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FACTORS INFLUENCING RATE AND SUCCESS OF INTRASPECIFIC KLEPTOPARASITISM AMONG KELP GULLS (*LARUS DOMINICANUS*)

William K. Steele and Philip A. R. Hockey
Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa 7700

Abstract.—Intraspecific kleptoparasitism among Kelp Gulls (*Larus dominicanus*) was studied at four sites in the southwestern Cape Province of South Africa. Sites included: (1) undisturbed foraging habitats; (2) a sandy beach and a rocky shore; and (3) areas where supplementary food was available—a fishing harbor and a refuse dump. Simple food-choice experiments were used to test hypotheses generated from field observations. Among-site variation in the rate and success of kleptoparasitism was related to prey attributes, of which prey size and handling time were the most important. In food-choice experiments, gulls selected small prey with short handling times. Prey with long handling times were the most likely to be stolen and the rate of keptoparasitism was higher when prey were dispersed than when they were clumped. There were marked age-related differences in the rate, although not the success, of kleptoparasitism among Kelp Gulls. Juvenile (first-year) gulls attempted kleptoparasitism significantly more often than expected and adults significantly less often. Subadults kleptoparasitized in proportion to their abundance in the population. If an age-related dominance hierarchy exists, it mediates kleptoparasitic behavior in Kelp Gull assemblages through older birds avoiding kleptoparasitic attacks rather than initiating them. Simple mathematical models, based on data collected during field observations, were used to investigate the conditions explaining the rate of intraspecific kleptoparasitism within Kelp Gull populations. Either few individuals can kleptoparasitize relatively frequently, or many individuals can kleptoparasitize infrequently. Apparently, both mechanisms operate within Kelp Gull populations because individuals attempt kleptoparasitism relatively frequently when they are juveniles and inefficient hunters, but infrequently once they are adult and efficient hunters. The viability of facultative intraspecific kleptoparasitism as a foraging technique relies on stolen prey being larger on average than the prey captured by hunting. *Received 18 July 1994, accepted 13 February 1995.*

Kleptoparasitism, or the stealing of already procured prey from one individual by another (Brockmann and Barnard 1979), has been extensively studied where it occurs interspecifically among birds (see reviews by Brockmann and Barnard 1979, Barnard and Thompson 1985, Furness 1987). Intraspecific kleptoparasitism among birds has received less attention in the scientific literature, but field evidence of its profitability or otherwise has been discussed by Kushlan (1978, 1979), Dunbrack (1979), Hansen (1986), and Ens et al. (1990).

Intraspecific kleptoparasitism differs from the interspecific behavior because the rate of intraspecific kleptoparasitism within a population is constrained by factors that do not operate interspecifically (Barnard and Sibly 1981, Vickery et al. 1991). Some individuals must hunt, and all individuals cannot resort to kleptoparasitism as a foraging technique, except at a very low rate. Thus, intraspecific kleptoparasitism within populations can be controlled in two ways: either few individuals kleptoparasitize relatively frequently, or many individuals kleptoparasitize relatively infrequently. Alternatively, individuals can change their role as either a "producer" or a "scrounger," depending on the nature of the food resource or the composition of the foraging group (Giraldeau and LeFebvre 1986). Although differential frequencies of kleptoparasitism among age classes within gull populations have been shown (Burger and Gochfeld 1979, Carrol and Cramer 1985, Hesp and Barnard 1989, Hockey et al. 1989, Hockey and Steele 1990), the constraints that determine this division are poorly understood.

The Kelp Gull (*Larus dominicanus*) is widespread throughout the higher latitudes of the Southern Hemisphere (Harrison 1983), and is common along much of the southern African coastline (Crawford et al. 1982, Steele and Hockey 1990). These gulls are separable into age classes in the field on the basis of plumage and soft-part coloration (Kinsky 1963, Harrison 1983), allowing age-related differences in foraging and kleptoparasitic behavior to be studied. Field observations of flocks of foraging Kelp Gulls, supported by food-choice experiments, were used to determine the factors that influence the rate and success of intraspecific kleptoparasitism.

Because it was impossible to quantify the full foraging repertoire of all gulls, a mathematical model was used to estimate the proportion of foraging time an individual should devote to kleptoparasitism if all birds were facultative producers/scroungers. A second, empirically-based model was used to investigate the proportion of birds in flocks of different sizes that could be obligate kleptoparasites (and still maintain an intake rate at least equal to producers). That is, what would be the stable ratio of producers to scroungers if all individuals used only one or the other foraging technique.

METHODS

Field observations.—Three age classes of Kelp Gull were recognized on the basis of plumage and bare-part coloration: juvenile (first-year birds), subadult (second- and third-year birds), and adult. Four sites in the Western Cape Province of South Africa, where flocks of Kelp Gulls regularly foraged, were selected to include a range of feeding habitats. Olifantsbos Bay (OB; 34°16′S, 18°23′E) is a stretch of undisturbed rocky shore in the Cape of Good Hope Nature Reserve, and 16 Mile Beach (SMB; 33°18′S, 18°17′E) is a sandy beach within the West Coast National Park where humans have had little impact. By contrast, at both Strandfontein refuse dump (SD: 34°05′S, 18°30′E) and Hout Bay fishing harbor (HB; 34°04′S, 18°21′E), supplementary food is available to the gulls as a result of human activities.

We conducted 220 h of observations on flocks of foraging gulls at the four sites from 1986 through 1989. The numbers of gulls present during observation periods were counted hourly by age class. For each observed attempt at kleptoparasitism, the success, age class of host, number and age class(es) of pursuer(s), and age classes of successful kleptoparasites were noted. Prey-handling times and kleptoparasitic pursuits were timed to the nearest second. An index of the rate of kleptoparasitism among gulls at different sites was calculated as the number of observed kleptoparasitic incidents per hour for each 100 gulls present.

Food-choice experiments.—To test trends observed in the field, controlled feeding of gulls was carried out on open sandy beaches at Kalk Bay harbor (34°09′S, 18°07′E) and Bloubergstrand (33°47′S, 18°27′E), where all interactions between gulls were clearly visible. At Kalk Bay harbor, a food-choice experiment was used to test the effects of prey size on food selection and kleptoparasitic behavior. Three pieces of fish offal of different size classes (small, ca. 25 × 25 × 50 mm; medium, ca. 25 × 25 × 100 mm; large, ca. 25 × 25 × 150 mm) were placed equidistant from the main group of gulls. The order in which the food items were placed was varied each time ($n = 50$ replicates).

It has previously been determined that Kelp Gulls rapidly crush and swallow small sand mussels (*Donax serra*), whereas large *Donax* require a complex handling technique, in which the gulls fly up and drop the mussel to break the shell open (Steele 1992). In order to test the effect of prey-handling time on food selection, Kelp Gulls at Bloubergstrand were presented simultaneously with two large *Donax* of equal size, but one having had its adductor muscle cut so that the valves gaped open slightly and gulls could gain direct access to the flesh ($n = 51$ replicates).

In order to test effects of prey "quality" (defined as energy content per unit mass) on kleptoparasitic behavior, independent of prey size, gulls at Kalk Bay harbor were presented simultaneously with 10 portions each of fish offal and bread of the same size (ca. 25 × 25 × 25 mm). Bread was dampened to make it easier for gulls to swallow. These food items were placed alternatively in a grid pattern, over 1.5 × 1.0 m, to ensure that gulls could select the item of their choice immediately on landing ($n = 34$ replicates).

Finally, to test the effects of prey dispersion independent of prey size and quality, Kelp Gulls were videotaped at Hout Bay harbor while feeding on pilchards (*Sardinops ocellata*) presented as one pile of 20 fishes ($n = 10$ replicates), five piles of 4 ($n = 10$), and 20 individually spaced fishes ($n = 10$). All fishes were of approximately the same size, and all presentations were evenly spaced over a 10 × 10 m area. The order in which different presentations were used varied randomly, and no more than three replicates were presented on any given day.

During controlled feeding, the age ratio of Kelp Gulls present was recorded at 30-min intervals, and the order of food selection, as well as the rate and success of kleptoparasitic attacks, were recorded by age class. A second and smaller gull species, Hartlaub's Gull (*L. hartlaubii*), was also present at Kalk Bay harbor during controlled feeding and participated in the food-choice experiments. The mean number of gulls present at Kalk Bay harbor during controlled feeding was 12 Hartlaub's and 30 Kelp gulls ($n = 7$). Although Hartlaub's Gulls also were present at Hout Bay harbor, controlled feeding took place on the harbor breakwater, which was the main Kelp Gull loafing area, and Hartlaub's Gulls were totally excluded from the food by the larger gulls.

Models.—During observations at Strandfontein dump, individual Kelp Gulls scavenging for food were selected at random and watched for 5 min, until they went to the loafing area, or were lost to sight. The size of food items was estimated relative to bill length (ca. 54 mm; Maclean 1993) during both scavenging and kleptoparasitic attempts, and a number of other foraging variables were determined (Appendix 1). These variables were then used to model aspects of the foraging behavior of Kelp Gulls at the dump. Kelp Gulls at Strandfontein dump theoretically have a choice among three foraging "strategies": (1) the "scavenger" does not resort to kleptoparasitism, but scavenges/hunts for food; (2) the "kleptoparasite" obtains food through kleptoparasitism alone; and (3) the "scavenger-kleptoparasite" employs a combination of the two foraging techniques. Using the Strandfontein data, we developed two models to find the stable rate of kleptoparasitism depending on whether the behavior was facultative or obligate.

Model I assumes that all Kelp Gulls in the flock are able to vary the proportion of available foraging time they devote to kleptoparasitism (i.e. the flock comprises scavengers and/or scavenger-kleptoparasites). Individual reward, in terms of the equivalent number of average-sized food items consumed per hour, was calculated for a range of rates of kleptoparasitism, and the theoretical proportion of foraging time that Kelp Gulls at Strandfontein dump should devote to kleptoparasitism in order to maximize their rate of food intake was determined. The parameters, assumptions, and calculations used for this model are detailed in Appendix 1.

The case where flocks of Kelp Gulls at the Strandfontein dump comprise a mixture of obligate scavengers and obligate kleptoparasites was considered in Model II. A model similar to that of Barnard and Sibly (1981) was developed to determine the stable ratio of kleptoparasites to scavengers within Kelp Gull flocks of varying size. Individual reward, in terms of the number of average-sized food items consumed per hour, was calculated for gulls following one of these two foraging strategies (Appendix 2). The calculated reward for both strategies was compared for various flock sizes and compositions. For each flock size, the composition (ratio of scavengers to kleptoparasites) at which point no individual could better its food intake by changing its foraging strategy was determined.

RESULTS

FACTORS INFLUENCING RATE AND SUCCESS OF KLEPTOPARASITISM

There were many more Kelp Gulls at sites where supplementary food was available than at undisturbed sites (Table 1). The number of Kelp Gulls at each study site actively foraging every hour was much lower than the total number of gulls present. The mean number of foraging Kelp Gulls at Olifantsbos Bay during hourly counts was 7.3 ± SD of 8.0 ($n = 27$) and at Strandfontein dump was 26.9 ± 21.9 ($n = 33$). The number of gulls foraging at 16 Mile Beach and Hout Bay harbor fluctuated so widely throughout the day according to tidal conditions and/or harbor activity that it was meaningless to calculate an average value. The indexes of rates of kleptoparasitism varied greatly between sites (Table 1), being highest at 16 Mile Beach and lowest at Olifantsbos Bay—the two undisturbed study sites. Many attempts at kleptoparasitism took place among gulls on the ground, and these often were impossible to observe when large numbers of gulls were feeding together. Furthermore, it was only possible to follow a single kleptoparasitic attempt at a time and, therefore, the number of recorded kleptoparasitic incidents is an underestimate.

Prey size and handling time.—Prey-handling

TABLE 1. Summary of feeding and kleptoparasitic behavior of Kelp Gulls at study sites.

	Undisturbed		Food-supplemented	
	OB	SMB	HB	SD
Mean number at site[a]	23.4 ± 26.3 (17)	24.7 ± 22.4 (10)	243 ± 150 (17)	546 ± 296 (19)
Site surface area (m^2)	2,000	10,000	25,000	25,000
Principal prey	Dipteran larvae and pupae	*Donax serra*, invertebrates	*Engraulis capensis*, invertebrates	Domestic waste
Mean prey-handling time (s)[a]	<1.0	175.6[b] ± 129.4 (52)	2.1 ± 0.4 (8)	3.8 ± 11.9 (40)
Mean pursuit time (s)[a]	4.0 (1)	5.0 ± 11.4 (30)	2.8 ± 1.8 (12)	8.3 ± 11.4 (138)
Kleptoparasitism rate (incidents·[100 gulls]$^{-1}$·h^{-1})	0.1	6.8	0.7	1.2
Individual kleptoparasitic success (%)	0.0	25.5	15.2	14.0

[a] $\bar{x}$ ± SE (n).

[b] For *Donax* only.

TABLE 2. Effect of prey size on food choice, and frequency and success of kleptoparasitism by Kelp and Hartlaub's gulls.

	Prey size (n = 50 for each size)[a]		
	Small	Medium	Large
Order of selection (%)			
First	46	42	10
Second	30	46	16
Third	24	8	56
Not taken	0	4	18
Percentage taken by			
Kelp Gull adult	24	42	34
Kelp Gull subadult	24	47	29
Kelp Gull juvenile	43	23	34
Hartlaub's Gull	75	20	5
Probability of retaining prey by			
Kelp Gull adult	1.00	0.75	0.22
Kelp Gull subadult	1.00	0.50	0.33
Kelp Gull juvenile	0.87	0.87	0.67
Hartlaub's Gull	0.93	0.50	0.00

[a] Small, 25 × 25 × 50 mm; medium, 25 × 25 × 100 mm; large, 25 × 25 × 150 mm.

time affected both the overall rate (Table 1) and success of kleptoparasitism among gulls. At Olifantsbos Bay, where the mean prey-handling time was less than 1 s, the rate of kleptoparasitism was very low and restricted to uncommon, large prey items (e.g. mussels, limpets and fishes). At 16 Mile Beach the principal prey of Kelp Gulls was *Donax,* which required a long handling time; at this site the rate of kleptoparasitism was higher than at any other (Table 1). At Strandfontein dump, successful kleptoparasitic attempts involved significantly larger prey ($\bar{x}$ = 75 ± 52 mm, n = 68) than failed attempts ($\bar{x}$ = 61 ± 41 mm, n = 146; t = 2.07, df = 212, $P < 0.05$).

At Kalk Bay harbor, when presented with evenly spaced prey of three different size classes simultaneously, gulls selected the smallest prey item first significantly more often than expected by chance ($X^2 = 4.2$, df = 1, $P < 0.05$); the largest item was usually selected last (Table 2). This order of selection reflects the risk of losing prey to kleptoparasites: 63.4% of all large food items were stolen, compared to 29.2 and 6.0% of medium-sized and small-sized items, respectively.

Prey-handling technique.—The handling technique used for *Donax* at 16 Mile Beach, where prey are dropped during flight, made prey readily available to potential kleptoparasites. At this site, Kelp Gulls also fed on three-spotted swimming crabs (*Ovalipes punctatus*), which required a long handling period (sometimes >10 min). However, in contrast to the handling technique used for *Donax,* gulls feeding on *Ovalipes* stood over, and were able to protect their prey. As a result, no crabs were lost to kleptoparasites.

During feeding experiments, Kelp Gulls at Bloubergstrand selected partially opened *Donax* before similarly sized *Donax,* which were closed (41 of 51 occasions, $X^2 = 18.8$, $P < 0.01$).

Prey quality and abundance.—It is difficult to compare relative prey "quality" between sites in the field. When offered prey of similar size and handling time, but of different energetic content, gulls clearly selected "high-quality" prey (Table 3). Fish offal (19.0 kJ/g; Hockey unpubl. data) was selected before bread (11.1 kJ/g; N.R.I.N.D. 1986) significantly more often than expected ($X^2 = 16.0$, $P < 0.01$). Fifteen kleptoparasitic attacks were directed at hosts with fish and only one at a host with bread; gulls directed attacks disproportionately more frequently at hosts with high-quality prey ($X^2 = 4.9$, $P < 0.05$). Only 1.2% of fish pieces offered were left at the end of experimental runs compared to 53.5% of the pieces of bread.

At Strandfontein dump, food was usually abundant and comparatively few gulls resorted to kleptoparasitism (Table 1). Although supplementary food also was available at Hout Bay harbor, this was only for limited periods, when boats unloaded catches or cleaned nets. The highest observed rate of kleptoparasitism was at 16 Mile Beach, where large *Donax* afforded an opportunity for kleptoparasites. These mussels were relatively uncommon, with only one or two being handled by gulls at any one time. The success of kleptoparasitic attempts by Kelp Gulls at 16 Mile Beach was high in comparison to the other sites (Table 1).

TABLE 3. Effect of prey quality (in terms of energy content per unit mass) on order of food choice (n = 340 for bread and for offal) by Kelp and Hartlaub's gulls.

Order of selection	Bread	Fish offal	Unknown
First item taken[a]	14.7	82.4	2.9
Second item taken[a]	5.9	82.4	11.7

[a] Percent of time particular item taken.

TABLE 4. Effect of prey dispersion on rate of kleptoparasitism among Kelp Gulls (n = 10 for each column).

	1 pile of 20 fishes	5 piles of 4 fishes	20 spaced fishes
No. fishes taken	180 (90%)	176 (88%)	191 (96%)
Kleptoparasitic attempts	7 (3.9%)	13 (7.4%)	20 (10.5%)

Prey dispersion and group size.—The rate of kleptoparasitic attempts on Kelp Gulls carrying fishes at Hout Bay harbor increased as prey dispersion increased ($X^2 = 5.5$, df = 2, $P < 0.01$). When 20 individually spaced fishes were presented to Kelp Gulls, the rate of kleptoparasitism was twice as high as when the same number of fishes were presented in one pile (Table 4).

The chance of an individual kleptoparasite gaining food decreased as the number of kleptoparasites in a group pursuit increased (Fig. 1), and pursuits by a lone kleptoparasite were more frequent than attempts involving several gulls (Fig. 2). Participation in kleptoparasitic attempts by groups of Kelp Gulls showed no age-related bias (Fig. 3).

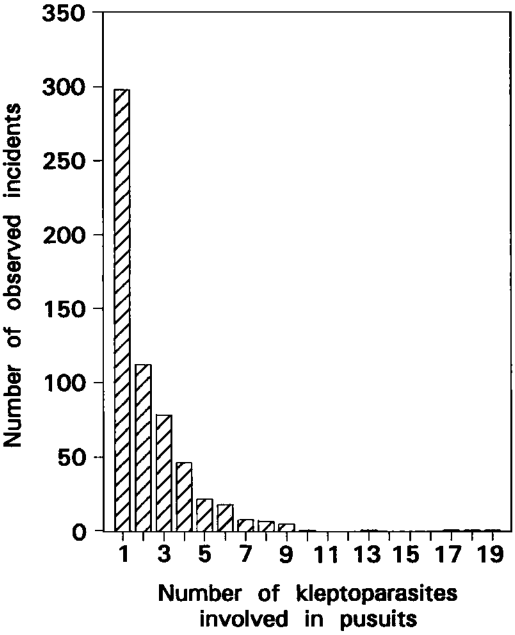

Fig. 2. Frequency distribution of singleton and group kleptoparasitic pursuits by Kelp Gulls at study sites.

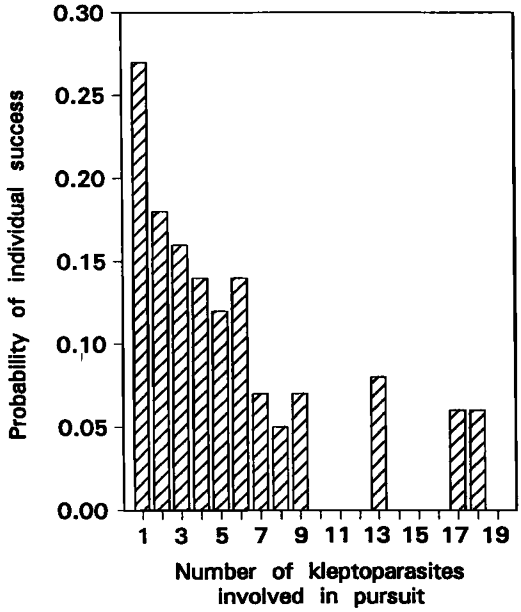

Fig. 1. Probability of individual Kelp Gull kleptoparasite successfully gaining prey item in relation to number of kleptoparasites involved in pursuit (n = 671).

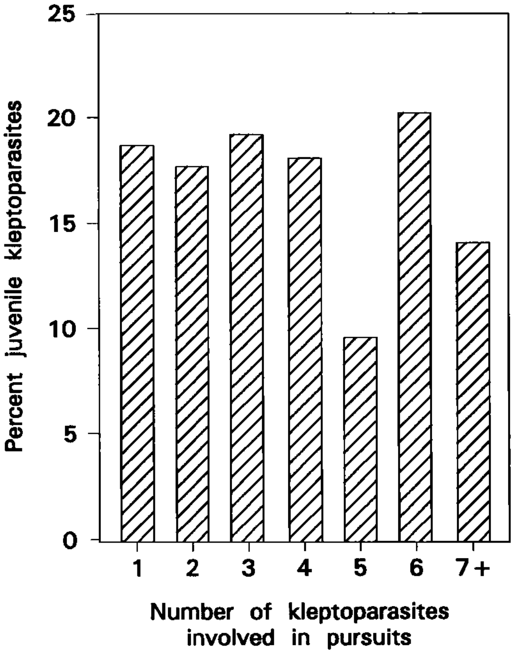

Fig. 3. Proportion of juvenile Kelp Gulls involved in group kleptoparasitic pursuits.

TABLE 5. Frequency and success of Kelp Gull kleptoparasitic activity by age class.

	Undisturbed		Food-supplemented	
	OB	SMB	HB	SD
Adult				
Mean no. at site (percent of population)	20.7 (88.4)	20.6 (83.5)	150 (61.8)	403 (73.9)
No. observed as kleptoparasites (percent of all kleptoparasitic attacks at site)	0 (0)	46 (48.9)	50 (29.2)	586 (60.7)
Percent success as kleptoparasite	—	28.3	14.0	15.7
No. observed as host (percent of hosts)	1 (100.0)	71 (89.9)	14 (38.9)	181 (69.6)
Percent of hosts retain prey	100.0	71.8	57.1	60.2
Subadult				
Mean no. at site (percent of population)	1.9 (8.2)	2.4 (9.7)	42.3 (17.4)	73.7 (13.5)
No. observed as kleptoparasites (percent of all kleptoparasitic attacks at site)	0 (0)	12 (12.8)	48 (28.1)	218 (22.6)
Percent success as kleptoparasite	—	33.3	20.8	10.1
No. observed as host (percent of hosts)	0 (0)	5 (6.3)	6 (16.7)	46 (17.7)
Percent of hosts retain prey	—	60.0	50.0	63.0
Juvenile				
Mean no. at site (percent of population)	0.8 (3.4)	1.7 (6.8)	50.5 (20.8)	68.8 (12.6)
No. observed as kleptoparasites (percent of all kleptoparasitic attacks at site)	1 (100)	36 (38.3)	73 (42.7)	162 (16.8)
Percent success as kleptoparasite	0	19.4	12.3	16.1
No. observed as host (percent of hosts)	0 (0)	3 (3.8)	16 (44.4)	33 (12.7)
Percent hosts retain prey	—	33.3	68.7	63.6

Combining data from all study sites, group pursuits on average lasted significantly longer (8.5 ± 10.2 s, $n = 121$) than chases by single gulls (4.8 ± 7.9 s, $n = 96$; $t = 2.93$, df = 215, $P < 0.01$). The average durations of successful and unsuccessful pursuits were not significantly different in either group or singleton pursuits (t-test).

Gull age.—At all sites where intraspecific kleptoparasitism among Kelp Gulls occurred often, the rate of attempted kleptoparasitism, by age class, was significantly different from that expected from the age structure of the population (SD, $X^2 = 353.9$; HB, $X^2 = 26.9$; SMB, $X^2 = 151.3$; all $P < 0.01$; Table 5). Juvenile Kelp Gulls kleptoparasitized conspecifics more frequently than expected given their abundance in the population (SD, $X^2 = 37.9$; HB, $X^2 = 13.1$; SMB, $X^2 = 9.0$; all $P < 0.01$).

Adult Kelp Gulls never were observed attempting intraspecific kleptoparasitism at Olifantsbos Bay and, at all other sites, adults attempted intraspecific kleptoparasitism significantly less often than expected (SD, $X^2 = 311.2$; HB, $X^2 = 37.6$; SMB, $X^2 = 16.1$; all $P < 0.01$). Subadults generally were involved in kleptoparasitic incidents in proportion to their relative abundance in the population (Table 5).

During food-choice experiments, kleptoparasitism was significantly asymmetrically distributed among age classes of Kelp Gull ($X^2 = 32.7$, $P < 0.01$). Juveniles constituted 28.5% of all Kelp Gulls present ($n = 105$ counts), but accounted for 53.3% of kleptoparasitic pursuits. In contrast, 53.5% of Kelp Gulls present were adults, but these accounted for only 38.1% of kleptoparasitic attacks.

Although juvenile Kelp Gulls attempted kleptoparasitism more often than expected, we found no differences among age classes either in their success at stealing food ($X^2 = 1.4$, ns) or at retaining prey during a kleptoparasitic attack ($X^2 = 1.2$, ns; Table 5).

CONTROL OF INTRASPECIFIC KLEPTOPARASITISM

Model I indicates that individual rewards for Kelp Gulls at Strandfontein dump employing a mixed foraging strategy are greatest when a small proportion of the available time is allocated to kleptoparasitism (Fig. 4). The stable composition for flocks of Kelp Gulls at Strandfontein dump comprising individuals following one of two foraging strategies, kleptoparasitism and scavenging (Model II), is calculated in Table 6. Although simplistic, this calculation

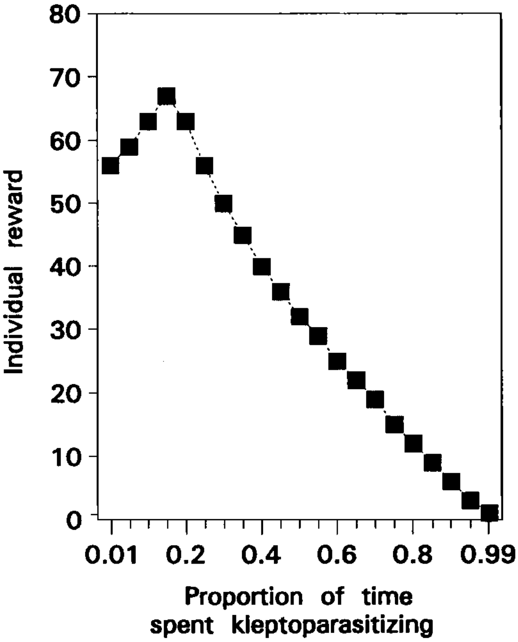

Fig. 4. Average equivalent number of food items consumed per hour (individual reward) by individual Kelp Gulls at Strandfontein dump for different kleptoparasitism frequencies.

demonstrates that in any flock the number of individuals obtaining food solely through intraspecific kleptoparasitism represents a very small proportion of that flock.

For example, in a flock of 13 gulls where all individuals are scavengers and do not resort to kleptoparasitism, each gull will gain the equivalent of 55.2 average-sized food items per hour. If one of these gulls changed foraging strategy and became a kleptoparasite, it would improve its hourly reward to the equivalent of 58.0 average-sized food items. However, if a second gull also became a kleptoparasite, the two kleptoparasites would each only gain the equivalent of 26.6 average-sized food items per hour. As this is less than the hourly reward of a scavenging gull, it would not benefit the second gull to become a kleptoparasite. Therefore, a flock of 13 gulls would be stable when 12 of the gulls are scavengers and only 1 a kleptoparasite.

DISCUSSION

Factors influencing rate and success of kleptoparasitism.—Prey characteristics are important in determining both the rate and success of intraspecific kleptoparasitism among Kelp Gulls. Prey cannot be stolen if their handling time is less than the time needed for a kleptoparasitic attack (Barnard and Thompson 1985). At Olifantsbos Bay, where Kelp Gulls fed on small invertebrates with handling times of less than 1 s, kleptoparasitism rarely was possible. Large prey take longer to handle than small prey, and gulls preferentially selected small, rapidly handled prey that had a concomitantly low probability of being stolen (Table 2).

Studies of a range of kleptoparasitic interactions have shown that increasing prey size and handling time increase both the rate (Hopkins and Wiley 1972, Fuchs 1977, Fischer 1985, Hackl and Burger 1988, Hockey and Steele 1990, Burger and Gochfeld 1991) and success (Gochfeld and Burger 1981, Barnard and Thompson 1985, Hackl and Burger 1988, Hockey and Steele 1990) of kleptoparasitism. However, both Dunn (1973) and Fuchs (1977) found that kleptoparasitic success among terns (*Sterna* spp.) was inversely related to prey size, and attributed this to increased host vigilance when carrying large prey. Prey size was positively related to kleptoparasitic success among Kelp Gulls in the southwestern Cape.

While the rate of kleptoparasitism may decrease as food availability increases (Dunn 1973), it has been suggested that hosts may give up food more readily when food is abundant (Birt and Cairns 1987). This is supported by the results of our study, where high kleptoparasitic success rates were recorded at the two sites where food availability was high (Table 1). Although the success of kleptoparasitic attempts at 16 Mile Beach (where large *Donax* were captured infrequently) was even higher (Table 1), almost certainly this was a consequence of the prey-handling technique, where the gulls lose direct contact with their prey when mussels are dropped to break them open. The risks to the host attending this prey-handling technique are directly proportional to the number of times the shell has to be dropped before it breaks (Hockey and Steele 1990). Kleptoparasitism under these conditions is a very different behavior than when the parasite is "chasing" or "food snatching." However, certain preconditions apply to all of these behaviors, in particular the availability of hosts and the opportunity to the kleptoparasites. Thus, we have treated all forms of intraspecific kleptoparasitism as falling along a behavioral continuum.

TABLE 6. Calculated average reward for individual kleptoparasites (in terms of number of equivalent mean-sized food items consumed per hour) in different-sized flocks of foraging Kelp Gulls at Strandfontein dump, comprising scavengers and kleptoparasites. Individual reward for scavengers is 55.2 (see Appendix 2). Stable composition for each flock (i.e. the point at which no individual can improve its rate of food consumption by changing foraging strategy) is given in bold.

Flock size	Number of kleptoparasites									
	1	2	3	4	5	6	7	8	9	10
2	4.8									
3	9.7	2.4								
4	14.5	4.8	1.6							
5	19.3	7.2	3.2	1.2						
6	24.2	9.7	4.8	2.4	1.0					
7	29.0	12.1	6.4	3.6	1.9	0.8				
8	33.8	14.5	8.1	4.8	2.9	1.6	0.7			
9	38.6	16.9	9.7	6.0	3.9	2.4	1.4	0.6		
10	43.5	19.3	11.3	7.2	4.8	3.2	2.1	1.2	0.5	
11	48.3	21.7	12.9	8.5	5.8	4.0	2.8	1.8	1.1	0.5
12	53.2	24.2	14.5	9.7	6.8	4.8	3.5	2.4	1.6	1.0
13	**58.0**	26.6	16.1	10.9	7.7	5.6	4.1	3.0	2.1	1.4
14	**62.8**	29.0	17.7	12.1	8.7	6.4	4.8	3.6	2.7	1.9
15	**67.6**	31.4	19.3	13.3	9.7	7.2	5.5	4.2	3.2	2.4
16	**72.5**	33.8	20.9	14.5	10.6	8.1	6.2	4.8	3.8	2.9
17	**77.3**	36.2	22.5	15.7	11.6	8.9	6.9	5.4	4.3	3.4
18	**82.1**	38.6	24.2	16.9	12.6	9.7	7.6	6.0	4.8	3.9
19	**86.9**	41.1	25.8	18.1	13.5	10.5	8.3	6.6	5.4	4.3
20	**91.8**	43.5	27.4	19.3	14.5	11.3	9.0	7.2	5.9	4.8
25	115.9	**55.5**	35.4	25.4	19.3	15.3	12.4	10.3	8.6	7.2
30	140.1	**67.6**	43.5	31.4	24.2	19.3	15.9	13.3	11.3	9.7
35	164.2	**79.7**	51.5	37.4	29.0	23.3	19.3	16.3	14.0	12.1
40	188.4	91.8	**59.6**	43.5	33.8	27.4	22.8	19.3	16.6	14.5
45	212.5	103.8	**67.6**	49.5	38.6	31.4	26.2	22.3	19.3	16.9
50	236.7	115.9	75.7	**55.5**	43.5	35.4	29.7	25.4	22.0	19.3
55	260.8	128.0	83.7	**61.6**	48.3	39.4	33.1	28.4	24.7	21.7
60	285.0	140.1	91.8	**67.6**	53.1	43.5	36.6	31.4	27.4	24.2
65	309.1	152.1	99.8	73.7	**58.0**	47.5	40.0	34.4	30.1	26.6
70	333.3	164.2	107.9	79.7	**62.8**	51.5	43.5	37.4	32.7	29.0
75	357.4	176.3	115.9	85.7	67.6	**55.5**	46.9	40.5	35.4	31.4
80	381.6	188.4	124.0	91.8	72.5	**59.6**	50.4	43.5	38.1	33.8
85	405.7	200.4	132.0	97.8	77.3	**63.6**	53.8	46.5	40.8	36.2
90	429.9	212.5	140.1	103.8	82.1	67.6	**57.3**	49.5	43.5	38.6
95	454.0	224.6	148.1	109.9	86.9	71.6	**60.7**	52.5	46.2	41.1
100	478.2	236.7	156.2	115.9	91.8	75.7	64.2	**55.5**	48.8	43.5

An increase in the rate of kleptoparasitism with increasing spacing of prey (Table 4) appears initially to be counterintuitive. However, Kelp Gulls apparently were better able to judge the amount of available food remaining when prey were dispersed. As prey abundance decreased, newly arrived gulls resorted to kleptoparasitism in order to obtain some of the few remaining prey. When fishes were presented in a single pile, a dense crowd of fighting gulls immediately formed over the food and approaching gulls joined this crowd, which persisted for some time after all the food was taken, rather than attempting to kleptoparasitize birds leaving the area with fish.

Krebs and Barnard (1980) suggested that the rate of kleptoparasitism should increase with population density. Barash et al. (1975) found that gulls modified their prey-handling technique as gull density increased, apparently to limit prey loss through kleptoparasitism. In our study the rate of kleptoparasitism was highest at 16 Mile Beach, where gull density was lowest (Table 1); however, we did not set out specifically to test this relationship. While the density of gulls foraging at a site is likely to have a marked effect on the rate of kleptoparasitism within a population, prey abundance and handling time probably are of greater importance.

Prey loss by hosts through kleptoparasitism has been correlated with the number of kleptoparasites involved in the pursuit (Hatch 1970, 1975, Barnard and Thompson 1985, Hackl and Burger 1988), although the probability of an individual kleptoparasite gaining food decreases as the number of pursuers increases (Hatch 1970, 1975; Fig. 1), accounting for the relatively low frequency of group pursuits (Fig. 2).

Our findings support conclusions of several prior studies of both inter- and intraspecific kleptoparasitism that a suite of factors influence the rate and success of this behavior. These factors include characteristics of both prey items and the gull population. Although the rate of kleptoparasitism at most sites generally is low, the risk of food loss through kleptoparasitism is sufficiently great to influence food choice by gulls.

Mechanisms controlling the rate of intraspecific kleptoparasitism.—There has been debate regarding the efficacy of kleptoparasitism as a foraging technique, and it has been suggested that kleptoparasitism is a less efficient means of gaining food than is hunting (e.g. Furness 1977, Kushlan 1978, 1979, LeBaron and Heppner 1985). However, Ens et al. (1990) have shown that, for Eurasian Curlews (*Numenius arquata*) on mudflats in the Netherlands, kleptoparasitism is a profitable form of foraging, despite the low proportion of success. Similarly, Dunbrack (1979) concluded that, contrary to Kushlan's (1978) findings, kleptoparasitism was profitable in terms of prey returns for Great Egrets (*Casmerodius albus*) foraging in Florida.

The results generated by Model I indicate that kleptoparasitism can be an efficient method of foraging, and that the inclusion of a low rate of kleptoparasitism in a gull's foraging repertoire can raise its food intake rate above that achieved by scavenging alone. Based on manipulation of parameter values in Model I (see Appendix 1), the key condition producing this result is that the prey items obtained through kleptoparasitism must, on average, be larger than those obtained by scavenging. If individuals were to obtain the same-sized food items through kleptoparasitism and scavenging, then kleptoparasitism would always reduce the individual reward to the kleptoparasite and, thus, would not be a viable foraging technique. However, because successful kleptoparasites gain larger than average-sized food items, low rates of kleptoparasitism can enhance the rate of food intake.

Although intraspecific kleptoparasitism is a functional parallel of the interspecific behavior (Brockmann and Barnard 1979), it presents a more complex situation. Intraspecific kleptoparasitism may be an efficient foraging technique for some species in some situations, but not all individuals within a flock can resort to intraspecific kleptoparasitism, except at very low frequencies. Obviously, some individuals within the population must hunt in order to provide the resource base on which the kleptoparasitic behavior depends.

The results of Model II give an indication of how few obligate intraspecific kleptoparasites a Kelp Gull flock can support. The average group of 30 Kelp Gulls actively foraging at Strandfontein dump would be able to support a maximum of only 2 obligate kleptoparasites (Table 6). However, it was clear from field observations that more than two individuals were responsible for the kleptoparasitizing of conspecifics.

Field observations and experimental studies of age-related kleptoparasitism among Kelp Gulls indicate that the frequency with which this technique is used to obtain prey decreases with age and, thus, is not an individually fixed, obligate trait. This is supported by the empirically based models: the stable ratio of obligate scroungers to obligate producers predicted by Model II is too low to accord with the number of birds observed kleptoparasitizing in the field.

Among Bald Eagles (*Haliaeetus leucocephalus*), populationwide frequencies of intraspecific kleptoparasitism and hunting are balanced at the evolutionarily stable strategy (ESS) point (sensu Maynard-Smith and Parker 1976), such that the rewards accrued through each strategy are nearly equal (Hansen 1986). This situation is the evolutionarily stable population strategy described by Treisman (1977). Similarly, the populationwide rate of intraspecific kleptoparasitism that maximizes the rate of food intake for Kelp Gulls foraging at Strandfontein dump, as shown in Model I, would be an evolutionarily stable population strategy. Every gull in the flock would not have to allocate 15% of its available foraging time to kleptoparasitism in order to maximize individual rate of food intake (Fig. 4), but the overall average food intake rate would be maximized when the populationwide average percent of available time allotted to kleptoparasitism was about 15%.

Studies of several gull species have shown that juveniles are less efficient at hunting than adults at both natural (e.g. Searcy 1978, Greig et al. 1983, Maron 1983, Hockey et al. 1989) and supplemented feeding sites (e.g. Verbeek 1977a, 1977b, Maclean 1986). In many cases, juvenile gulls also have been shown to be less efficient at kleptoparasitism than adults (Burger and Gochfeld 1979, 1981, Carrol and Cramer 1985, Hesp and Barnard 1989, Hockey et al. 1989). Juvenile Kelp Gulls in our study, however, were as efficient at kleptoparasitism (both in effecting it and avoiding it) as were adults; similar results have been reported by Verbeek (1977c) and Hackl and Burger (1988). Thus, it is predictable that juvenile Kelp Gulls should use intraspecific kleptoparasitism in order to exploit the greater hunting capabilities of the adults, and should resort to kleptoparasitism more often than adults (see also Pettitt 1953, Burger and Gochfeld 1979). Juvenile gulls beg from, and are fed by, their parents for a short period after fledging (e.g. Burger 1981, Holley 1982). Intraspecific kleptoparasitic behavior may develop from this begging behavior, particularly at the time when adults stop feeding the juveniles.

The observation that inefficient hunters (juveniles) rely more heavily on intraspecific kleptoparasitism than experienced, older birds has a counterintuitive corollary that older birds do not exert their presumed dominance by stealing from young birds. Among Eurasian Oystercatchers (*Haematopus ostralegus*), the amount of food gained by kleptoparasitism increases with dominance status (Ens and Goss-Custard 1984). However, young oystercatchers when they first arrive on the nonbreeding grounds obtain more of their food by kleptoparasitism (directed both at other juveniles and adults) than do adults (Gross-Custard and dit Durell 1987). The frequency of this behavior subsequently decreases because of the establishment of dominance hierarchies, and remains low for several years (Goss-Custard and dit Durell 1987). Comparable effects of dominance are not evident among Kelp Gulls; older birds initiate fewer attacks than younger birds (Hockey and Steele 1990, current study). However, a larger than expected proportion of all attacks are directed at juveniles and subadults. This suggests that if dominance influences kleptoparasitic behavior in Kelp Gulls, as clearly is the case in Eurasian Oystercatchers, it functions through dominant birds being targeted less often for attack rather than using their dominance to initiate attacks.

Dominance hierarchies exist in gulls (e.g. Monaghan 1980), but whether generalizations can be made between species is debatable. Adult Herring Gulls (*L. argentatus*) in northeastern England use supplementary feeding sites, such as dumps, more often than juveniles. These apparently are preferred feeding sites for adult males, which dominate adult females and juveniles, and are able to relegate the latter to less preferred sites (Monaghan 1980). Among Kelp Gulls in both South Africa and Chile, it is juveniles that aggregate disproportionately at such feeding sites (Hockey and Steele 1990). This suggests either that higher-quality food was available at the English refuse dumps than at those studied in South Africa and Chile, or that dominance hierarchies in the two species operate differently.

Kelp Gulls kleptoparasitize interspecifically, as well as intraspecifically, stealing food from a variety of species, including other gulls and African Black Oystercatchers (*H. moquini*; e.g. Hockey 1980). While the physical act of food stealing might be similar, independent of the host species, inter- and intraspecific kleptoparasitism may not have the same evolutionary origins. Although the opportunities for kleptoparasitism always are limited by host availability, intraspecific kleptoparasitism is further constrained by an additional feedback loop. Time spent in kleptoparasitism can be equated with lost hunting time, thereby reducing the overall availability of prey that can be stolen. Thus, it is incorrect to view intraspecific kleptoparasitism as simply an extension of the interspecific behavior.

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APPENDIX 1. Parameters, assumptions, and calculations used to model individual reward for Kelp Gulls at Strandfontein dump, at varying rates of kleptoparasitism. Individual reward expressed as number of food items, standardized to average size consumed per hour.

Parameters.—Mean food-handling time (TH) = 3.8 ± 11.9 s ($n = 40$); mean interval between food items during scavenging (including TH) = 59.8 ± 47.8 s ($n = 133$). Therefore, mean food intake rate during scavenging (FR) = 60 items/h. Mean kleptoparasitic pursuit time (TP) = 8.3 ± 11.4 s ($n = 138$). Mean food length during scavenging = 32 ± 27 mm ($n = 165$); mean length of food items successfully kleptoparasitized = 75 ± 52 mm ($n = 68$). Therefore, mean length of food items lost to kleptoparasitism, relative to mean food size and expressed as a proportion (K) = 2.3. Proportion of successful kleptoparasites during both group and singleton pursuits (KS) = 0.14. Proportion of available foraging time allocated to scavenging (Q) = variable (between 1.00 and 0.01). The proportion of available foraging time allocated to kleptoparasitism (P) = variable (between 0 and 0.99).

Assumptions.—(1) Number of Kelp Gulls in flock able to interact with each other (N) = 100; (2) 25% of all food items found during scavenging are large enough to warrant kleptoparasitic attempt; (3) all Kelp Gulls in flock follow same foraging "strategy" and kleptoparasitize at same rate.

Calculations.—Value 1: Food items found during scavenging = ($QM \cdot FR$). Value 2: Food items lost to kleptoparasites = ($Q \cdot FR \cdot 0.25 \cdot KS \cdot K$). Value 3: Food items consumed by individual during scavenging = (Value 1 − Value 2). Value 4: Maximum number of kleptoparasitic pursuits possible per hour = $P/[TP + (KS \cdot TH)]$. Value 5: Number of food items available to be kleptoparasitized = $(N \cdot Q \cdot FR \cdot 0.25)/(N \cdot P)$. Value 6: Actual number of kleptoparasitic pursuits possible = Value 5 up to, but not exceeding, Value 4. Value 7: Number of successful kleptoparasitic attempts = Value 6·KS. Total food intake = (Value 7·K) + Value 3.

APPENDIX 2. Parameters, assumptions, and calculations used to model stable composition of different sized flocks of foraging Kelp Gulls at Strandfontein dump, which are comprised of obligate scavengers and obligate kleptoparasites. Stable point is that at which no individual can improve its rate of food intake per hour by changing foraging strategy.

Parameters.—Mean interval between food items during scavenging (including food handling time) = 59.8 ± 47.8 s ($n = 133$). Therefore, mean food intake rate during scavenging (FR) = 60 items/h. Mean food length during scavenging = 32 ± 27 mm ($n = 165$); mean length of food items successfully kleptoparasitized = 75 ± 52 mm ($n = 68$). Therefore, mean length of food items lost to kleptoparasitism relative to mean food size expressed as a proportion (K) = 2.3. Proportion of successful kleptoparasites during both group and singleton pursuits (KS) = 0.14; number of kleptoparasites in flock (P) = variable (between 1 and 10); number of scavengers in flock (Q) = variable (between 1 and 99).

Assumption.—Of all food items found during scavenging, 25% are large enough to warrant a kleptoparasitic attempt.

Calculations.—Individual kleptoparasite reward (Y) = $(Q \cdot FR \cdot 0.25 \cdot KS \cdot K)/P$; individual scavenger reward = $[(Q \cdot FR) - (Y \cdot P)]/Q$.

Thus, individual scavengers gain equivalent of 55.2 mean-sized food items. Therefore, unless kleptoparasites gain more than this amount it would benefit them to change strategy to become scavengers.