish in their bill. Yet, it is hard to conceive how food visibility *per se* can cause an increase in success rate even though it may have a great effect on host selection and searching time. One likely explanation is that hosts are more inclined to drop food items not already swallowed. Correspondingly, Arnason and Grant (1978) observed that jaegers chased kittiwakes before they swallowed their fish. A reduced facility at dropping food could even have led to the physical contacts that we observed toward the kittiwakes although jae-

gers' success did not improve. Andersson (1976) did not find any effect of physical contact on the success rate of Great Skuas (*Catharacta skua*) chasing Northern Gannets (*Sula bassana*), another species that swallows its food. Nevertheless, it could be argued that a parasite seeing a prey should try harder in pursuing its host and hence obtain a greater success, or could reduce the host suitability assessment time and increase its surprise effect, and consequently, its success (Furness 1978, Taylor 1979).

Efficiency at securing a dropped fish is positively correlated with the height from which it was dropped (Grant 1971, Arnason and Grant 1978). Kittiwakes which were harassed by jaegers often, even when not physically attacked, lost some altitude up to the point that they flew just above the water. In comparison, terns always tried to escape by having an erratic flight, gaining some altitude and performing loops. This difference in escape behavior may have caused the greater efficiency at securing fish dropped by terns than by kittiwakes. Other factors that may affect securing efficiency include the suitability of the prey, the substratum in which the prey land if not secured in the air, the chasing group size, the position of the parasite in the line of pursuit, and the presence of kleptoparasites (Grant 1971, Arnason and Grant 1978, Birt and Cairns 1987, Furness 1987b). All these factors were trivial in our study except for the position of the parasite in the line of pursuit when chasing terns. The backward trend in securing efficiency observed with increasing group size could have resulted from the interference that the individuals made on each other as they selfishly tried to recuperate the falling fish. This trend, which was also reported by Arnason and Grant (1978), is not supported by Birt and Cairns' (1987) observations that only the first jaegers in line obtained fish. Unfortunately, these authors did not report the range and frequency of the different chasing group sizes observed. Since jaegers frequently change positions in the course of a chase, and there are no constraints on joining groups or dominance within groups, it is hardly conceivable that jaegers can position themselves in an optimal position (Arnason and Grant 1978). This, together with the fact that the host has to be maintained under pressure for the jaegers to be successful, could explain why jaegers do not strive for a particular position during a chase.

ACKNOWLEDGMENTS

We are grateful to Adalbert Bouchard for bringing to light the existence of the Portneuf Sandbar, and to Guy Beauchamp, Luc-Alain Giraldeau, Harry Williams, and two anonymous referees for making helpful suggestions on previous drafts of this paper. Field work was financially supported by two grants of the PQSPB (Québec) to MB, and writing by an NSERC (Canada) undergraduate student research award to MB. Finally, MB thanks Gilles Isabelle for his support to a young and inexperienced researcher when the idea of this project emerged in 1989.

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