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Fishing success of gulls at a southeast Alaska smelt run

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ABSTRACT. We observed foraging behavior and success of gulls (*Larus* spp.) at spawning runs of eulachon (*Thaleichthyes pacificus*; Osmeridae) in Berners Bay, Alaska, in spring 1996–1998. Adults foraged more effectively (≥56% of dives were successful) than immatures (≤56%) when diving for fish, but there was little difference in the effectiveness of piracy (≤23% success for all gull species and age classes). The hypothesis that larger birds would be better pirates and less likely to lose prey to pirates was not well supported, although smaller species seldom attacked larger ones. Age classes less successful at foraging were more likely to act as pirates, but this relationship did not hold among species or between years. The frequency of piracy attempts was positively correlated with the availability of fish captured by other birds.

SINOPSIS. **Éxito de captura de peces por parte de gaviotas durante la corrida de *Thaleichthyes pacificus***

Observamos la conducta de forrajeo y el éxito de captura de peces por parte de gaviotas (*Larus* spp.) durante la corrida de *Thaleichthyes pacificus*; Osmeridae. El trabajo se llevó acabo durante la primavera de 1996–1998 en la Bahía Bernes, Alaska. Los adultos forrajearon con mayor efectividad (≥56% de las zambullidas fueron éxitosas) que los inmaduros (≤56%). Sin embargo, hubo muy poca diferencia en la efectividad del pirateo de presas (≤23% de éxito para toda las especies de gaviotas y de diferentes clases de edades). La hipótesis de que las aves más grandes pudieran ser más efectivas pirateando y menos propensas a perder sus presas a otros piratas, no tuvo mucho apoyo, aunque las especies más pequefias pocas veces atacaron a las más grandes. Los individuos menos éxitosos forrajeando (de cualquier clase de edad) fueron más propenso actuar como piratas. Sin embargo, esta relación no se sostuvo entre especies o entre aves en los diferentes años de estudios. La frecuencia de intentos de piratería se correlaciona positivamente con la disponibilidad de peces capturados por otras aves.

Key words: foraging success, kleptoparasitism, *Larus, Thaleichthyes pacificus*

Opportunistic food piracy or kleptoparasitism is a common mode of foraging for many animals (Songe 1986; Thompson 1986), especially gulls and raptors (Brockmann and Barnard 1979; Furness 1987). Piracy may be expected when the potential benefit to the pirate is high compared to the cost, or when the chances of success are greater than for capturing food independently. Piracy is often thought to be most common in situations where potential hosts are congregated or foraging on relatively large and profitable prey, because there are multiple opportunities and good chances of success, but it may also occur under conditions of low food abundance and food stress, when the need is great (Brockmann and Barnard 1979; Furness 1987; Jorde and Lingle 1988; LeSchack and Hepp 1995; Beintema 1997).

An opportunity to examine hunting success by diving and by piracy was offered in Berners Bay near Juneau, Alaska, where large numbers of gulls (*Larus* spp.), Bald Eagles (*Haliaeetus leucocephalus*), and pinnipeds gather to forage on spring spawning runs of eulachon (*Thalichthyes pacificus*, Osmeridae-smelt) (B. Marston et al., in press). In our area, eulachon are important prey for many species, because they are high in lipids and are abundant in early spring, when the predators are migrating or preparing for reproduction.

We tested several *a priori* predictions, including the following: (1) immature birds forage less successfully than adult conspecifics, both as pirates and as independent foragers, as found for many species previously; (2) larger gulls are more likely to attempt to steal fish from smaller gulls and are more likely to be successful than smaller gulls attempting to steal from larger ones, because larger birds can be more intimidating or because they handle prey more rapidly and leave less opportunity for theft; (3) species and age categories that are less successful at foraging are more likely to attempt piracy

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(Hockey et al. 1989; LeSchack and Hepp 1995; Steele and Hockey 1995); and (4) frequency of piracy attempts increases with increased abundance of prey caught by diving. In addition, we asked if foraging success differed among gulls foraging in groups of differing size.

STUDY AREA AND METHODS

This study was conducted in Berners Bay, about 65 km north of Juneau, Alaska, where two river systems converge on a broad delta of extensive tidal sand flats. Both river systems are composed principally of channels made opaque by glacial silt. Eulachon spawn in the lower reaches of both river systems, and avian predators were concentrated there. Observations were made from late April to mid May in 1996 and 1997, and briefly in late April to early May in 1998. The numerical response of gulls to the eulachon run was rapid and huge: the numbers of gulls present rose to over 40,000 in just a few days (B. Marston et al., in press).

Gulls hunted eulachon by two principal methods: diving, consisting of plunging into the water, either from the air or the water surface, and piracy or kleptoparasitism, consisting of stealing prey by chasing birds that had already caught a fish. In addition, occasionally gulls would stand in the shallows and pluck fish from the water or glean dead fish from tide flats.

Gulls were recorded by size category: large "pink-legged" gulls, which included Herring, Thayer's, and some Glaucous-winged Gulls (*L. argentatus*, *L. thayeri*, and *L. glaucescens*, respectively), the medium-sized Mew Gull (*L. canus*), and the small Bonaparte's Gull (*L. philadelphia*). The large gull species were difficult to distinguish at the range of our observations and at the speed with which many foraging events occurred, so they were pooled. Adult gulls were defined as those with adult plumage; immature gulls included all younger age classes. For the large gulls, immatures comprised more than one year-class, because these species take longer to reach maturity than the smaller gulls.

Data were collected by picking a focal foraging bird in flight or on the water surface and following it until it caught a fish or disappeared from sight, recording the number of dives or piracy attempts, elapsed time, and size of foraging group. Foraging groups of gulls usually consisted of mixed species and age groups. Whenever possible, data were taken on multiple categories of predators in the same group, to minimize the potentially confounding effects of differing prey availability. In most cases, two observers worked together to increase the rate of data recording.

Foraging gulls were distributed unevenly across the study area, some foraging singly, while others congregated temporarily in certain areas. These congregations were called foraging "groups." Because of the large number of gulls and because groups of foraging gulls continually merged, split, and moved around, we think that the likelihood of recording the same gull more than once was small. Therefore, we consider the observations to be independent. The continuously varying distribution of foragers meant that gulls continually had a choice of joining foraging groups of different size or of foraging singly. Therefore, we asked if foraging success differed among gulls foraging singly, in small groups, or in large groups within any one year. Group size was defined for each year separately: small groups had fewer than the mean number of birds per group and large groups had more. Although gull abundance and mean group size differed between years, between-year comparisons were not addressed, because birds could only choose size of foraging group within a year.

Most statistical analyses were nonparametric, because most of the data were not normally distributed even after transformation.

RESULTS

Diving. The prediction that adults would be better at dive-foraging than conspecific immatures was upheld for all taxa (Table 1), although in one case the difference was not statistically significant. In most cases, adults were at least 30% better than immatures. Adults of all gull taxa had similar foraging success (56–69%), as did immatures of all taxa (39–56%, except Bonaparte's Gull, for which the sample size was small). Immature "pink legs" had poor foraging success compared to adults, in both years, but immature Mew Gulls foraged almost as successfully as adult Mews in 1997 (Table 1).

The interval between consecutive dives in a foraging bout was similar for adult and imma-

Table 1. Percent of dives that were successful for gulls feeding on eulachon, Berners Bay, Alaska (N = number of dives; Mann-Whitney U-test comparing adults and immatures).

Species	Yr	Adult			Immature		Adult/ Immature[1]
		Mean (SE)	N	P	Mean (SE)	N	
Bonaparte's Gull	1996	56 (4)	107	0.004	14 (7)	9	4.0
Mew Gull	1996	64 (3)	211	0.001	48 (3)	239	1.3
	1997	61 (4)	120	0.401	56 (6)	64	(1.1)
"Pink-legged" gull	1996	69 (5)	306	0.001	44 (3)	219	1.6
	1997	56 (5)	77	0.049	39 (7)	45	1.4

[1]Ratio of diving success of adults compared to immatures.

ture gulls of each taxon (median = 5 s in 1996, 23 s in 1997; sample sizes in Table 1). Bonaparte's Gull (in 1996) consistently had about 50% longer intervals between dives within a bout than the larger species (median = 10 s, Kruskal-Wallis, $P = 0.00$, followed by multiple comparisons).

In general, diving success was greater for gulls foraging singly rather than in groups (Table 2). Mean group size was smaller in 1997 than in 1996, and small groups were more successful, on average, than large groups in 1997. In 1996, however, larger groups tended to be more successful than small ones.

Piracy. Most piracy attempts involved short chases (median duration <7 s), with little detectable difference among taxa and age classes. The only significant difference was found in 1997, when immature Mew Gulls were slightly more persistent pirates than other gulls (median duration 8 s, vs. 5–6 s for others; Kruskal-Wallis test followed by multiple comparisons, $P = 0.00$).

Piracy attempts had three possible outcomes: pirate wins and victim loses, victim wins and pirate loses, or both pirate and victim lose (if the fish is dropped and lost). A fourth possibility—that pirate and victim shared the prey—was never observed. We present the probability of winning for both pirate and victim, since they are not reciprocals of each other (Table 3). Victims of piracy attempts were usually successful in keeping prey with little evident difference in vulnerability related to body size for Mew Gulls and "pink-legs" (Table 3); even Bonaparte's Gull was usually successful in retaining prey (54%, $N = 41$, present in 1996 only), although this species was more vulnerable than the larger species.

The overall probability of success in piracy was low (Table 3). The prediction that large size increases the probability of success was not sup-

Table 2. Foraging success of individual gulls (percentage of attempts that are successful) in groups of differing numbers of gulls, Berners Bay, Alaska.

		Mean group size	Group size					
			1	small	large	K-W	N	P[1]
Mew Gull								
adult	1996	165	71%	66%	51%	5.9	151	0.05
	1997	28	75	71	42	11.2	120	0.004
immature	1996	128	55	45	46	2.4	163	NS
	1997	21	—	77	51	550.0	58	0.025
"Pink-legged"								
adult	1996	292	81	60	75	5.6	261	0.06
	1997	93	—	62	42	702.0	93	0.09
immature	1996	270	84	27	56	40.3	199	0.00
	1997	70	50	40	25	0.1	45	NS
Bonaparte's Gull	1996	131	59	52	64	1.4	83	NS

[1] Kruskal-Wallis or Mann-Whitney U-tests on each row.

Table 3. Success of piracy attempts of gulls, Berners Bay, Alaska. Data are the percentage of events in which the pirate obtains a fish from a victim (P wins) and in which the victim keeps the fish (V wins). The two values do not add to 100% because sometimes the fish is dropped and no one wins. The sample sizes (*N*) give a rough indication of the frequency of attacks for each combination.

		Pirate					
		Adult Mew		Immature Mew		Immature "pink-legged"	
Victim		1996	1997	1996	1997	1996	1997
Mew Gull							
adult	P win	22% (36)	0% (41)	14% (79)	3% (89)	14% (29)	9% (34)
	V win	72	95	80	78	62	59
immature	P win	4 (32)	0 (21)	19 (74)	23 (69)	12 (25)	No data
	V win	81	76	73	39	72	No data
"Pink-legged"							
adult	P win	100 (2)	0 (3)	15 (13)	0 (3)	11 (28)	4 (23)
	V win	0	100	85	100	82	70
immature	P win	0 (3)	0 (6)	0 (13)	0 (5)	13 (32)	6 (17)
	V win	33	67	100	100	75	88

ported by our observation that the success of immature "pink-legs" attacking Mew Gulls or conspecifics was similar (Table 3). Nevertheless, Mew Gulls seldom attacked the larger "pink-legs" and tended to be more successful against the smaller Bonaparte's Gulls (33%, $N = 24$, 1996 only) than against other species, suggesting that size may sometimes matter. Likewise, there was little evidence of consistent age differences in piracy success. However, immatures seemed to engage in piracy more often than conspecific adults (Table 3); adult "pink-legs" were rarely observed to engage in piracy. Immature "pink legs" often appeared to be waiting for opportunities to steal fish. In a conspicuous behavior pattern, they commonly stood about on sand bars, watching other birds dive, and chased others when a fish had been caught.

If the frequency of piracy attempts is greater for birds that have poorer foraging success, we should observe an inverse relationship between foraging success and observed piracy attempts when relative abundance of species/age categories is accounted for. The frequency of piracy attempts was related inversely to diving success in comparisons between age classes but not among species. Adults had higher diving success than immatures and made fewer attempts at piracy, although adult "pink legs" and Mew Gulls were at least as abundant as immatures (B. Marston et al., in press; Table 3). However, immature Mew Gulls were at least as successful in diving and generally less numerous than immature "pink-legs," but they were more often seen pirating. Adult Mews and "pink-legs" were about equally successful in diving, and adult "pink-legs" were generally more numerous than Mew Gulls, but adult Mews were observed to pirate more often.

Did the frequency of piracy attempts depend on the availability of fish caught by other gulls? In 1998, we examined the relationship between the number of piracy attempts and presence of captured fish in the bills of other birds over the same time period (a measure of availability to would-be pirates, and which, in turn, depended on the number of foraging gulls nearby and their diving success). Piracy frequency was significantly correlated with fish availability ($r = 0.62$, $N = 21$, $P = 0.002$). The ratio of the rate of piracy attempts (per bird/min) to the number of fish captured by others (per bird/min) averaged 0.86, so that there was almost one piracy attempt per fish caught. The ratio of piracy rates to fish availability did not vary systematically with group size.

DISCUSSION

The prediction that adults have better diving success than immatures was upheld for all gull species, as reported for many species (e.g., Verbeek 1977; Schnell et al. 1983; Carroll and Cramer 1985; Hesp and Barnard 1989; Hockey et al. 1989; Amat and Aguilera 1990; Gilardi 1994; Goss-Custard et al. 1998; cf. Oro and

Martínez-Vilalta 1994; Cummins 1995; Steele and Hockey 1995; Shealer et al. 1997). We also observed that adult Bald Eagles foraging on eulachon were more successful (71–87% of dives in two years) than immatures (64–68%). Success of piracy attempts by gulls showed few consistent age differences, as also found for some other species (Hansen 1986; Oro and Martinez-Vilalta 1994; Hackl and Burger 1988). Immature Mew Gulls were closer to conspecific adults in their foraging skills than immature "pink legs," perhaps because they mature at younger ages than "pink legs." Maturing more rapidly, they should gain foraging skills more rapidly, and fewer immature age classes would be represented in the Mew Gull population.

The prediction that larger gulls are more successful pirates and less vulnerable as victims than smaller gulls did not receive general support, although smaller gulls did not attack larger ones very often (see Fischer 1985; LeBaron and Heppner 1985; Amat and Aguilera 1990; Temeles 1990; Kasoma 1995; Steele and Hockey 1995; Tuckwell and Nol 1997; cf. Hackl and Burger 1988). Large Bald Eagles, in contrast, were both more likely than small individuals to attack and to be successful in piracy attempts (Hansen 1986).

Bonaparte's Gulls, observed in 1996, cruised more extensively between dives than the larger gulls. Their smaller size may limit their dive depth, such that fewer eulachon were available to them. They also appeared to have difficulty handling eulachon (average mass about 33 g), especially large ones, and often dropped their prey even when not attacked by pirates. The longer interval between dives may indicate that they were "picking their shots" more than the other predators, to improve the success of handling prey once caught and reduce the risk of piracy.

The notion that piracy attempts should be inversely related to diving success was supported by comparisons of age classes but not of species or years, suggesting interspecific differences in trade-offs between hunting modes. Instead, the frequency of piracy attempts was correlated with the availability of dive-caught fish, suggesting that frequency was related to piracy opportunity. In contrast, the frequency of piracy attempts by Bald Eagles did not differ with food abundance, although the probability of success was greater when food was abundant (Hansen 1986).

Single gulls foraged more successfully than gulls in groups and were subject to piratic attacks less often, probably because they could swallow their prey more quickly than an attacker could approach. The foraging success of singletons raises the obvious question of why forage in groups at all. Three nonexclusive possibilities are that (1) certain individuals are more likely to forage singly and are able to be successful in so doing; (2) there are more opportunities to steal fish from others in groups, even though piracy is not a highly successful foraging technique; and (3) group foraging reduces the risk of piratic attack, especially by eagles, on any particular individual. The second possibility is bolstered by the correlation between frequency of piracy attempts and availability of captured fish. We cannot evaluate the first possibility, because we lacked marked birds, or the third, because eagle attacks were rare.

As found in this study, the success rate of piracy attempts is often low (e.g., Birt and Caims 1987; Fumess 1987; Hockey et al. 1989; Sumba 1989; Vickery and Brooke 1993; Shealer et al. 1997; Goss-Custard et al. 1998), although there are examples of high success rates (e.g., Fischer 1985; Hansen 1986; Amat and Aguilera 1990; Osorno et al. 1992; Oro and Martinez-Vilalta 1994; González 1996). Even when success is low, piracy may be retained in the foraging repertoire because it increases the overall net energy intake (e.g., by focusing selectively on larger prey, Steele and Hockey 1995; Ratcliffe et al. 1997), or because it is relatively inexpensive in energy and of low risk, or because it provides other kinds of benefits (e.g., LeBaron and Hepner 1985; Ens et al. 1990; Goss-Custard et al. 1998).

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