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# AGE-SPECIFIC FORAGING ABILITY AND THE EVOLUTION OF DEFERRED BREEDING IN THREE SPECIES OF GULLS

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ABSTRACT.—From 1976 to 1978, I studied the foraging performances of all age classes of the Bonaparte's Gull (*Larus philadelphia*), the Ring-billed Gull (*L. delawarensis*), and the Herring Gull (*L. argentatus*). In all species, immatures foraged less efficiently than did adults. There was improvement in performance with age, the adult level of efficiency being achieved in the spring of the final year of adolescence. A correlation was established between the extent of performance depression in the immatures and the length of the species-specific prereproductive period. Search, pursuit-capture, and handling improved at different rates and in different sequences in the three species. Implications for deferred breeding are discussed. *Received 25 May 1984, accepted 20 Sept. 1985.*

Central to the discussion of deferred breeding is the fact that reproductive activities carry both benefits and costs. The benefits include genetic representation in future generations. The costs have been defined as "any decrement in either the effectiveness of another function or in the probability of surviving to perform that function, or both" (Williams 1966). Recent theoretical treatment of deferred breeding by Goodman (1974), Wittenberger (1979), and Stearns and Crandall (1981), among others, has demonstrated that deferred breeding will be favored only when the benefits, expressed as increments in the lifetime production of offspring, exceed the costs of forfeiting one or more years of potential reproductive output.

Of the various theories proposed to account for the presence of greater cost factors in immatures, the most widely accepted is that proposed by Ashmole (1963), who suggested that young lack certain of the skills required for their own maintenance and, hence, survival. He further suggested that these skills were acquired gradually, through experience, and that until these skills were perfected, the young birds, as a class, would exhibit elevated mortality relative to that of adults. Ashmole specifically mentioned foraging ability as one such skill. A number of studies have since confirmed that young of gulls exhibiting deferred breeding do indeed forage less efficiently than do their conspecific adults (Searcy 1978, Burger 1981), but none of the studies has attempted to correlate the extent of foraging inefficiency or the rate of foraging improvement with the length

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of the period through which breeding is deferred. If, as Ashmole suggests, the acquisition of certain skills influences the age at which breeding commences, then the rate at which these skills are acquired should be correlated with the speed with which reproductive activities are assumed.

I studied the foraging behavior of all recognizable age classes within three species of gulls: the Bonaparte's Gull (*Larus philadelphia*) the Ring-billed Gull (*L. delawarensis*), and the Herring Gull (*L. argentatus*), birds that breed for the first time when they are two, three, and four year of age, respectively. I sought to answer the following questions: (1) Do immatures of each species forage less efficiently than do adults? (2) Is there any evidence, within each species, of an improvement in foraging ability with age? (3) Is there any correlation between the extent to which foraging performance is depressed in the immature and the length of the period through which immatures defer breeding?

## METHODS

The study was conducted along a 2-km stretch of the Niagara River that flows past Queenston, Ontario, Canada (43°10′N, 79°04′W).

Preliminary studies to determine the suitability of the region were conducted between October 1975 and March 1976. Formal observations were conducted in September–November, 1976 and 1977, and March and April, 1977 and 1978. On each day, observations began at 05:00 h and ceased at 17:00 h.

Foraging success was recorded for all age classes of all species on each day of observation. Individual birds were selected haphazardly, identified as to species and age (using plumage characteristics), and observed continuously thereafter with 10 × 40 binoculars. No data were recorded until the bird was seen to capture and consume a prey. As soon as a bird that had consumed its food resumed flying, a stopwatch was engaged and all behavioral patterns observed were recorded into a tape recorder. Observation and data collection ceased when the bird next consumed prey.

Only behavioral patterns involved in "independent foraging" (Table 1) are included in this paper. Piracy, while important, (and especially prevalent in the Ring-billed and Herring gulls), is not discussed here, but rather in a separate paper (MacLean, in press). Prey taken included fish, insects, and edible "garbage" that the birds took from the water.

A census of the foraging population was conducted twice daily; first at 05:00 h, and again at 12:00 h. Each age class of each species was censused separately. Each census represents the numbers of birds that crossed a visual plane drawn across the study area during a one-min interval.

Data analysis involved the use of nonparametric tests. The data presented in this paper are combined for each age class in each season. Although performance did vary with such parameters as wind speed, presence of rain or snow, sunny or overcast skies, etc., the variance in performance caused by these factors did not differ between adult and immature classes and hence the data were lumped for the purposes of presentation (though not for statistical analysis). Further details may be found in MacLean (1982).

## RESULTS

*Inefficiency of immatures.*—Immature age classes of all species required more time than did conspecific adults to capture and consume prey, at

TABLE 1

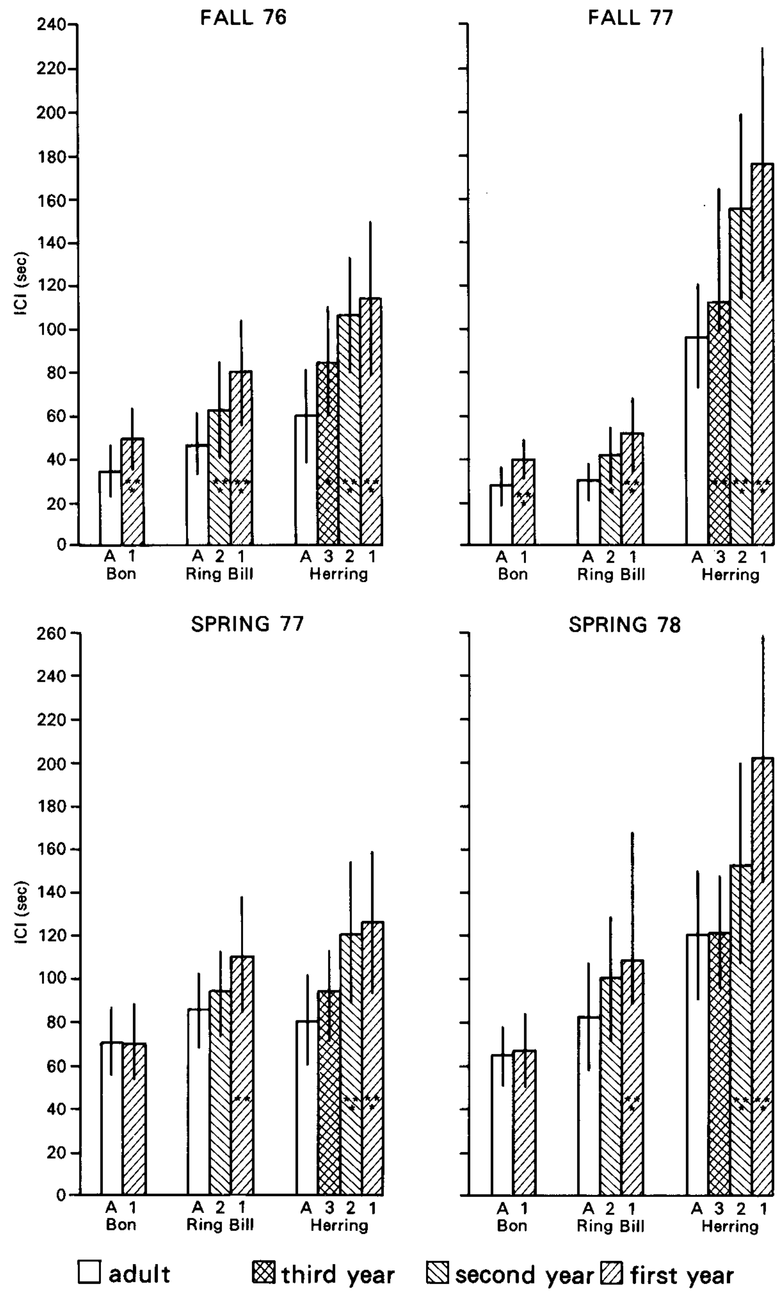
BEHAVIORAL PATTERNS OF FORAGING BONAPARTE'S, RING-BILLED, AND HERRING GULLS

| Behavioral patterns | |
|---|---|
| Dives | Any entry into the water, other than sitting, of any part of the bird. |
| Unsuccessful dive | A dive that did not result in the capture of prey. |
| Successful dive | A dive in which prey was captured and consumed. |
| Drops | Loss of a prey item after capture. |
| Intention movements | Dives that were terminated prior to contact with the water. Termination of the dive occurred at any distance above the water line. No prey was captured. |
| Intercatch interval (ICI) | The time between one successful dive and the next successful dive. |
| Diving rate | The number of dives performed by an individual per unit time. |
| Capture efficiency | The percentage of dives performed that resulted in the capture of a prey item. |

least during fall of each year (Fig. 1). In both fall seasons, the difference between adult and first-year immature performances was highly significant in all three species ($P < 0.001$). The older immature classes of both Ring-billed and Herring gulls also had significantly longer intercatch intervals (ICIs) than did conspecific adults. The pattern that emerged, however, was of a gradual improvement in ability. Second-year Ring-billed Gulls (R2), for example, although less efficient than the adult (RA), were, nevertheless, more efficient than the first-year birds (R1) in both fall seasons. Similarly, in Herring Gulls, third-year birds (H3) were less efficient than the adults (HA), but more efficient than second-year birds (H2), which, in turn, were more efficient than first-year birds (H1). All differences between age classes in each species were statistically significant.

This pattern changed somewhat in spring. Although in spring the ICIs of all age classes were greater than those seen in fall (probably a consequence of reduced fish densities and of the ice cover on the river, which effectively shielded many prey and thereby increased search time) the performance of each immature age class relative to adults improved (Fig. 2). In all three species, all immature age classes improved their performances significantly ($P < 0.05$) between fall and spring, with the oldest immature classes (the R2 and H3) achieving a level of performance that was not statistically different from that of adults.

Thus, in all three species the immatures took significantly more time than did their conspecific adults to capture and consume each prey item, and in each there was a gradual reduction in the average ICI over time.


FALL 76
FALL 77
SPRING 77
SPRING 78
ICI (sec)
ICI (sec)
240
220
200
180
160
140
120
100
80
60
40
20
0
260
A 1
Bon
A 2 1
Ring Bill
A 3 2 1
Herring
adult
third year
second year
first year

The rate of this improvement varied, however, among the three species (Fig. 2, Table 2). For example, in fall, the ICI for the immature Bonaparte's Gulls (BI) was 41% longer than that of the adults. By spring, the two age classes were performing at the same level of efficiency. First-year Ring-billed Gulls (R1), in contrast, had both a greater initial disadvantage (the R1 ICI for fall of 1976 was 70% longer than that of adult birds) and a slower rate of improvement, having achieved only 59% of the reduction in the ICI required to attain the adult level of success. The data for the Herring Gulls indicate even greater initial disparities and slower improvement (Table 2).

*Sources of inefficiency.*—In fall, the immatures of all three species made fewer dives per unit time than did the adults, although the older age classes were relatively more proficient than the younger age classes (Table 3). During fall the immatures also made significantly more intention movements than did the adults (Table 3). The lower diving rates indicate that the young birds of all species do not detect potential prey as readily as do the adults. The data on intention movements (representing as they do terminated dives) indicate that the young birds make more "mistakes" either in the identification of suitable prey or in judging the accessibility of those prey.

In all three species, older age classes of immatures dove more frequently and aborted fewer dives than did younger age classes. As was the case with the ICI, the rate at which this occurred varied among the species, with immature Bonaparte's Gulls improving most rapidly and immature Herring Gulls improving least rapidly (Table 2).

In addition to taking more time and effort in the search for suitable prey, immatures of all species were significantly less efficient than conspecific adults in the capture of prey once these had been found (Fig. 3). In fall, immature classes captured fewer prey per attempt than did adults, and there was gradual improvement in the efficiency of young birds from year to year. All of these increases were significant except for the fall–spring data for R1 in 1977–1978. Performance levels were most depressed in the Herring Gull, the species exhibiting the longest period of immaturity, and least depressed in the Bonaparte's Gull, the species with the shortest adolescence. There are, however, exceptions to this general pat-

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FIG. 1. Intercatch interval (ICI) for three species of gulls. Bars indicate average ICI for each age class, vertical lines indicate ± 1 SD. Asterisks indicate level of significance for adult-immature comparisons: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

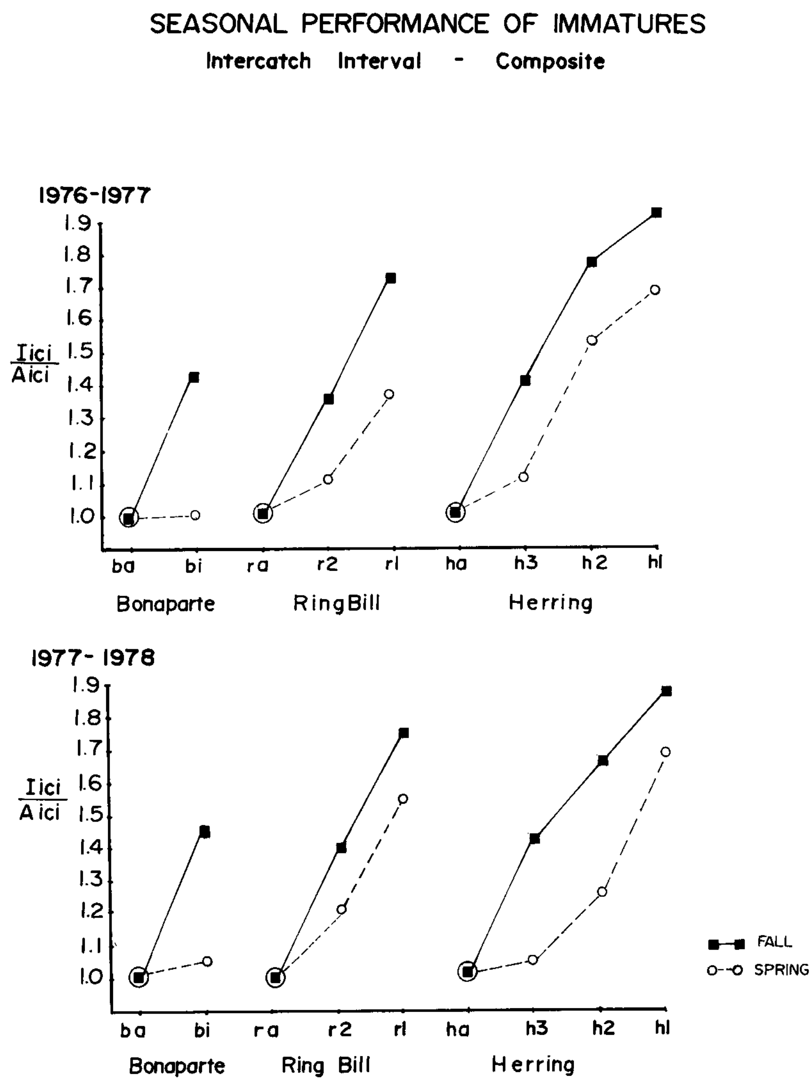


FIG. 2. Intercatch interval (ICI) data for all three species of gulls. Immature performance in a season is expressed as a percentage of the adult performance observed during that same season. Species-age abbreviations as in text.

tern. For example, the relationship between the performances of the first-year Ring-billed and Herring gulls (R1 and H1) is far from clear-cut. In some seasons the relative performance of the R1 is better than that of the H1 (spring 1977); in others it is essentially comparable (fall 1977), and

TABLE 2
SEASONAL IMPROVEMENT OF FIRST-YEAR IMMATURES

| Parameter | Year | % reduction needed to attain adult level | | |
|---|---|---|---|---|
| | | Bonaparte's | Ring-billed | Herring |
| Intercatch interval | 1976–77 | 100 | 59 | 38 |
| | 1977–78 | 100 | 24 | 17 |
| Diving rate | 1976–77 | 100 | 68 | 19 |
| | 1977–78 | 100 | 15 | 0 |

in others it is actually worse (fall 1976, spring 1978). Generally, the discrepancy seems to lie with the performance of the first-year Herring Gulls during 1977–1978 when that age class had a relatively high capture rate.

Handling abilities also varied between immatures and adults (Fig. 4). In all three species the young dropped significantly more prey than did the adults. Improvement in handling ability occurred later in adolescence than did ICI and capture efficiency.

*Foraging period.*—Immatures of all three species compensated for their reduced food intake by foraging for longer periods each day (Table 4). The typical adult pattern was to forage intensively in the morning and again prior to sunset, spending the afternoon resting on a nearby hydroelectric plant roof. Immatures, too, followed this pattern, but their morning feeding bout was extended relative to that of adults, and the rest period was foreshortened. For example, in fall 1976, 1514 adult Bonaparte's Gulls were counted during the morning censuses, but only 288 birds of this class were observed during the noon count. That is, only 19% of the morning flock continued to forage at noon. Extended searches of the surrounding area did not reveal a disproportionate number of these birds foraging elsewhere. In contrast, 44% of the immature Bonaparte's Gulls noted during the morning count were still present and feeding in the study area during the noon census. Similar figures were obtained for immature age classes of the other two species.

## DISCUSSION

My observations demonstrate that immatures of three species of gulls forage less efficiently than do adults during at least some portion of each year. They further indicate that foraging performance improves gradually in all species, with the adult level of performance being achieved only by the spring of the final year of adolescence. Similar adult-immature discrepancies have been noted in other studies (Greig et al. 1983). The

TABLE 3

DIVING RATES AND INTENTION MOVEMENTS OF BONAPARTE'S, RING-BILLED, AND HERRING GULLS

| Season | Parameter | Type gull | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | BA | BI | RA | R2 | R1 | HA | H3 | H2 | H1 |
| Fall 1976 | Dives/min | 2.24 | 2.21 | 1.79 | 1.59 | 1.35[b] | 1.25 | 0.98[b] | 0.95[b] | 0.93[b] |
| | Intentions/capture | 0.74 | 1.01 | 0.81 | 0.92 | 1.03[b] | 0.75 | 0.95[b] | 1.02[b] | 1.56[c] |
| Spring 1977 | Dives/min | 0.98 | 1.04 | 0.75 | 0.74 | 0.69 | 0.86 | 0.78 | 0.65[a] | 0.68[a] |
| | Intentions/capture | 0.94 | 1.04 | 0.53 | 0.60 | 1.11[c] | 0.64 | 0.68 | 0.96[b] | 1.71[c] |
| Fall 1977 | Dives/min | 2.20 | 1.79[b] | 2.19 | 1.82[a] | 1.63[b] | 0.70 | 0.54[b] | 0.53[b] | 0.50[b] |
| | Intentions/capture | 0.28 | 0.42[a] | 0.70 | 0.84[a] | 0.95[a] | 0.85 | 1.16[b] | 1.50[c] | 1.90[c] |
| Spring 1978 | Dives/min | 0.96 | 1.01 | 0.83 | 0.74 | 0.65[a] | 0.64 | 0.64 | 0.52 | 0.45[a] |
| | Intentions/capture | 0.97 | 1.01 | 1.00 | 1.00 | 1.35[b] | 0.82 | 0.97[a] | 1.53[c] | 2.13[c] |

[a] Significant difference ($P < 0.05$) between adults and immatures.
[b] Significant difference ($P < 0.01$) between adults and immatures.
[c] Significant difference ($P < 0.001$) between adults and immatures.

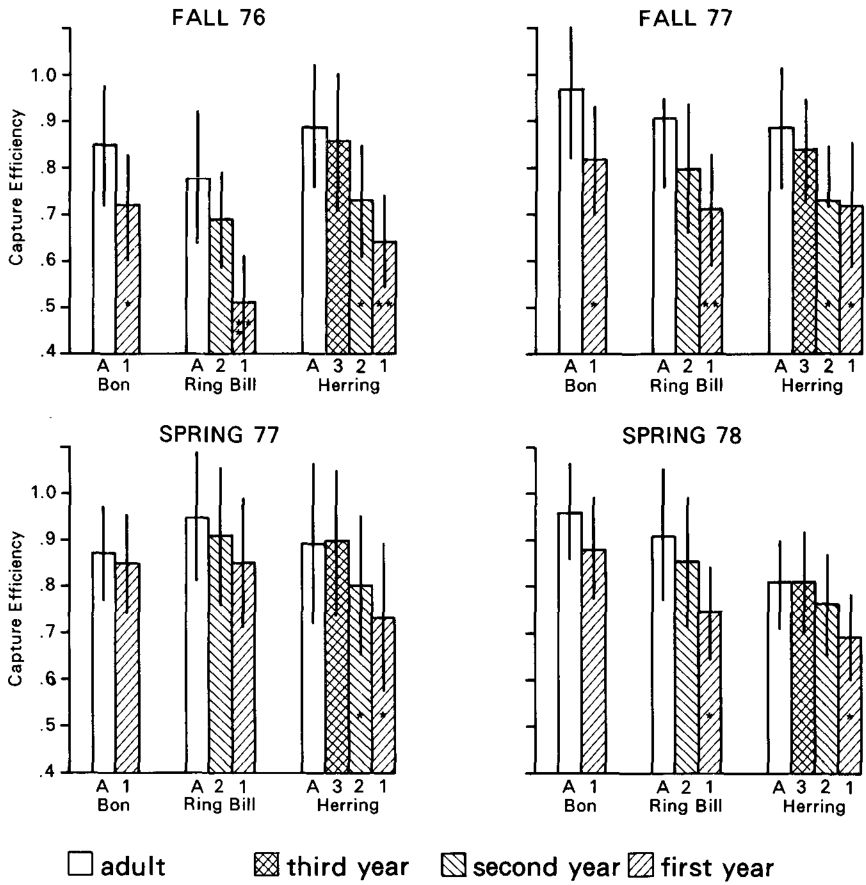


FIG. 3. Capture efficiency in three species of gulls. Bars represent average performance for each age class, vertical lines through bars represent standard deviation. Asterisks indicate level of significance for adult-immature comparisons: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

tendency for young birds to forage for longer periods than do adults has been noted by Schreiber (1968), Spaans (1971), and Davis (1975). Additionally, young have been shown to be less successful pirates than adults (Schnell et al. 1983; Carroll and Cramer 1985). The evidence thus seems overwhelming that such differential efficiency does exist and may contribute, as Ashmole (1963) suggested, to the postponement of breeding. Before the latter connection can be made, however, it is necessary to demonstrate not only the presence of inefficiency in immatures, but also

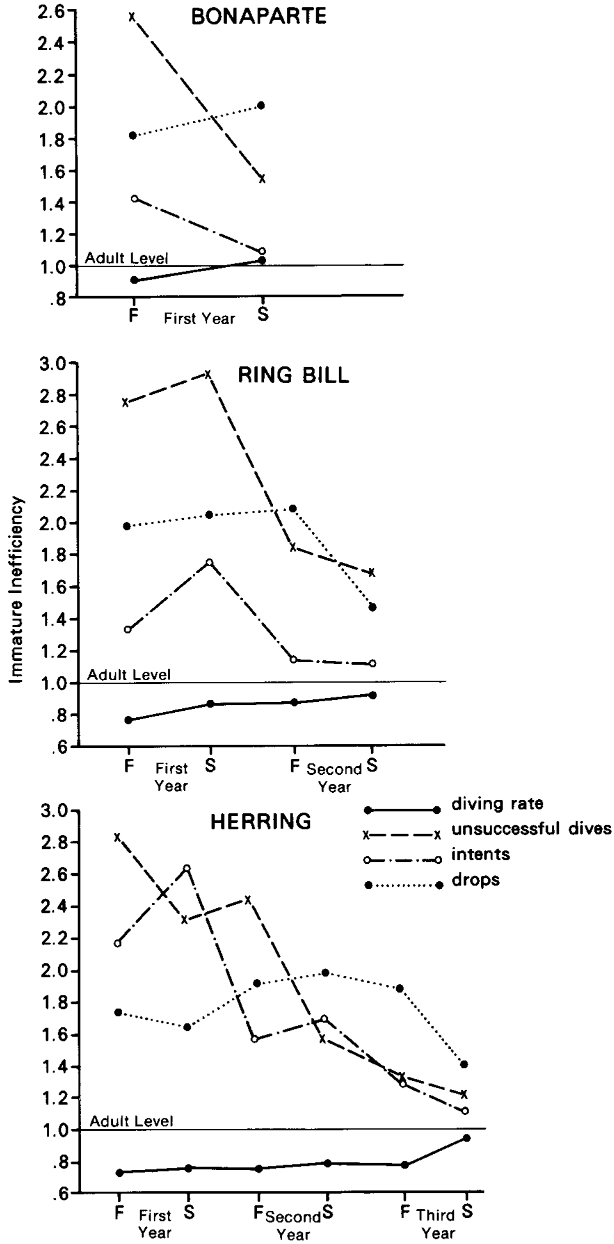


FIG. 4. Summary of various parameters of foraging ability. Immature inefficiency is calculated as the ratio of immature performance to adult performance. F = fall performances, S = spring performances.

TABLE 4

NUMBERS OF BONAPARTE'S, RING-BILLED, AND HERRING GULLS FEEDING ON THE STUDY SITE

| Type gull | Fall 1976 | | Spring 1977 | | Fall 1977 | | Spring 1978 | |
|---|---|---|---|---|---|---|---|---|
| | Morning[a] | Noon | Morning | Noon | Morning | Noon | Morning | Noon |
| BA | 1514 | 288 (19)[b] | 2282 | 342 (15) | 2311 | 208 (9) | 2198 | 132 (6) |
| BI | 458 | 201 (44) | 848 | 263 (31) | 203 | 69 (34) | 202 | 48 (24) |
| RA | 1376 | 220 (16) | 648 | 58 (9) | 812 | 106 (13) | 328 | 33 (10) |
| R2 | 256 | 87 (34) | 150 | 50 (33) | 314 | 63 (20) | 171 | 26 (15) |
| R1 | 562 | 253 (45) | 170 | 68 (40) | 310 | 118 (38) | 236 | 76 (32) |
| HA | 466 | 56 (12) | 232 | 32 (14) | 352 | 35 (10) | 359 | 57 (16) |
| H3 | 148 | 30 (20) | 120 | 25 (21) | 92 | 16 (17) | 103 | 25 (24) |
| H2 | 204 | 59 (29) | 168 | 54 (32) | 120 | 42 (35) | 177 | 71 (40) |
| H1 | 230 | 113 (49) | 244 | 117 (48) | 140 | 73 (52) | 222 | 122 (55) |

[a] Counts represent numbers of birds foraging in the study area during morning (05:00) and noon (12:00) on each day of observation. All comparisons between morning and noon counts within an age class are significant ($P < 0.001$).

[b] The percent of the morning flock foraging during the noon census.

that the extent of foraging inefficiency in the young is correlated to the length of the period during which these birds defer breeding. The data I collected indicate such a correlation. For example, in terms of capture rate, as one passed from Bonaparte's to Ring-billed to Herring gulls, the relative efficiency of the first-year birds declined from 59% to 30% to 10% during fall 1976, and the rate of improvement in performance was most rapid in the Bonaparte's Gull and least rapid in the Herring Gull.

One might also ask whether the species differ not only in the *rate* at which their foraging abilities improve but also in the *ways* in which their foraging abilities improve. That is, given that the immatures of all three species improve their foraging abilities with time (albeit at significantly different rates), is the mechanism for improvement the same in all species? What is being improved, and when?

Searching ability improves abruptly in the Bonaparte's Gull, occurs at a fairly even pace throughout immaturity in the Ring-billed Gull, and is restricted primarily to the final year of immaturity in the Herring Gull (Fig. 4). Similar, and even more marked, differences among species are evident in the "pursuit-capture" component of foraging behavior (Fig. 4). Young Bonaparte's Gulls improved their searching abilities (diving rate), while simultaneously improving their pursuit-capture abilities, as indicated by the decrease in both the numbers of unsuccessful dives and intention movements performed. This was not the case in either Ring-billed or Herring gulls. In the Ring-billed Gull there appears to be a stepwise improvement in abilities (Fig. 4). First, the searching ability (diving rate) improved. But, while this resulted in the young bird locating more prey than it had previously done, it lost more prey than previously as a result of inefficient pursuit and capture, as illustrated by the increase in both unsuccessful dives and intention movements during the first year. The pursuit-capture abilities of the young Ring-billed Gulls began to improve only during their second year. Handling ability improved even later during the second year (Fig. 4).

In the Herring Gull the pursuit-capture component of foraging performance improved first (Fig. 4). The number of unsuccessful dives was reduced as the number of intention movements increased. The birds were apparently catching their mistakes earlier in the diving sequence. Thereafter, both intention movements and unsuccessful dives declined in frequency. Handling ability (prey dropped) improved most slowly; the improvement was noticeable only during the final year of adolescence. Improved searching abilities were primarily restricted to the older immature classes (H2 and H3), although there was some improvement earlier.

It would thus appear that young gulls improve their overall foraging performance not only at different rates but also in somewhat different ways. In the Bonaparte's Gull, search and pursuit improve simultaneously; handling ability only improves later. In the Ring-billed Gull, searching ability improves first, pursuit and capture abilities next, and handling ability last. In the Herring Gull, pursuit improves first, and handling and searching abilities second. In future studies it may be beneficial to examine not only the presence or absence of immature foraging inefficiencies, but also the sequence in which the various aspects of foraging behavior are improved. This type of information, previously noted in only a few studies (e.g., Bildstein 1983, 1984), together with data on rates of improvement, might then allow us to understand better the determinants of the length of the prereproductive period.

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