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FORAGING EFFICIENCY IN GULLS: A CONGENERIC COMPARISON OF AGE DIFFERENCES IN EFFICIENCY AND AGE OF MATURITY

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ABSTRACT.—I studied feeding efficiency in 15 species of gulls in North America, Africa, Australia, and Europe in different feeding situations and habitats to test the hypotheses that (1) foraging efficiency increases with age, and that (2) the disparity between young and adults is greater in species with the most delayed maturity. Efficiency was measured by timing the interfood interval (time between successful food captures) for actively feeding individuals. Regression analysis indicated that the variance in the interval was explained by species, age, food type, method, and habitat. Adult interfood intervals were shorter than those of young for all species in all but 5 feeding situations. In general, the disparity between adult and young was greater for the large gulls, supporting the hypothesized relationship between deferred maturity and foraging efficiency of gulls.

All birds are faced with the task of finding food resources to provide adequate food for themselves throughout the year, and for developing young during the breeding season. Foraging theory suggests that birds should concentrate their foraging efforts where there is abundant, easily obtained, high quality food (Schoener 1971, Krebs et al. 1981). For most seabirds, food is patchily distributed, distant, and ephemeral (Ashmole 1963, Diamond 1984). Seabirds have some of the largest foraging ranges of any vertebrate (Dunnet and Ollason 1982, Duffy 1983, Ainley et al. 1984). Further, many seabirds forage primarily by plunge-diving for food, a difficult task for young to perfect (Ashmole 1971). The difficulties of learning where to forage and how to plunge-dive are reflected in age-related differences in foraging: young are significantly less efficient in many aspects of foraging behavior (Orians 1969, Searcy 1978). Age-related differences in feeding ability have been noted for seabirds such as gulls *Larus* (Verbeek 1977, Ingolfsson and Estrella 1978, Searcy 1978, Ulfstrand 1979, Burger and Gochfeld 1981, 1983; MacLean 1986), terns *Sterna* (Dunn 1972, Buckley and Buckley 1974), pelicans *Pelecanus occidentalis* (Orians 1969), frigatebirds *Fregata magnificens* (Gochfeld and Burger 1981), and cormorants *Phalacrocorax olivaceus* (Morrison et al. 1978). In all cases adults had lower interfood intervals, higher foraging success, spent less time foraging for, obtaining, and handling food items, foraged for less of the day than young, or exhibited a combination of these factors. These age-related differences have been cited as a cause for delayed maturity in seabirds, many species of which do not breed until their fourth year or later (Lack 1967, Ryder 1980).

Although many groups of seabirds have diets mainly limited to fish or other pelagic organisms, the *Larus* gulls have diversified in foraging method and habitat. Gulls forage in a variety of habitats from wet fields to the open ocean, and employ a variety of feeding methods appropriate to habitat and prey type (Hunt and Hunt 1973, Mudge and Ferns 1982). Further, they exhibit species-related differences in maturation from species that start to breed in their second year to those that breed in their fourth or even fifth year (Dwight 1925). Thus, gulls provide an excellent opportunity to study species, habitat, method, and age-related differences in foraging behavior among congenerics, and I do so in this paper. I use the interfood interval as an index of foraging efficiency, defining it for an actively foraging bird as the time between obtaining one item and obtaining a second food item.

Based on optimal foraging theory and the variability of gulls in size, age of sexual maturity, feeding methods, and prey items, I made the following predictions.

1. For all foraging situations and prey items adults should have shorter interfood intervals than young (see references above).
2. The ratio of young to adult interfood interval should increase with increasing difficulty of the task as measured by adult interfood interval (see Burger and Gochfeld 1983).
3. The ratio of young to adult interfood interval should relate directly to size and age of sexual maturity. That is, gulls that do not breed until they are four or five years old should exhibit a greater age-related difference in interfood interval than those breeding in their second year.

I tested these hypotheses by examining the interfood intervals of 15 species of gulls foraging in a variety of habitats in North America, South America, Europe and Australia. Table 1 lists the species examined with their scientific names.

METHODS

From 1977 to 1985, I collected data on interfood intervals on gulls wherever and whenever there was a

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TABLE 1
DATA SETS, BODY LENGTH AND AGE OF FIRST BREEDING FOR *LARUS* GULLS STUDIED (1977–1985)

Gull species	Scientific name[a]	Number of data sets[b]	Mean length (cm)[c]	Age at first breeding[c,d] (year)
Heermann's	*Larus heermanni*	3	46–53	3
Ring-billed	*L. delawarensis*	12	45–53	3
Mew[d]	*L. canus brachyrhynchus*	11	40–46	3
Common[d]	*L. c. canus*	3	40–46	3
Herring	*L. argentatus*	21	56–66	4
California	*L. californicus*	1	51–58	3–4
Western	*L. occidentalis*	11	61–68	4
Kelp	*L. dominicanus*	1	58	4
Great Black-backed	*L. marinus*	2	71–79	4–5
Glaucous-winged	*L. glaucescens*	8	61–68	4
Laughing	*L. atricilla*	6	38–43	3
Grey-headed	*L. cirrocephalus*	2	41–43	3
Silver	*L. novaehollandiae*	1	38–43	2
Black-headed	*L. ridibundus*	8	38–43	2
Bonaparte's	*L. philadelphia*	9	33–36	2
Black-legged Kittiwake	*Rissa tridactyla*	7	39–46	2

[a] Order follows Morony et al. 1975.
[b] A data set usually consists of at least 20 interfood intervals each for adults and young of the year.
[c] From Harrison 1983, 2 years = 27–28 months old, 3 = 39–40 months old, 4 = 51–52 months old.
[d] Common and Mew are conspecific, but have non-contiguous ranges.

group including adults and young. The study was primarily coastal and did not involve observations from large, offshore vessels. Data were collected on all actively foraging gulls encountered whenever the flock met the following criteria: there were at least 20 individuals each of adults and young foraging at close range so food items could be identified, and success determined. Data were collected from 1977 through 1985 in the following locations for the following species: Heermann's (California, USA), Ring-billed (California, Texas, and New Jersey, USA; Alberta, Canada), Mew (=Common, California and Alaska, USA), Herring (Slimbridge, England; Ekkeroy, Norway; Leningrad, Tbilisi, and Baku, USSR), California and Western (California, USA), Kelp (Durban, South Africa), Great Black-backed (New Jersey, USA), Glaucous-winged (California and Alaska, USA), Laughing (New Jersey, Texas, USA), Grey-headed (Naivasha, Kenya), Silver (Brisbane, Australia), Black-headed (Guayaquil, Ecuador; Naivasha, Kenya; Moscow and Leningrad, USSR; Slimbridge, England), Bonaparte's (California, Alaska and New Jersey, USA; Alberta, Canada), Black-legged Kittiwake (Ekkeroy, Norway; Alaska, USA).

Data collected at each field site included: place, date, time, habitat, species, feeding method, and food. Habitat types included ocean, bay, mudflat, pond, lake, river and field. Food types included natural foods such as midges (Chironomidae), other insects, fish, worms, crabs, and other invertebrates, and man-made food such as offal (e.g., fish parts from canneries) and garbage. Except for small invertebrates picked from the water's surface, the food type could be easily identified. Feeding methods (modified after Ashmole and Ashmole 1967, Ashmole 1971) included surface-diving, plunge-diving, picking up items from the ground, piracy, aerial dip, surface dip and jump dive. Dipping could thus occur by flying or hovering above the water, or by swimming and dipping with the head down. If a bird flew up 20 to 50 cm and dove into the water it was called a jump dive. "Adult" was defined as adult-plumaged birds with all white tails, and "young" was defined as birds that were less than one year old (i.e., had hatched the last breeding season). The few birds in intermediate age classes were excluded from this paper.

In almost all cases a data set includes data on twenty adults and twenty young of one species. If feeding ceased during the observation period the data set might have fewer observations. On a randomly chosen individual, I recorded the interfood interval to be used as a measure of foraging ability. The interfood interval is the time between first obtaining a food item and successfully obtaining a second food item. I then switched to another individual, alternating adult and young when possible.

During the study I recorded interfood intervals for 4502 birds in 106 data sets (Table 1). Most species were examined from more than one location (see above) and habitat. Table 1 also lists the mean length of gulls and the usual age of first breeding.

I used stepwise multiple regression model procedures to determine the factors that should be entered in the model contributing to explaining the variance in interfood intervals. Ordinal variables could be analyzed without transformation. For each non-ordinal variable, I created a new variable which compared the dependent measures at each variable value against all other variable values, examining each value in turn. Thus for age of maturity, those that mature at 2 years of age were compared to those maturing at all other ages; then those that mature at 3 years were compared to all others, and so on. If any one of the values was significant it was entered in the model (see Burger et al. 1984). The stepwise procedure first selects the variable that contributes the most to the coefficient of determination (R^2), and then selects the second variable

TABLE 2

REGRESSION MODELS FOR INDIVIDUAL SPECIES EXPLAINING VARIATION IN INTERFOOD INTERVALS FOR A VARIETY OF FEEDING SITUATIONS

	Model				Factors entering models			
Species	F	R^2	df	*P*	Method	Food	Habitat	Age
All Species[a]	61.5	0.70	126,4376	0.0001	53.9 (0.0001)	291.4 (0.0001)	15.7 (0.0001)	37.9 (0.0001)
Heermann's	23.9	0.51	2,46	0.0001	29.3 (0.0001)	—	—	18.6 (0.0001)
Ring-billed	29.3	0.44	13,419	0.0001	24.0 (0.0001)	23.0 (0.0001)	14.6 (0.0001)	29.5 (0.0001)
Mew	32.9	0.50	15,500	0.0001	13.5 (0.0001)	75.9 (0.0001)	8.81 (0.003)	28.4 (0.0001)
Common	26.1	0.59	4,73	0.0001	33.3 (0.0001)	5.73 (0.01)	—	32.3 (0.0001)
Herring	25.9	0.51	24,599	0.0001	26.6 (0.0001)	55.8 (0.0001)	7.62 (0.0001)	39.11 (0.0001)
California	2.41	0.09	2,51	NS				
Western	25.8	0.45	14,439	0.0001	16.8 (0.0001)	45.6 (0.0001)	39.8 (0.0001)	—
Kelp	9.84	0.40	2,14	0.0001	—	—	—	9.84 (0.001)
Great Black-backed	0.18	0.01	1,14	NS				
Glaucous-winged	13.6	0.40	9,184	0.0001	20.2 (0.0001)	—	—	8.13 (0.0001)
Laughing	13.7	0.32	5,144	0.0001	—	32.9 (0.0001)	—	—
Grey-headed	16.8	0.48	3,59	0.0004	—	—	—	16.8 (0.0004)
Silver	37.83	0.63	2,35	0.0001	31.7 (0.0001)	—	—	44.2 (0.0001)
Black-headed	48.2	0.62	8,23	0.0001	36.5 (0.0001)	120.8 (0.0001)	—	16.5 (0.0001)
Bonaparte's	15.7	0.33	9,291	0.0001	25.3 (0.0001)	15.9 (0.0001)	—	10.7 (0.001)
Black-legged Kittiwake	43.1	0.57	8,257	0.0001	22.0 (0.0001)	—	—	3.02 (0.05)

[a] For this model, species ($F = 86.2$, $P < 0.0001$), foraging plane ($F = 2.26$, $P < 0.05$), and species × age ($F = 70.7$, $P < 0.0001$) also entered the model.

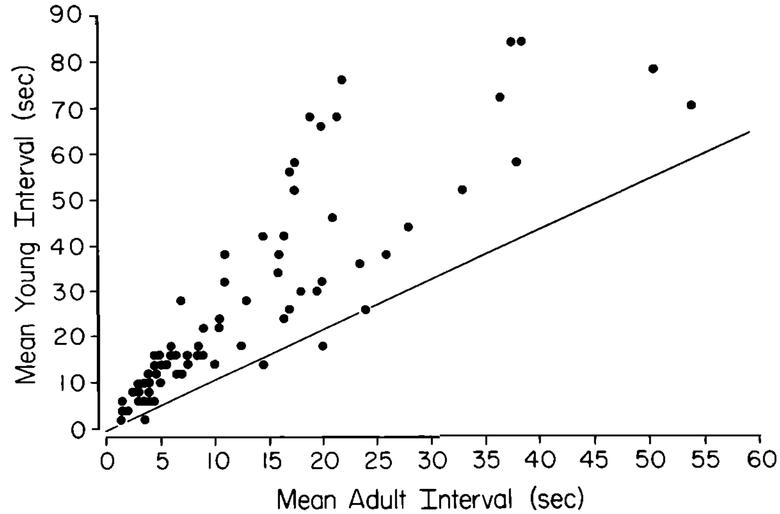

FIGURE 1. Relationship of mean interfood interval of young to mean interfood interval of adult gulls. Shown also is the line of equivalency where the mean interval for adults = the mean interval for young.

that gives the greatest increase in R^2. This procedure continues until all variables not included are not statistically significant ($P > 0.05$). If variables are highly correlated, only the one giving the highest R^2 is added. The model selection process determines the "best" model, gives the R^2 values and levels of significance for the model as well as for each contributing factor. I used Kruskal-Wallis χ^2 tests to determine significant differences in interfood interval as a function of age for each data set. I used analyses of variance to determine differences among classes of variables. All tests were performed on log-transformed data.

RESULTS

Factors Influencing Foraging Efficiency

I used multiple regression techniques to determine the factors influencing the variability in interfood interval (see methods). Over 60% of the variance in interfood interval for the 4502 individuals examined in this study was explained by (in order of contribution): food type, species, species × age, foraging method, age, habitat, and foraging plane (Table 2). Thus, food type was more important than species in explaining the variance in the interfood interval (see below).

I then examined the relative contribution of the variables to the variance in interfood interval for each species (Table 2). For all species except California and Great Black-backed gulls, the models explained a significant amount of the variation in interfood interval. This may be due to having only one and two data sets for the latter two species, respectively (thus there could be only one or two differences in the class variables such as method, food type and habitat).

The models indicate several things: (1) Between 30 and 60% of the variability in interfood interval was explained by the models. (2) Age was a significant factor for 12 of the 13 significant species models, but did not enter for Laughing Gull. (3) Method, food, and habitat entered fewer

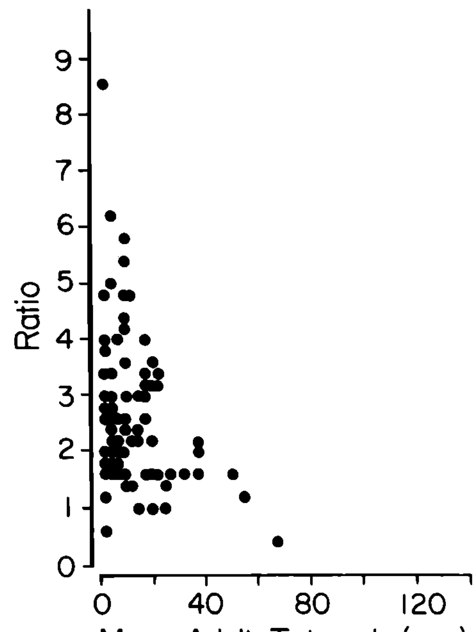

FIGURE 2. Relationship of rate of mean young and mean adult interfood interval to mean adult gull interfood interval for each of 106 data sets.

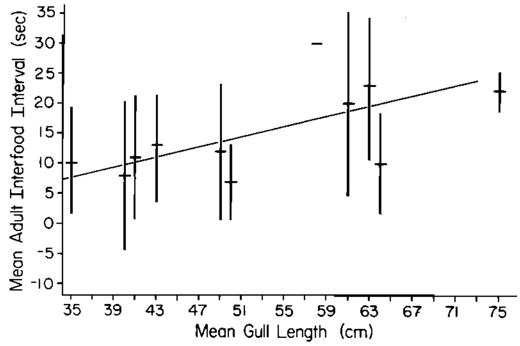

FIGURE 3. Relationship of mean interfood interval to mean body length for gulls.

of the significant models. Thus, for most species, age was one of the most important contributors to explaining variation in the interfood interval.

Effect of Age on Interfood Interval

Adults had significantly shorter interfood intervals in 96 of these data sets (91%). These results generally support prediction one: adults have lower interfood intervals than young. Exceptions were Great Black-backed Gulls feeding on garbage, Herring Gulls picking up worms, Laughing Gulls picking up insects from a wet field, Black-headed Gulls aerial dipping for invertebrates on a bay, and Bonaparte's Gulls picking up insects from a mudflat, plunging for fish and dunking for invertebrates on a lake. The exceptions are of interest since all of them fed on natural foods except the Herring Gull and were among the gulls that mature earliest.

The interfood interval for young was positively related to the adult interval (Kendall tau = 0.71, df = 210, $P < 0.0001$, Fig. 1). The ratio of young to adult foraging interval, however, was inversely related to the length of the foraging interval (Kendall tau = −0.18, df = 212, $P < 0.007$, Fig. 2). Thus, as the interval gets longer, the difference between adult and young decreases rather than increases, and prediction 2 is rejected.

Interfood Interval, Body Size and Age of Maturity

In gulls, age of maturity is related to body length: larger gulls mature and breed at a later age than smaller gulls (see Table 1, tau = 0.76, n = 16, Z = 4.09, $P < 0.001$). For the gulls studied, mean interfood interval increased as body size increased (F = 5.79, $r^2 = 0.39$, df = 1,9, $P < 0.03$, Fig. 3). The ratio of young to adult interfood interval increased significantly with increasing gull length (F = 4.23, $r^2 = 0.42$, $P < 0.0002$, Fig. 4). That is, as gull size increased the

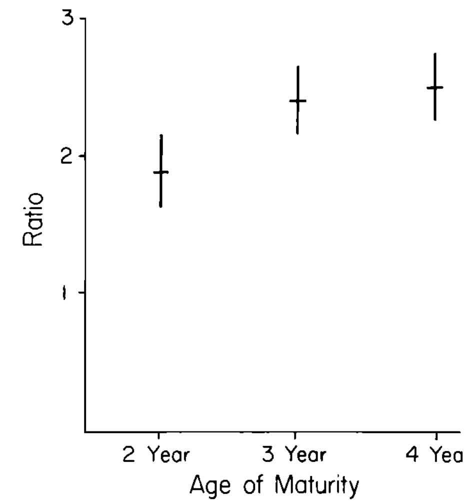

FIGURE 4. Mean foraging ratio (young interfood interval/adult interfood interval) as a function of body length in gulls.

disparity between the mean interfood interval of adults and young increased, confirming prediction 3.

Although the gulls range in length from 33 to 79 cm, they can be grouped into three "maturity age" classes. The small gulls first breed when they are two years old, the intermediate-sized gulls breed when they are three, and the large gulls breed when they are four or five years old. For the 106 data sets examined the disparity between adult and young interfood interval differed significantly among the three "maturity age" classes (F = 4.12, df = 2, $P < 0.01$, Fig. 5). The difference between species with a two year vs. three year cycle was significant ($P < 0.05$) as were the two vs. four-year species ($P < 0.01$). There was no significant difference between species with three and four year cycles. Thus the interfood interval of young gulls that will breed in their second year was closer to the interfood intervals of adults than was the young to adult ratio for the larger gulls that breed in their fourth or fifth year, confirming prediction 3.

DISCUSSION

Methodology Problems

In this study, I examined only foraging situations where both adults and young foraged together. I selected these situations because all birds could theoretically feed on the same species and size of prey items, using the same methods. Although adults frequently fed in other foraging situations without young, it would bias the data to compare adult rates in these situations with young foraging in others. By selecting foraging

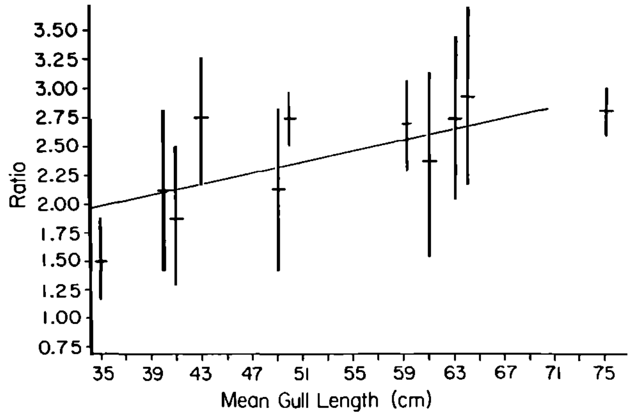

FIGURE 5. Foraging ratio (young interfood interval/adult interfood interval) as a function of age of maturity.

sites with both foraging adults and young, I eliminated those foraging sites with long interfood intervals for adults, but where young were unable to feed. In some cases, one or two young were present but they obtained no food.

Secondly, I examined only foraging situations where there were 20 or more of both adults and young. In foraging sites where there were many adults but only a few young, the young were usually completely unsuccessful at obtaining food items or required over three times the time adults required to find food items (unpublished data). Thus, I did not include in the data set foraging situations with very large differences in interfood intervals between adults and young. Had I included these two types of foraging sites, the disparity between adults and young would have been even larger than those I report, so it would strengthen the differences rather than weaken them. They were not included because it was impossible to obtain sufficient sample sizes of young for statistical analysis.

By using interfood interval, I have chosen not to examine habitat location or selection. Both aspects of foraging behavior are extremely important, and young are presumably less able to locate feeding sites, to decide whether to forage there, and to decide when to abandon a site in search of a more productive one.

Interfood Interval and Age

For over 90% of the data sets examined in this study adults had significantly shorter interfood intervals than young. Thus, assuming that they are capturing the same size prey within any given feeding situation, adults are obtaining more food per unit time than young. Comparable results have been reported for several other seabirds, but this report illustrates the consistency of this finding for a large number of congeners feeding in very different habitats on a variety of food items.

The interfood interval includes search, capture, and manipulation time since all three activities occur between successfuly capturing a first and second food item. From the results of this study it is not possible to determine which of these three (or combination thereof) is difficult for the young gulls. The literature (Verbeek 1977, Ingolfsson and Estrella 1978, Gochfeld and Burger 1981, MacLean 1986), however, suggests that across species young birds may be less efficient at all three tasks.

Ratio of Young to Adult Interfood Interval and Foraging Task Difficulty

I had originally predicted that the ratio of young to adult interfood interval would increase with the difficulty of the task as measured by adult interfood interval. This turned out not to be the case. This can be accounted for by two factors: (1) adult interfood interval may not be the best measure of foraging difficulty and (2) young gulls actively avoid difficult foraging situations, resulting in only those young gulls that are proficient in foraging in these sites. Adult interval may not be the best basis to assess foraging difficulties if in short interfood interval situations young have difficulty maneuvering prey. If adult interval is only 2 sec, and young require 2 sec longer to handle food, then they are twice as slow as adults whereas when adult interfood interval is 120 sec an additional 2 sec by young in food handling does not appreciably increase young interfood interval.

Young gulls clearly avoid the most difficult foraging tasks (i.e., plunge-diving) and it was often difficult to find enough young for a sufficient sample. Thus perhaps only the young already proficient at difficult tasks choose to forage there, minimizing the differences between adult and young intervals. Alternatively, since all young must feed somewhere, the less proficient young might concentrate in relatively easy foraging situations, maximizing the differences between adult and young interfood intervals.

Interfood Interval, Gull Size and Age of Maturity

One factor that supposely contributed to the evolution of delayed maturity in seabirds is the difficulty young and subadults have in foraging efficiently (e.g., Lack 1967, Ashmole 1971). This assumption can be indirectly tested by examining the disparity between the foraging efficiency of adults and young of closely related species that mature at different ages. An important purpose in this study was to examine the disparity in *Larus* gulls to determine if the disparity is greater in gull species with greater delayed maturity. Data from 106 foraging sets with 15 species of gulls maturing from two years to five years of age confirmed the prediction that disparity is greater for gulls that mature later. Age of maturity and size are directly related, and in this study the disparity was also directly related to size of the gull species. These results are clearly consistent with the theory that foraging difficulties contributed to the evolution of delayed maturity in gulls.

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