Prey choices and foraging efficiency of recently fledged California Gulls at Mono Lake, California

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PREY CHOICES AND FORAGING EFFICIENCY OF RECENTLY FLEDGED CALIFORNIA GULLS AT MONO LAKE, CALIFORNIA

Chris S. Elphick¹ and Margaret A. Rubega²

ABSTRACT.—We studied the foraging biology of recently fledged California Gulls (Larus californicus) at Mono Lake during August–September 1991. We made behavioral observations to collect information on the relative proportions of different prey types in the diet of these birds and took plankton tows to determine the relative abundance of each prey in the water column. These data show that alkali flies (Ephydra hians) were the primary constituent of the diet and that they were eaten at a much higher rate than one would expect based on their abundance. We also determined the number of feeding attempts and successful captures made during each behavioral observation. From these, we calculated the birds’ feeding efficiencies on emergent adult alkali flies and on all other prey types combined. We found that foraging efficiencies on emergent flies were very high and significantly greater than those obtained on other prey types. These results suggest that flies were actively sought in preference to the alternative prey type, brine shrimp (Artemia monica), presumably because they are easier to capture and of greater nutritional value.

Key words: California Gull, Larus californicus, diet, foraging efficiency, Mono Lake.

California Gulls (Larus californicus) breed widely in the arid West, with the largest concentrations at two saline lakes: Great Salt Lake in Utah and Mono Lake in east central California (Conover 1983). Various factors may influence the size and reproductive success of the California Gull colony at Mono Lake: predation, food supply, weather, parasitism, nesting habitat, and access to freshwater (Winkler 1983, Winkler cited in Botkin et al. 1988). Of these, increased risk of predation caused by the exposure of a "land-bridge" between the mainland and islands on which the birds breed has received most attention (Patten et al. 1987, Botkin et al. 1988).

The role of food abundance has received relatively little discussion, primarily because information on the diet of California Gulls at Mono Lake is limited. Brine shrimp (Artemia monica) and alkali flies (Ephydra hians) are the main sources of food available to gulls, although other items (e.g., cicadas, fish, and garbage) are occasionally taken (Patten et al. 1987). Previous reports have focused on the food brought to chicks at the nest. Some of these studies show chick diets to be dominated by brine shrimp (Grinnell and Storer 1924, Winkler et al. 1977, Jehl and Mahoney 1983), while others found high proportions of alkali flies (Nichols 1938, Young 1952, Mason 1967). Diet data for other age classes of gulls are not widely available. Young (1952) dissected two individuals and found their guts to be full of alkali fly pupae, and Jehl and Mahoney (1983) found high proportions (>90% by volume) of shrimp in a sample of free-swimming gulls (18 adults, 20 fledglings). These studies show that both brine shrimp and alkali flies are used by California Gulls at Mono Lake under certain circumstances. The factors that determine which of the two prey species, or which life stages of alkali flies, are taken are not known. Do the patterns simply reflect variation in relative abundances of prey species, or is one species preferred but not always available?

During three summers of fieldwork we noticed that over the latter part of summer California Gulls feed extensively on alkali flies, particularly recently emerged adults. Flies of this age class are immotile and presumably easier to catch than either brine shrimp or fly larvae (though not necessarily fly pupae). We therefore hypothesized that they would be a preferred prey source when available. In this paper we quantify the incidence of alkali flies in the diet of recently fledged California Gulls.

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We restricted our study to juvenile gulls because inexperienced birds are typically the least proficient foragers (Porter and Sealey 1982, Burger 1987, Wunderle 1991) and hence most likely to benefit from the availability of easily captured prey. We demonstrate that under certain circumstances alkali flies (1) constitute a major proportion of the diet and (2) are not eaten in direct proportion to their abundance. As a potential explanation for the birds' apparent preference for alkali flies when available, we also test the hypothesis that fledgling gulls are able to achieve greater feeding efficiencies when eating emergent adult flies than when foraging on alternative prey.

METHODS

Data were collected on five days during August and September 1991 from waters just off the northeastern shore of Mono Lake, where feeding gulls were numerous.

Feeding Observations.—We obtained feeding data by videotaping foraging birds with a Sony 8 mm HandyCam video recorder with an 8X zoom lens (n = 50) or by direct observations (n = 20). In all cases the focal bird was within 10 m of the observer, and foraging behavior was scored over a 1-min feeding trial. No more than 10 birds were observed at any site to reduce the chance of obtaining repeated samples of the same individual.

Feeding trials were scored for the number of feeding attempts and successful captures, which were divided by one minute to give attempt and success rates. When possible, prey items were identified. An attempt was defined as any occasion on which the bird's bill entered the water or the bird lunged for a prey item on the water's surface. Attempts were deemed successful if (1) the gull was seen “head-throwing” (i.e., inertial feeding; Gans 1961) and swallowing after the attempt, (2) the prey item was observed in the bird's mandibles and not dropped, or (3) the prey item was visible on the water surface before the capture attempt and was picked off by the gull. Filmed trials were scored at half-speed to improve accuracy. Data from the one day when both methods were used were compared to assess the relative accuracies of videotaping and direct observation.

Diet.—We used two measures to determine the incidence of alkali flies in the diet of juvenile gulls. First, we used the number of attempts directed at flies (all life stages), divided by the total number of attempts, as a measure of the proportion of foraging effort directed at alkali flies. Second, we calculated the minimum proportion of the birds’ diet that constituted flies:

\[
\text{fly captures} \div \text{attempts on all prey minus known failures.}
\]

Prey Abundance.—Prey abundance was determined from horizontal plankton tows taken at the site of, and immediately after, a series of feeding trials. Tows were made with a 0.5-μm mesh plankton net, 1 m in diameter, and supported at the surface by floats. The tows sampled approximately 6 m³ of water, down to a maximum depth of about 60 cm. Samples were sorted and individuals of each alkali fly life stage counted. Because shrimp were too numerous to count, their numbers were calculated from a previously determined wet weight to number relationship (Rubega unpublished data):

\[
\text{Weight (g)} = 0.002207 \times \text{Number} (r^2 = .96, n = 10).
\]

Feeding Efficiency.—We calculated feeding efficiency of juvenile gulls by dividing the number of successful prey captures by the number of attempts for both emergent adult alkali flies and all other prey types combined. These values were compared using a paired t test in which the two efficiency measures for each individual were paired. Feeding efficiency could not be calculated individually for other prey types because, unlike adult flies, they occurred below the water's surface and often could not be seen unless they were captured. Hence, usually we were unable to determine the object of the foraging attempt unless the attempt was directed at an adult fly. All estimates are given in means (± standard error).

Results

Table 1 compares the minimum proportions of the total diet for each prey type with the relative abundances of each prey in plankton tows. Alkali fly adults and pupae both were eaten in much higher numbers than expected if prey were taken in proportion to their abundance. The minimum proportion of
foraging attempts directed at flies (all life stages) and the minimum proportion of the diet comprised of flies were 41.7 ± 3.0% and 40.8 ± 3.0%, respectively (n = 70). In comparison, only 0.7 ± 0.8% (n = 22) of prey items sampled in the water column were alkali flies; the remainder were all brine shrimp. These data indicate that alkali flies were favored over brine shrimp.

The two sampling methods are compared in Table 2a. Attempt and success rates for all prey types combined did not differ significantly between the videotaped feeding trials and those obtained by direct observation (t33 = -0.1, P = .933 and t33 = 1.56, P = .128, respectively). Proportions of different prey types recorded did differ, however, with videotaped trials, underrecording the number of pupae captured by an average of 79.7% on the day for which a comparison was possible. Similar numbers of adult flies were detected by the two methods. This discrepancy was probably because, unlike adult flies, pupae do not float on top of the water surface and are difficult to see on film due to reflection. Values given above for the incidence of alkali flies in the diet are therefore underestimates.

Mean foraging efficiency for recently fledged gulls feeding on emergent alkali flies was very high and significantly greater than mean efficiency on all other prey (Table 2b; paired t45 = 10.8, P < .0001). In addition, a comparison of the two measures for each individual showed that in all but one case a bird’s efficiency was greater when feeding on emergent flies. Although our foraging efficiency data for alkali fly pupae are limited because we did not always know what prey type an attempt was directed at, they do indicate that pupae were caught as easily as adult flies (Table 2a).

### Table 1. Mean proportions (± SEM) of different prey types in the diet of fledged California Gulls (n = 70) and in plankton tows taken where birds were feeding (n = 21).

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Abundance in diet (% by number)</th>
<th>Abundance in plankton tow (% by number)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alkali fly adults</td>
<td>22.59 ± 0.35</td>
<td>0.01 ± 0.003</td>
</tr>
<tr>
<td>Alkali fly pupae</td>
<td>15.29 ± 0.39</td>
<td>0.67 ± 0.40</td>
</tr>
<tr>
<td>Alkali fly larvac</td>
<td>—</td>
<td>0.05 ± 0.0007</td>
</tr>
<tr>
<td>Alkali flies</td>
<td>—</td>
<td>0.74 ± 0.04</td>
</tr>
<tr>
<td>(all life stages)</td>
<td>≥ 22.59 ± 0.35</td>
<td>0.74 ± 0.04</td>
</tr>
<tr>
<td>Brine shrimp</td>
<td>—</td>
<td>90.25 ± 0.04</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The large difference between alkali fly use and abundance strongly suggests that flies were actively sought in preference to brine shrimp and that flies were an important component in the diet of the birds we observed. It is likely that our prey sampling regime underestimated the availability of alkali flies because (1) we sampled deeper in the water column than gulls forage and (2) emergent flies are most abundant at the surface. It is unlikely, however, that this could account for the 60-fold difference between observed and expected values for fly abundance in the birds’ diet. Two factors may contribute to the apparent preference for flies over shrimp. First, we have shown that 27% higher foraging efficiencies can be attained when feeding on emergent alkali flies than on alternative prey types combined. Second, Herbst (1986) reported that alkali flies are larger and have a greater nutritional value than the alternative food, brine shrimp. Both factors mean that there is an increase in food intake per unit effort when feeding on emergent flies. Although we have no quantitative data for adult gulls, observations made during the course of this study suggest that they also fed predominantly on alkali flies. A supply of easily caught prey, however, would be expected to benefit juveniles more that adults because the former lack foraging experience and are more likely to have difficulty feeding on more motile prey.

Conclusions that can be drawn from these results are obviously limited. Our sampling was restricted to a few dates in one year and one portion of Mono Lake. Our anecdotal observations from two additional years and surveys conducted across the entire lake suggest that these findings are not atypical for late summer; when emergent flies and dislodged pupae are common at the water surface. We have no data for other time periods; however, chick diet data collected earlier in the summer suggest that flies were eaten throughout the post-hatching period in 1991 (D. Shuford personal communication). Jehl and Mahoney’s (1983) data clearly show that under some circumstances brine shrimp make up a major portion of the diet of fledgling California Gulls. The difference between their result and ours mirrors the variation seen in the diet of chicks (Grinnell and Storer 1924, Nichols 1938, Young 1952,
Table 2. Mean feeding performance values (± SEM). Sample sizes given in parentheses. (a) Comparative values for the two observation methods from the one day on which both were used. (b) Values for the two prey classifications for which accurate data could be collected from all study days.

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Attempt/min</th>
<th>Success/min</th>
<th>Efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Comparison of observation methods</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alkali fly adults (video trials)</td>
<td>0.53 ± 0.06 (15)</td>
<td>0.53 ± 0.06 (15)</td>
<td>100 ± 0 (5)</td>
</tr>
<tr>
<td>Alkali fly adults (direct observation)</td>
<td>0.65 ± 0.05 (20)</td>
<td>0.65 ± 0.05 (20)</td>
<td>100 ± 0 (8)</td>
</tr>
<tr>
<td>Alkali fly pupae (video trials)</td>
<td>2.40 ± 0.31 (15)*</td>
<td>1.93 ± 0.286 (15)</td>
<td>81.75 ± 0.03 (8)*</td>
</tr>
<tr>
<td>Alkali fly pupae (direct observation)</td>
<td>9.50 ± 0.22 (20)*</td>
<td>10.47 ± 0.22 (20)</td>
<td>100 ± 0 (20)*</td>
</tr>
<tr>
<td>All prey (video trials)</td>
<td>16.67 ± 0.43 (15)</td>
<td>13.07 ± 0.40 (15)</td>
<td>78.25 ± 0.05 (15)</td>
</tr>
<tr>
<td>All prey (direct observation)</td>
<td>16.55 ± 0.31 (20)</td>
<td>10.15 ± 0.25 (20)</td>
<td>59.00 ± 0.80 (20)</td>
</tr>
<tr>
<td>(b) Comparison of prey types</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alkali fly adults</td>
<td>8.30 ± 0.15 (70)</td>
<td>7.79 ± 0.14 (70)</td>
<td>95.77 ± 1.0 (70)</td>
</tr>
<tr>
<td>All prey except adult flies</td>
<td>17.20 ± 0.99 (70)</td>
<td>11.99 ± 0.09 (70)</td>
<td>68.40 ± 0.23 (70)</td>
</tr>
</tbody>
</table>

*These data should be viewed with caution as attempt rates are minimums.

Mason 1967, Winkler et al. 1977, Jelh and Mahoney 1983). Alkali fly abundance varies seasonally with an increase during May and June, peak numbers between July and September, and a gradual decline thereafter (Herbst 1986). Research by Point Reyes Bird Observatory shows that the relative proportions of flies and shrimp in food brought to chicks differ considerably between samples collected during the day and night, and between years (D. Shuford personal communication). These observations not only suggest that relative availability of the two prey is quite variable at daily, seasonal, and annual time scales but also help explain the discrepancies between studies. Previous diet studies did not present data on relative prey abundances in areas where birds were foraging. In demonstrating a higher than expected abundance of alkali flies in the diet of fledgling gulls and the high foraging efficiencies that can be attained when feeding on them, our study suggests that flies are the preferred prey when they are available.

In light of recent research on Red-necked Phalaropes (Phalaropus lobatus), which are physiologically unable to survive on a diet of pure brine shrimp (Rubega and Inouye 1994), our data lead us to speculate that brine fly production may be an important factor in determining fledgling survival rates (currently unknown) for the Mono Lake gull colony. California Gulls clearly eat brine shrimp on a regular basis and apparently are not as dependent on alkali flies as Red-necked Phalaropes. However, it is not clear whether the prey supply is limiting the gull population size. Experiments needed to address that issue have yet to be performed. In addition, it is possible that gull predation plays an important role in determining alkali fly recruitment rates. The extent to which these issues are important can only be established through further study of the interactions between flies and gulls, both at Mono Lake and elsewhere.

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LITERATURE CITED


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