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INTRASPECIFIC FOOD ROBBING IN GLAUCOUS-WINGED GULLS

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Inter- and intraspecific food robbing, sometimes called kleptoparasitism or piracy, is common in birds, particularly, Falconiformes and Charadriiformes. A critical review of the literature by Brockmann and Barnard (1979) revealed principally descriptions of the behavior without explanations for functional significance. Findings from my investigation of intraspecific food robbing in Glaucous-winged Gulls (*Larus glaucescens*) are provided in response to recommendations by these authors for studies of costs and benefits of food robbing.

PRELIMINARY OBSERVATIONS AND METHODS

During informal visits to Lopez Island, Washington, between 1975 and 1977, I observed intraspecific food robbing in Glaucous-winged Gulls foraging on tidal mudflats at Mud Bay and MacKaye Harbor. During ebb, low and flood tides, gulls plunge-dived in shallow water, searched among seaweed and probed the mud with their bills. They captured clams, crabs, marine worms and organisms too small to be identified by observation. Gulls seized clams with the bill and flew to shore (drop flight) where they dropped the mollusks over firm ground (drop site) from a height of 3–8 m. Clam shells cracked upon impact and gulls descended to pick the meat from the fragments. Gulls cracked exoskeletons of crabs, too large to be swallowed whole, with forceful stabbing of their bills. All other prey was swallowed with one or two gulps without processing.

Three age classes of Glaucous-winged Gulls were recognized on the basis of plumage differences (Robbins et al. 1966). First-year birds were identified by uniform mottled-brown plumage; incomplete white body plumage and mottled-brown mantles with gray patches differentiated second- and third-year birds from adults which were characterized by uniform white body plumage and gray mantles. Robberies were committed within and among age classes. On the mudflats, gulls robbed by supplanting conspecifics dissecting crabs or by seizing clams from the bills of victims. On shore, gulls robbed at drop sites. As soon as conspecifics released clams to crack their shells, robbers dashed to the sites of impact and grasped the mollusks. In the air, victims surrendered prey to robbers during aerial chases. Robbers initiated such chases while victims were flying to drop sites on shore. Robbers retrieved surrendered prey from the ground or caught it on the wing.

These observations suggested that food robbing was profitable if caloric gains per unit time were greater for robbers than for individuals that did not rob. Because it was principally clams that were obtained by robbing, I confined my estimates of cost-benefit ratios to expenditures for handling clams and robbing and caloric gains from the meat of clams. The estimates did not include calculations for other expenditures related to foraging. Nevertheless, they revealed whether robbers acquired more calories for such expenditures as, for example, search of prey, metabolic regulations, growth, and reproduction, than individuals that did not rob. This assumption was made because with few exceptions robbers foraged intensively and robbed only when handling of prey rendered nearby conspecifics vulnerable.

From 5 May–15 July 1978 I observed Glaucous-winged Gulls on tidal mudflats at Mud Bay

and MacKaye Harbor, Lopez Island, Washington. Daily observation periods alternated between the two sites and were conducted from shore, usually with binoculars. Every 60 min, I counted the number of gulls engaged in foraging, feeding and processing food. I recorded the number of captured clams and robbery attempts as well as the types of robberies, types of booty, age classes of robbers and victims, and outcomes of both ground and aerial robberies on an hourly basis. Drop flights commencing with lift off upon capture of clams and terminating with releases of clams over drop sites were timed with a stop watch. Aerial chases commencing with the pursuit of the victims by the robbers and terminating with surrender of prey by the victims or abandonment of the chases by the robbers were also timed with a stop watch. Energy expended on drop flights and aerial chases was estimated with the equation kcal/h = 45.4 $W^{0.73}$ (Hart and Berger 1972) where W is the average weight of Glaucous-winged Gulls, i.e., 1.051 kg (Vermeer 1963). Energy expenditures for ground robberies were assumed to require about 0.01 kcal/robbery because at most they involved a dash over 2–5 m to snatch booty. Methods to estimate energy expenditure for such locomotion are not available (King 1974).

Sizes of captured and robbed clams were estimated. A sample of clams comparable in size and species to captured and robbed clams was collected. The widths of clams were measured and the caloric contents of clams estimated from the weights and calorie charts (U.S. Dept. Agriculture 1973). Focal animal sampling (Altmann 1974) was conducted to observe the behavior of foraging gulls and their interactions with one another. Intervals between consecutive captures of clams by gulls of different age classes were timed with a stop watch.

Captured and stolen clams were identified as sources of caloric gains for robbers. Energy expended for flights to shore to crack clams, dashes over the ground to snatch booty from victims in ground robberies and aerial chases in aerial robberies were identified as caloric expenditures. Robbery attempts were successful if they terminated in favor of the robbers. Caloric expenditure for locomotion on the ground in successful ground robberies and for aerial chases in successful aerial robberies was subtracted from the caloric content of the robbed clam and the difference was identified as a caloric gain. Caloric expenditure for unsuccessful robberies was identified as a caloric loss. Because the identities of gulls were unknown, the number of robbers/h among the foraging gulls was assumed to equal the number of robbery attempts/h.

Average hourly caloric gains and losses were calculated in kcal/robber/h for each age class of robbers at each study site (Table 1). Losses were then subtracted from gains. The difference was compared with a conjectural caloric gain from clams in kcal/gull/h for all age classes at each site in the hypothetical absence of robberies. This conjectural gain was calculated from the average hourly number of captured clams and their caloric contents, the average hourly number of gulls engaged in foraging, feeding and handling of prey, and caloric expenditures for flights to shore to drop and crack clams. The comparison served to determine whether food robbing was profitable.

Means, standard errors and proportions were used to present numerical findings, and differences were tested with the Mann-Whitney *U*-test (Remington and Schork 1970, Conover 1980).

RESULTS AND DISCUSSION

Glaucous-winged Gulls were the only species of gulls present at the study sites. I observed a total of 846 robberies perpetrated on the ground and by aerial chase (Mud Bay N = 428, MacKaye N = 418). None were committed over prey that gulls swallowed with one or two gulps

TABLE 1

EQUATIONS USED TO ESTIMATE CALORIC COST-BENEFITS OF FOOD ROBBING IN GLAUCOUS-WINGED GULLS ON LOPEZ ISLAND, WASHINGTON, 1978

Conjectural caloric gains/gull/h	$= \frac{\text{no. clams captured/h}}{\text{no. foragers/h}} \times (\text{kcal/clam} - \text{kcal/drop flight})$
Caloric gains from captured clams/gull/h	$= \frac{(\text{no. clams captured/h} - \text{no. robbery attempts/h})(\text{kcal/clam} - \text{kcal/drop flight})}{\text{no. foragers/h}}$
Caloric gains from successful ground robberies/robber/h	$= \frac{\text{no. successful ground robberies/h} \times (\text{kcal/clam} - \text{kcal/ground robbery})}{\text{no. robbers/h}}$
Caloric losses from unsuccessful ground robberies/robber/h	$= \frac{\text{no. unsuccessful ground robberies/h} \times \text{kcal/ground robbery}}{\text{no. robbers/h}}$
Caloric gains from successful aerial robberies/robber/h	$= \frac{\text{no. successful aerial robberies/h} \times (\text{kcal/clam} - \text{kcal/aerial chase})}{\text{no. robbers/h}}$
Caloric losses from unsuccessful aerial robberies/robber/h	$= \frac{\text{no. unsuccessful aerial robberies/h} \times \text{kcal/aerial chase}}{\text{no. robbers/h}}$

without processing. The majority (Mud Bay 98%, MacKaye 95%) was committed over clams and the remainder over crabs too large to be swallowed whole. Most ground robberies (Mud Bay 63%, MacKaye 86%) were perpetrated on shores when gulls dropped clams to crack their shells. Most booty (Mud Bay 98%, MacKaye 74%) surrendered by victims in aerial robberies fell to the ground from where robbers retrieved it (the shells invariably cracked upon impact). Therefore, most clams that were obtained by robbing both on the ground or by aerial chase required no further caloric expenditure for drop flights.

Frequencies of robberies were the same at both sites, 0.15/gull/h. However, ground robbery prevailed at MacKaye (69%) whereas robbery by aerial chase was more common at Mud Bay (94%). The usual high density of gulls rendered MacKaye (5.52 gulls/ha/h) conducive to ground robbery. Low density of gulls provided few opportunities for ground robberies at Mud Bay (1.11 gulls/ha/h) because distances between conspecifics handling prey were usually greater than 10 m. The high density of foraging gulls at MacKaye may have been attributable to the close proximity of this site to a nesting colony (2.41 km). Robbers failed in 67% of all attempts to rob at Mud Bay and 51% at MacKaye.

Clams (*Saxidomus* spp., *Tapes* spp., *Clinocardium* spp.) measuring 5–7 cm across their broadest widths were classified as medium while those less than 5 cm in width were small and those greater than 7 cm in width were designated large. At both sites, booty consisted principally of small (Mud Bay 42%, MacKaye 39%) and medium (Mud Bay 46%, MacKaye 42%) clams. The average weight of the meat of clams in a sample of small and medium specimens combined (N = 10) was 10.62 ± 2.26 g. Approximate caloric value of 10.62 g of raw clam meat is 8.16 kcal.

The weighted average durations of drop flights for all age classes were 14.78 ± 0.71 sec requiring 0.15 kcal/drop flight at Mud Bay and 18.91 ± 0.65 sec requiring 0.19 kcal/drop flight at MacKaye. Average durations of aerial chases at Mud Bay were 13.34 ± 0.60 sec for adults, 11.34 ± 0.99 sec for second- and third-year birds, and 15.24 ± 0.78 sec for first-year birds, requiring expenditures of 0.13, 0.11, and 0.15 kcal per chase, respectively. At MacKaye, average durations of chases were 12.31 ± 1.16 sec for adults, 15.22 ± 1.00 sec for second- and third-year birds and 11.00 ± 1.43 sec for first-year birds, requiring expenditures of 0.12 kcal, 0.15 kcal and 0.11 kcal per chase, respectively.

Conjectural caloric gains were 4.90 kcal/gull/h at Mud Bay and 1.64 kcal/gull/h at MacKaye (Table 2). Gulls obtained 3.89 kcal/gull/h from captured clams consumed without threats of robberies at Mud Bay and 0.46 kcal/gull/h at MacKaye. At Mud Bay, robbers gained 0.49 kcal/adult/h, 0.37 kcal/second- and third-year bird/h, and 0.49 kcal/first-year bird/h from

TABLE 2

DATA USED TO ESTIMATE COST-BENEFITS OF FOOD ROBBING IN GLAUCOUS-WINGED GULLS ON LOPEZ ISLAND, WASHINGTON, 1978

Data	Mud Bay Combined age classes			MacKaye Combined age classes		
No. clams captured/h	16.2879			17.0294		
No. foragers/h	26.6061			82.7647		
Kcal/clam	8.1600			8.1600		
Average duration of drop flight in sec	14.7663			18.9050		
Average caloric expenditure/drop flight	0.1500			0.1900		
No. robbers/h	3.3636			12.2941		
	adults	age 2 + 3	age 1	adults	age 2 + 3	age 1
No. robbers/h	2.0152	0.3333	1.0152	4.3539	1.4412	6.5000
No. successful ground robberies/h	0.1212	0.0152	0.0606	1.4706	0.5294	3.5882
No. unsuccessful ground robberies/h	0.1061	0.0152	0.0303	0.8824	0.3529	1.7059
Caloric expenditure/ground robbery in kcal	0.0100	0.0100	0.0100	0.0100	0.0100	0.0100
No. successful aerial robberies/h	0.3333	0.0758	0.2273	0.2050	0.0294	0.1765
No. unsuccessful aerial robberies/h	1.4545	0.2273	0.6970	1.7941	0.5294	1.0294
Average duration of chase in sec	13.3418	11.3435	15.2437	12.3081	15.2171	11.0000
Average caloric expenditure/chase	0.1300	0.1100	0.1500	0.1200	0.1500	0.1100

successful ground robberies and lost fewer than 0.01 kcal/robber/h in all age classes for unsuccessful ground robberies. At MacKaye, robbers gained 2.75 kcal/adult/h, 2.99 kcal/second- and third-year bird/h and 4.50 kcal/first-year bird/h from successful ground robberies, and also lost fewer than 0.01 kcal/robber/h in all age classes for unsuccessful ground robberies.

Robbers gained 1.33 kcal/adult/h, 1.83 kcal/second- and third-year bird/h and 1.79 kcal/first-year bird/h from successful aerial robberies at Mud Bay, but lost 0.09 kcal/adult/h, 0.07 kcal/second- and third-year bird/h and 0.10 kcal/first-year bird/h from unsuccessful aerial robberies. At MacKaye, robbers gained 0.38 kcal/adult/h, 0.16 kcal/second- and third-year bird/h, and 0.22 kcal/first-year bird/h from successful aerial robberies, and lost 0.05 kcal/adult/h, 0.05 kcal/second- and third-year bird/h, and 0.02 kcal/first-year bird/h from unsuccessful aerial robberies.

Accordingly, robbers gained a total of 5.61 kcal/adult/h, 6.02 kcal/second- and third-year bird/h, and 6.07 kcal/first-year bird/h at Mud Bay, and 3.54 kcal/adult/h, 3.56 kcal/second- and third-year bird/h, and 5.15 kcal/first-year bird/h at MacKaye. Cost-benefit ratios were smaller for ground robbery than for aerial robbery. Consequently, robbery was more profitable at MacKaye where most robberies were perpetrated on the ground

than at Mud Bay where aerial robbery prevailed. Caloric gains by robbers exceeded conjectural gains by 14% for the adult class, 23% for the second- and third-year class and 24% for the first-year class at Mud Bay, and by 116% for the adult class, 117% for the second- and third-year class, and 214% for the first-year class at MacKaye. The comparison between conjectural caloric gains and gains from captured clams and clams obtained by robbing suggested that robbery, in spite of infrequent successful attempts, was an expedient and advantageous acquisition of food. Gulls exploited conspecifics handling prey and augmented gains from foraging with booty that required no search and no greater, but often fewer, caloric expenditures.

Some first-year birds may have obtained a significant portion of daily food requirements from robbing. Unlike older conspecifics, they occasionally lay in wait for opportunities to rob. At MacKaye, I noticed that first-year birds retreated to shore after having been chased from the mudflat by older conspecifics. Body movements and tilt of their heads indicated that these birds observed drop flights of conspecifics. They dashed toward anticipated drop sites before clams hit the ground. Although first-year birds were outnumbered by older conspecifics at both sites (by a ratio of one first-year bird : two second- and third-year : five adults), they committed a considerable portion of ground robberies at Mud Bay (31%) and most ground robberies at MacKaye (56%). Furthermore, unlike their adult conspecifics, first-year birds exhibited inappropriate behavior upon finding clams. Instead of seizing a clam and flying to shore with it, some of these young birds turned the mollusk over several times, pecked at it, and occasionally abandoned it after having tossed it about. First-year birds dropped clams over the mudflats where the ground was too soft to crack shells and sometimes dropped clams in flight as if having lost a firm grip. Such behavior suggested that shell-cracking is a skill that gulls acquire over time. First-year birds seemingly had few opportunities to improve their skills because older conspecifics repeatedly supplanted them and even chased them from the mudflats. Focal animal sampling revealed that first-year birds were supplanted by adults nine times more frequently than were other adults (N = 43) and that adults captured two clams within shorter time periods (adults: 6.56 ± 1.25 min; second- and third-year birds: 25.72 ± 8.30 min; first-year birds: 21.90 ± 8.46 min) than immature conspecifics ($U = 7.15$, $P = 0.0075$, N = 26).

The methods of my investigation are open to valid criticism and provide merely estimates of cost-benefits in food robbing. Further cost-benefit studies of food robbing should be made with gulls whose identities are known, possibly through color-coded wing tags, to determine whether robbery is a strategy employed by a large proportion of a population at some time or by specific individuals specializing in robbery.

SUMMARY

Cost-benefits of intraspecific food robbing in Glaucous-winged Gulls (*Larus glaucescens*) were investigated to determine whether caloric gains per unit time were greater for robbers than for individuals that did not rob. During 10 weeks, gulls foraging on two clam beds were observed to commit 428 robberies at one study site and 418 at the other. Robberies were committed within and among three age classes of gulls and only over prey that required handling. With exception of some first-year birds, robbers foraged intensively and robbed only when handling of prey rendered nearby conspecifics vulnerable. Minimum caloric gains for robbers were estimated. Caloric expenditures for handling prey and robbing were subtracted from caloric contents of prey. Estimates revealed that caloric gains/h were greater for robbers than for individuals that did not rob. Most robbers augmented gains from foraging. But some first-year birds seemingly acquired crucial portions of daily food requirements from robbing. Suggestions for further study of food robbing were included.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

BROCKMANN, R. J. AND C. J. BARNARD. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

CONOVER, W. J. 1980. Practical nonparametric statistics. 2nd ed. Wiley and Sons Inc., New York, New York.

HART, J. S. AND M. BERGER. 1972. Energetics, water economy and temperature regulation during flight. Proc. XV Inter. Ornithol. Congr. The Hague, The Netherlands 15:189–199.

KING, J. R. 1974. Seasonal allocations of time and energy resources in birds. Pp. 4–85 *in* Avian energetics (R. A. Paynter, ed.). Nuttall Ornithol. Club 15.

REMINGTON, R. D. AND M. A. SCHORK. 1970. Statistics with applications to the biological and health sciences. Prentice Hall, Englewood Cliffs, New Jersey.

ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1966. Birds of North America. Golden Press, New York, New York.

U.S. DEPARTMENT OF AGRICULTURE. 1973. Calories and weight. Washington, D.C.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gulls (*Larus glaucescens*) on Mandast Island, B.C. B.C. Prov. Mus. Occ. Pap. 13.

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