

**The Diets of California Gull Nestlings at Mono Lake:
Seasonal and Diurnal Variation**

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ABSTRACT

We conducted detailed studies of the composition of prey fed to California Gull (*Larus californicus*) nestlings at Mono Lake, California, in 2000 and 2001. We observed fifty-nine nests on Little Tahiti Islet regularly from hatching until fledging or failure. At each nest, the breeding male and female each fed nestlings throughout the day, alternating foraging bouts. Nestlings received regurgitations an average of 0.72 times/hour in 2000 and 0.64 times/hour in 2001, with the duration of adult foraging trips away from the colony lasting on average 3.7 hours.

The dominant prey fed to nestlings varied considerably between years, with brine shrimp (*Artemia monica*) predominant in 2000 and cicadas (*Okanagana cruentifera*) and alkali flies (*Ephydra hians*) in 2001. In 2000, male and female breeders specialized on foraging for brine shrimp during morning hours, with females more likely than males to feed brine shrimp also in the afternoon. In 2001 the pattern was very different, partly due to the abundance of cicadas throughout much of the nestling period. Shrimp were the dominant prey fed to chicks only for the first week after nests began to hatch. Thereafter, both males and females delivered primarily cicadas and alkali flies throughout the day, with females more likely to deliver cicadas and males more likely to deliver alkali flies. In both years, gulls regularly fed nestlings long-legged flies (*Hydrophorus plumbeus*), which breed in, or adjacent to, the lake's littoral zone. They also infrequently fed nestlings a number of other prey items; some, such as garbage, reflected specialized foraging behavior by a small number of adults.

Although all nestlings were fed a mixed diet over time that included nearly all prey species, the overall proportion of each prey type in the diet varied considerably among nests. The largely mixed diet precluded meaningful comparisons of nestling growth-rates versus diet within each year. A comparison of the growth of nestlings in 2000 (diet mainly shrimp) versus 2001 (diet mainly cicadas and alkali fly pupae) showed significantly faster growth and larger final body size in 2001. Causative factors behind the high year-to-year variation in reproductive success in this California Gull colony remain elusive. In years when adult cicada populations are high, nestling survival may be particularly high, but it is not clear how often cicada populations are dense enough to be a significant food resource, and thus how much it could explain variation in reproduction. Early mild springs, which accelerate the growth of prey populations within the Mono Lake ecosystem, may be critical for high gull reproductive success during meromictic episodes. Variable weather conditions that either change the relative availability of alternative prey or alter the efficiency of feeding on them may then determine which prey species are dominant in nestling diets.

INTRODUCTION

Mono Lake is a moderate-sized lake in the high sagebrush desert of eastern California, instantly recognized by many for its stark landscape of tufa towers and unusual water chemistry - highly saline, alkaline, and sulfurous. The ecology of organisms within the Mono Lake Basin, and the limnology of the lake and its tributary streams, has been of considerable interest to biologists for nearly three decades. At least part of the fascination that biologists have with Mono Lake lies in the apparent simplicity of the food web, dominated by only a handful of vertebrate species and a similarly limited number of invertebrates, algae, and other microorganisms. However, this

perceived simplicity is counter-balanced by the complex chemical environment that influences all of the biological systems at the most fundamental level. Although the number of species is limited, the prodigious production of brine shrimp and alkali flies in the waters of Mono Lake supports one of the largest breeding aggregations of California Gulls (*Larus californicus*) in the world (Winkler 1996) and a very large proportion of the continent's populations of Wilson's Phalaropes (*Phalaropus tricolor*) and Eared Grebes (*Podiceps nigricollis*) during their fall migrations (Winkler et al. 1977).

Ecological studies at Mono Lake have provided a firm foundation for historical as well as ongoing conservation initiatives. In particular, nearly continuous monitoring of the breeding population size and nesting success of California Gulls, from the late 1970s to the present, has served as an invaluable source of information for ongoing assessment of the health of the Mono Lake ecosystem. This monitoring program, standardized and managed by David Shuford at the Point Reyes Bird Observatory since 1983, provides a baseline for focused questions about the ecological mechanisms underlying changes in gull numbers and breeding productivity. Concerns over very low reproductive success by the gull breeding population in recent years motivated the study reported here.

In 1996, due to high snowmelt and reduced diversion of water from incoming streams, the lake became meromictic - a condition in which the lake stratifies into two layers: a less dense (less saline) upper layer, and a deeper more highly saline layer. While the upper layer undergoes normal seasonal mixing and depletion of nutrients, the lower layer does not. One result is that nutrients and minerals become sequestered in the deep layer, out of reach of the biotic community. Meromixis has probably characterized Mono Lake sporadically over its long history; for example, it became meromictic in 1982-83 as a consequence of high run-off during an El Niño climatic event (Jellison and Melack 1993). Low gull productivity has been associated with both of the recent meromictic events. In the earlier episode, productivity dipped to levels about 35% of usual levels at the lake, but it gradually recovered to higher levels over a period of four years. In the present meromictic episode, gull productivity in 1996 through 1999 again dipped to levels about 35% of average for non-meromictic years (Shuford et al. 2000, J. Jehl, personal communication). However in 2000 and 2001, although Mono Lake was still meromictic, gull productivity was high and the number of nesting gulls increased on all islands (Wrege et al. 2001a, b; J. Jehl, personal communication).

The proximate factors affecting gull reproduction are not known. Intensive studies of the phenology of brine shrimp productivity, a major food resource for the gulls, show delayed time to maturation and slower rise to high population densities in meromictic years (Melack and Jellison 1998). However, it was unclear whether this directly affected chick diet or chick production. Similar long-term studies of the population ecology of alkali flies, the other major food resource for gulls, suggests that rising lake levels are beneficial to fly reproduction and alkali fly population density is increasing (D. Herbst, personal communication). Furthermore, the energy content per individual alkali fly pupa or larva is considerably higher than for brine shrimp, presumably making flies a more attractive food resource (Herbst 1986). One study of the diet preferences of juvenile California Gulls showed a clear preference for alkali flies over brine shrimp in late August (Elphick and Rubega 1995). Similarly, adult California Gulls breeding at Great Salt Lake, Utah, ate more flies than shrimp when both were available in high densities

(Winkler 1983). Still, there have not been intensive studies of diet preference combined with measures of the foraging efficiency of adults during the breeding season.

In 2000 and 2001, we conducted a detailed investigation of nestling diets and foraging efficiency of adults on alternative prey species. Here we present data on diurnal and seasonal variation in the composition of nestling diets throughout those two breeding seasons and discuss factors that might affect the availability of prey species and hence the productivity of breeding gulls. This study is the most detailed to date, with more than 4000 nest-hours of observation, including over 3500 observed feedings of nestlings.

METHODS

This study was conducted on the population of California Gulls nesting on various islands in Mono Lake, Mono County, California (38°N, 119°W). Shuford (1985) and Shuford et al. (1984, 1985) provide detailed descriptions of the site and population. Behavioral observations and nestling measurements were made in a 20 x 20 meter fenced plot on Little Tahiti Islet. Reproductive success within this plot did not differ significantly from that reported for other plots on this and other islets (Wrege et al. 2001a, b; J. Jehl, personal communication). Observations were made using binoculars and spotting scopes from an observation hide situated 9 meters above, and roughly 10 meters outside, the northwest corner of the plot.

California Gulls are important predators of the eggs and young of conspecifics at nesting colonies. To minimize this source of mortality due to our activities at the colony, we captured and marked adults and took repeated measurements of nestling growth only at night. Although adults did flush from portions of the colony when we entered the nesting area in the dark, they returned to nearby locations rapidly and appeared to resume incubation or brooding behavior soon after we departed the nest vicinity. Hatching success of nests at which we captured and marked adults did not differ from that at undisturbed nests elsewhere in the colony (unpublished data).

Nestling California Gulls about 2 weeks of age and older may run long distances to escape a predator (or researcher). Often such nestlings are subjected to severe punishment, sometimes resulting in death, from conspecific adults as they attempt to return to their nest site. To minimize such risks, and to aid in locating older chicks for measurements, we erected short (~ 60 cm high) fences of poultry wire around groupings of 6 to 10 nests. Nestlings returned to these enclosures after measurements were taken did not appear to suffer any physical abuse as they returned to their nest site. However, these fences did cause some disturbance. Adults at three focal nests that were directly adjacent to the fence frequently loafed on the opposite side of the fence from their brood, which certainly reduced the effectiveness of begging by the brood. Occasionally the adult tried to regurgitate to nestlings through the fence, which was usually ineffective. Also, late in the nestling period, neighbors or non-breeding adults visiting the colony frequently harassed nestlings. In some cases nestlings crowded into the fence to avoid aggressive attacks and, in doing so, damaged their bill and face on the rough wire. These injuries were not critical, but they conceivably could have affected begging behavior by these nestlings. One nearly fledged nestling was killed by a conspecific, which might not have occurred had the chick been able to run further from the marauding adult. Finally, two nestlings died as a direct result of becoming entangled in the fencing during our absence.

Marking methods

Using noose carpets placed around the nest, we captured a total of 25 adult males and 26 adult females (9 males, 12 females in 2000) at night during the incubation period. We took captured birds to a nearby processing area, where we gave them numbered leg bands, individually marked them with plumage dyes, weighed them and measured wing, tarsus, and bill length and bill depth. In 2000, we removed 200-300 microliters of blood from the brachial vein for use in isotopic analyses of diet. We sexed captured birds using morphological measurements as reported by Winkler (1983). Typically, only one individual of each pair was captured and marked.

We measured nestlings at all focal nests once (2001) or twice (2000) each week. To limit disturbance, each night we captured at one time about half of the nestlings to be measured and removed them to a nearby processing site. We individually marked newly hatched chicks with a section of rubber band placed around the tarsus and stapled together. Once chicks reached 7 days of age, we permanently marked them with aluminum numbered leg bands. We took the following measurements from each nestling: mass, tarsus and bill length, straightened-flattened wing length, and 200-300 microliters of blood for diet analyses (2000 only). We also recorded any food items that were regurgitated during processing.

Observations of diet

We used 3-hour focal watches at the colony to obtain detailed observations of the diet of 58 nestlings from 33 nests in 2000 and 47 nestlings from 28 nests in 2001. In 2000, we observed nests for six hours each day from hatching until chicks were 20-25 days old. Older chicks were then observed on two consecutive days each week, for six hours each day, and included in *ad libitum* observations for two additional days. In 2001, we made focal observations on nests for a total of nine hours each week, six hours on the day we measured them and three hours on the afternoon of the day before measurement. On other days these nests were included in *ad libitum* observations.

We conducted focal observations during all daylight hours. Sixty-five percent of observations, however, covered the time periods from 0800-1200 hrs and 1600-1900 hrs. We could nearly always determine the sex of the adult feeding chicks, either by observing known-sex, color-marked adults or by using a combination of distinguishing plumage characteristics and size comparison with the other parent.

It was possible to determine the prey composition of nearly all regurgitations that could be seen clearly from the observation hide, and it was possible to roughly estimate the relative amount of each prey type in mixed feedings. We were able to confirm the visual characteristics used to class prey types by comparing observation scores from late afternoon feedings with actual regurgitations by specific nestlings during nighttime processing.

At each feeding bout, a returning adult regurgitated to the brood a variable number of times. The number of individual regurgitations depended mostly on the age and number of nestlings, but was influenced also by interference by conspecifics and sometimes by type of prey. We constructed observations for analyses by viewing all separate regurgitations on a given parental

provisioning trip as though they represented a single feeding, with each prey type scored as a proportion of all prey types fed during a given feeding bout.

Focal nests represented a reasonable sample of hatching dates (Figure 1), with slightly more emphasis on early and late-hatching nests in 2000. Because nearly all focal nests were observed from hatching until nestlings were either fledged or nearly so, our observations reflect the results of foraging decisions by each parent during the period of maximum nestling food demands.

RESULTS AND DISCUSSION

Sex Roles and Parental Care

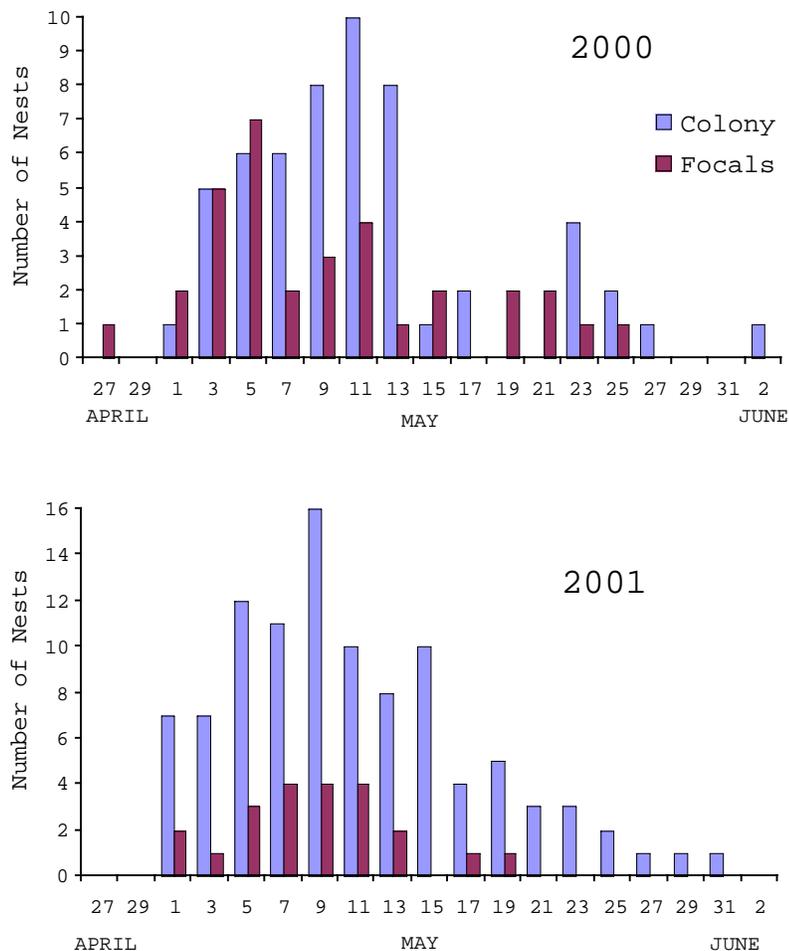


Figure 1. The seasonal distribution of laying dates for focal nests (dark bars) and a sample from the colony at large (light bars) for 2000 and 2001. Laying dates were grouped into two-day intervals with labels along the abscissa indicating the start of the interval.

Male and female California Gulls appear to contribute about equally to all phases of reproduction. Both males and females were captured on the nest at night, indicating that either

sex may incubate during this time period. Similarly, both sexes were likely to bring food to nestlings at any time of day, typically alternating between nest attendance and absences from the colony to obtain food. Females provisioned the chicks slightly more often than males, and both sexes decreased the number of feeding trips as the chicks got older (Table 1). Most of the sexual difference in provisioning rate occurred during morning samples (marginally significant interaction term, Table 1). However, the difference was rather small: after controlling for the influence of other variables, the adjusted mean for females and males provisioning at any time of day was 0.22 feeds/hr and 0.20 feeds/hr, respectively.

Table 1. Analysis of variance of sex and time of day influences on feeding rates ($n = 2362$ focal samples from 61 nests). Although highly significant ($p < 0.01$), the model explains only 6% of variation in feeding rate. The variable 'dayblock' coded whether more than 50% of the observation time occurred prior to 1200 hrs (morning focals) or after 1245 hrs (afternoon focals)

| Source | Coefficient | Sum-of-Squares | df | F-ratio | P |
|--------------|-------------|----------------|----|---------|--------|
| YEAR | 0.0056 | 0.0715 | 1 | 2.33 | 0.13 |
| CHICK AGE | -0.0036 | 4.5908 | 1 | 149.71 | < 0.01 |
| DAYBLOCK | 0.0044 | 0.0396 | 1 | 1.29 | 0.26 |
| SEX | 0.0112 | 0.2697 | 1 | 8.79 | < 0.01 |
| SEX*DAYBLOCK | 0.0076 | 0.1220 | 1 | 3.98 | 0.046 |

Seasonal variation in the mean feeding rate by males and females was remarkably small in both years. A significant linear decrease in feeding rate as the season progressed (and chicks got older, see Table 1) was due entirely to an increasing number of foraging bouts after which the returning parent did not feed the brood (Figure 2; data similar for 2001). When these bouts are omitted from the analysis, feeding rates remained remarkably constant through the entire season. Thus, from the perspective of the chicks, the number of foraging bouts resulting in food delivery remained constant throughout their development. As the season progressed, both males and females spent less time on each foraging excursion and returned more often to the colony without food for the chicks.

The relatively consistent feeding rate throughout development suggests that parents were adjusting either the amount of food delivered during each feeding bout, and/or the quality (energy content) of prey, as examined below.

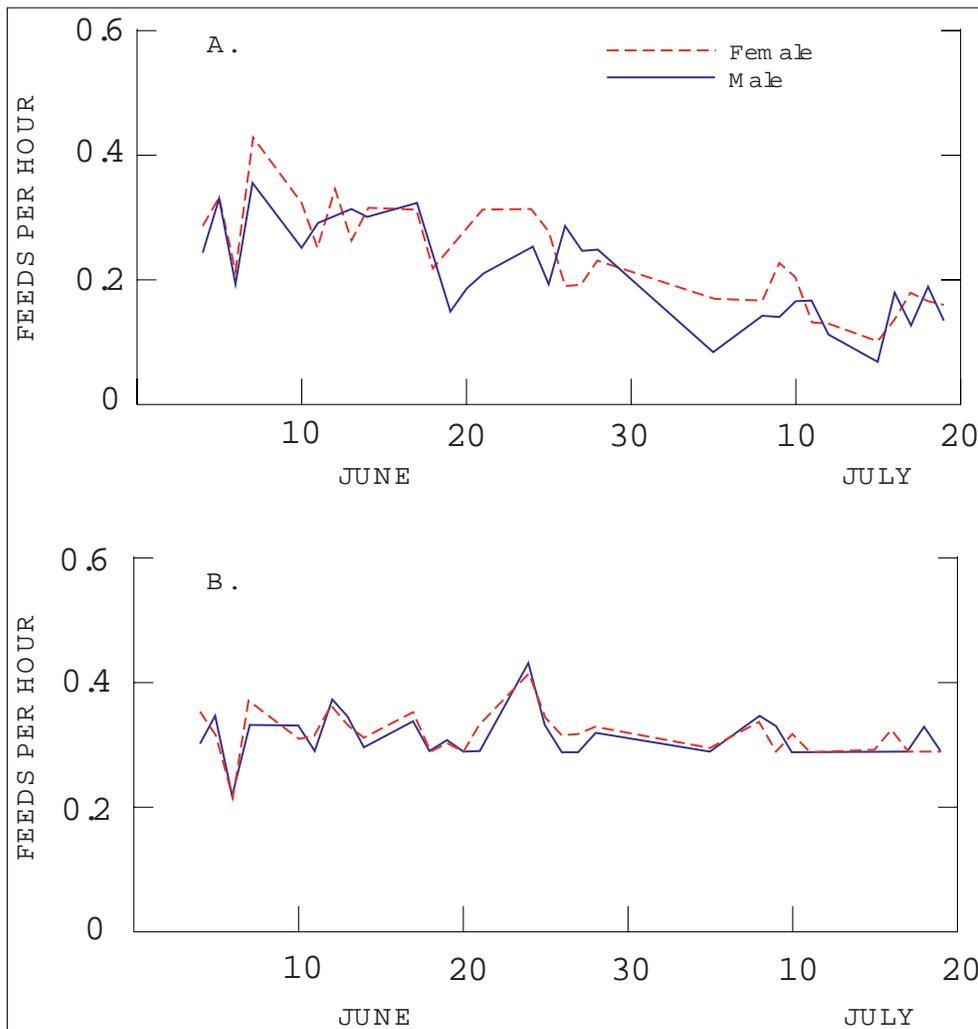


Figure 2. Seasonal variation in mean hourly feeding rates by female and male gulls in 2000. Panel A: mean rates include returns by parents during which no feeds were made to the brood. Panel B: mean rates include only feeding bouts with at least one regurgitation to the brood.

General Diet and Diel Patterns

Brine shrimp were by far the most common prey type fed to nestlings in 2000, whereas cicadas and alkali flies dominated in 2001 (Figure 3).

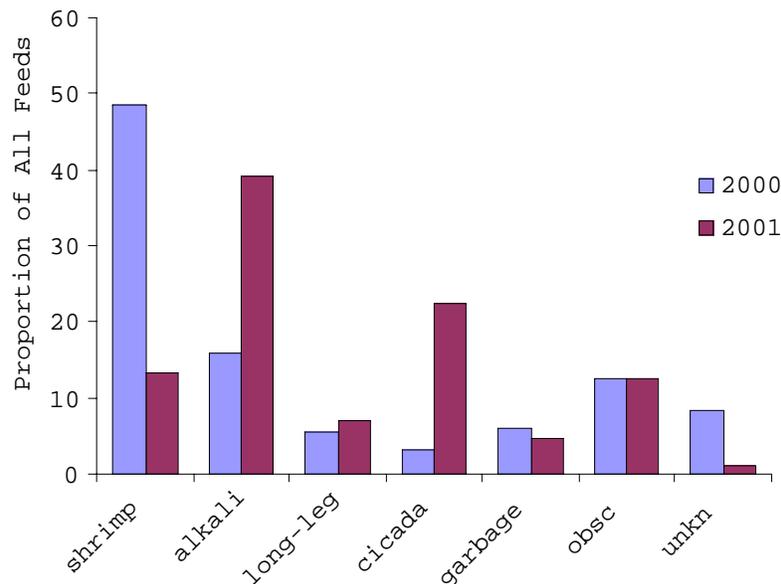


Figure 3. Relative frequency of prey types from feeding bouts throughout the nesting season. Shrimp= *Artemia monica*; alkali= larvae, pupae, and adults of *Ephydra hians*; long-leg = larvae of *Hydrophorus plumbeus*; cicada = adult *Okanagana cruentifera*; garbage= fish, fish parts, and food remains discarded in area landfills, picnic areas, etc.; obsc = feeds obscured by an adult or chick; unkn= type of prey not identified.

The general pattern of prey choice (Figure 3) hides considerable sexual, diurnal, and seasonal variation in diet (Figure 4). In 2000, prey selection by males and females was quite similar during the morning hours, when both fed strongly on brine shrimp. Afternoon prey selection tended to be much more evenly distributed among prey types, with strong differences in selectivity between males and females (Figure 4). In 2001, males and females were more similar to one another in terms of prey selection in both morning and afternoon. Cicadas and alkali flies dominated until late in the breeding season. In both years males were more likely than females to feed garbage to the brood.

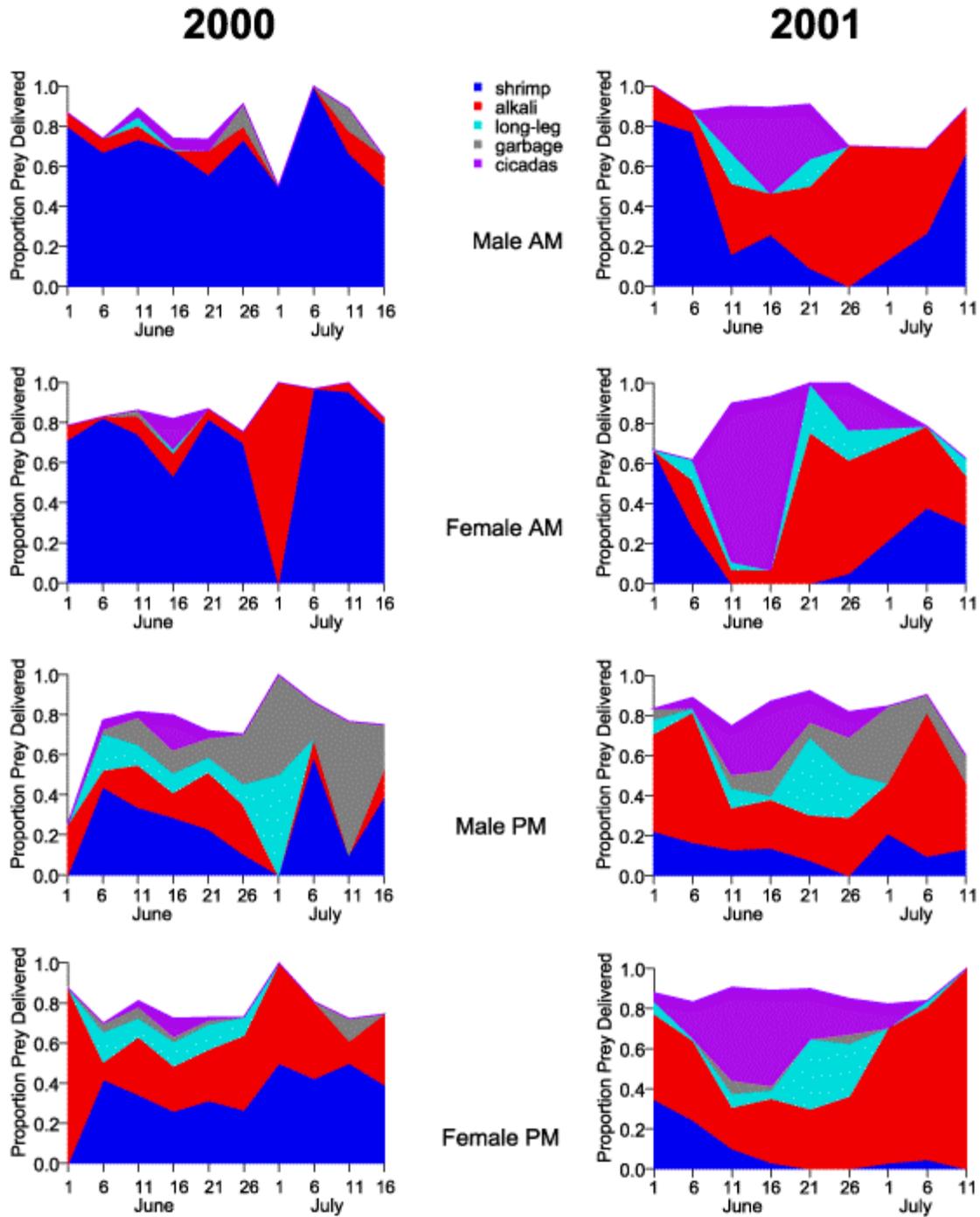


Figure 4. Diurnal and sexual patterns in the proportion of five major prey items fed by adults to their brood throughout the reproductive season. Points are 5-day average proportions, plotted on the first day of each interval. Shrimp = *Artemia monica*, alkali = *Ephydra hians*, long-leg = *Hydrophorus plumbeus*, cicada = *Okanagana cruentifera*. Based on 33 and 28 nests in 2000 and 2001 respectively. Sample sizes vary from point to point because observations were not always made on all five days of a time period, nor on all mornings and afternoons each day.

Long-legged flies were exploited only rarely in 2000, and they represented up to 20% of the diet over short time periods. However, in 2001 this prey species was more commonly observed in the diet of chicks, and populations of long-legged flies were found at many more locations around the lake (unpublished data). Increased use of long-legged flies in 2001 might partly reflect peculiarities in weather conditions that year (see below) or generally increasing populations of this species as a response to a lake environment that is less saline (D. Herbst, personal communication).

Previous studies of California Gulls at Mono Lake used the regurgitations of nestlings during banding operations to infer diet (e.g. Winkler 1983, Jehl and Mahoney 1983). Jehl and Mahoney (1983) suggested that differences between the apparent diet of chicks based on regurgitations during the day versus at night might be explained by foraging differences between males and females, with males foraging more broadly in the basin, returning to feed nestlings predominantly in the afternoon hours. We have shown that, while males and females fed chicks nearly equally throughout the day (Table 1), males were indeed primarily responsible for the more unusual prey items (e.g. 'garbage' in Figure 4).

Shrimp Vs. Alkali Flies

Heavy exploitation of cicadas in 2001 makes it difficult to draw general inferences about prey preferences by the Mono Lake gull population. The bloody cicada, *Okanagana cruentifera*, is not one of the periodic cicadas but appears to have vast year-to-year fluctuations in adult population size (DWW unpublished data). Hence this species is probably neither a typical nor predictable prey item for gulls breeding at Mono Lake. In 2001, however, breeders at every focal nest fed cicadas to their brood. It is unclear how foraging for cicadas might have affected selection of brine shrimp and alkali flies. As noted above, the relative importance of shrimp and alkali flies was reversed in the two years of study.

In 2000, brine shrimp maintained dominance in the diet throughout the gull breeding season. We suggest that the dominance was due partly to availability close to the breeding colony and possibly an interaction between weather conditions and the availability of alternate prey. These same factors, the combination of which influences the profitability of prey, may also explain the greater use of alkali flies in 2001. We will return to this hypothesis after a more detailed examination of the pattern of prey choice in the two years of this study.

The proportion of key prey items in the chick diet did not necessarily reflect their relative abundance in the lake. Although alkali flies consistently represented 15-20% of the chick diet across the season in 2000 (Figure 5), fly abundance in the Mono Lake system, and presumably their availability to gulls, increased throughout the summer (D. Herbst, personal communication). The relatively low rate of exploitation of alkali flies for feeding chicks was surprising given their higher nutrient value per individual prey item when compared to brine shrimp (Herbst 1986). It may be significant that the increased use of alkali flies between about 15 June and 4 July in 2000 (Figure 5) corresponded with the period of the season when cumulative energy demand at our focal nests was highest, as the maximum number of young were in the linear growth phase (from 5- 30 days of age). On a lake-wide basis brine shrimp populations at this time were still increasing toward their maximum abundance for the year

(R. Jellison, personal communication). The shift toward more intensive use of alkali flies during the period of highest demand may indeed reflect a need for delivering more nutrition per feeding trip, but begs the question of why the species was not more heavily exploited at other times.

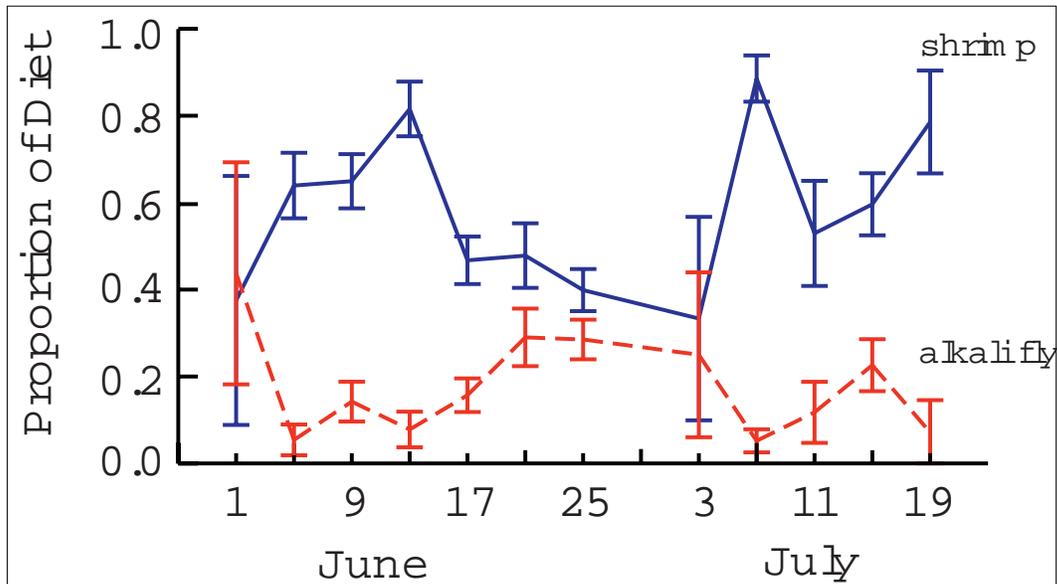


Figure 5. Proportion of brine shrimp and alkali flies in chick diets throughout the 2000 nesting season. Four-day means and SE are plotted (axis labels represent first day of the 4-day time period). Alkali fly means combine larvae, pupae, and adult stages. Means include only feeding bouts that included a transfer of prey and exclude four nests where garbage was a major component of the diet throughout the season.

Brine shrimp were not nearly as important in the diets of nestlings in 2001 as in 2000 (Figure 3). We argue below that one factor that might have influenced the dominant exploitation of shrimp in 2000 was the availability of this prey close to the colony. While shrimp were also abundant near the colony in 2001, adults were flying off of the lake and into the surrounding sagebrush habitat in order to capture cicadas, both for feeding chicks and presumably for their own nutrition. This activity involved flying over shoreline habitats where gulls could access alkali fly populations without incurring additional traveling-time (or energy) costs to get there. In 2001, alkali fly pupae represented a much higher proportion of the diet, both in absolute and in relative terms, compared with other fly life-stages (Figure 6). That both adult flies and pupae were sufficiently abundant to appear in nestling diets at high frequencies early in June might be explained by the warm spring in 2001 and concomitant acceleration of development in the population of overwintering alkali fly larvae (P. Levine, personal communication).

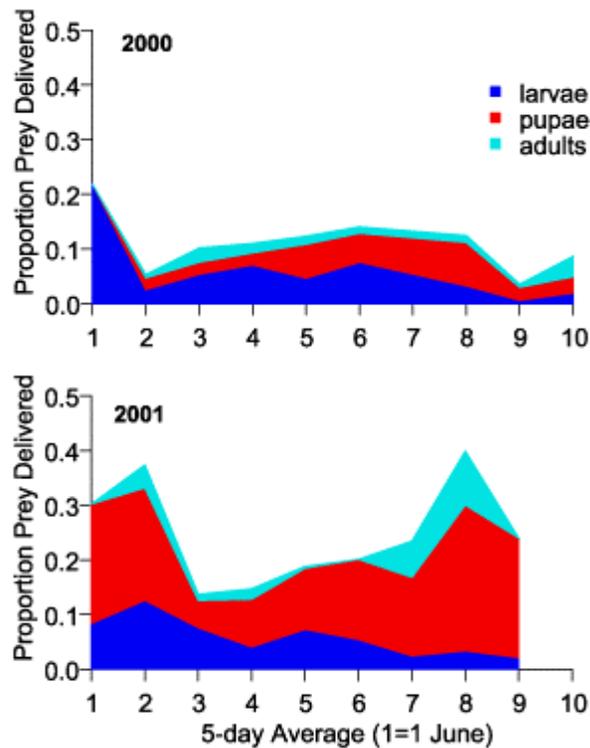


Figure 6. The relative proportion of three life-stages of alkali flies in chick diets. Points are 5-day average proportions, plotted on the first day of each interval.

Impact of prey choice on chick growth

The fitness implications of individual variation in diet will be expressed ultimately through their effect on reproductive success. Although there was clearly between-nest variation in the proportion of certain prey types, it would be difficult to detect an effect of this variation on growth because chicks in nearly all nests were fed each type of prey at least some of the time. Indeed, multiple regression analysis of growth-rate in both mass and tarsus or wing, controlling for nestling age, failed to show any significant effect of diet on the overall growth trajectory within either year.

Fledging success was higher in 2001 than in 2000, and cicadas were an abundant food resource fed to chicks in 2001 but not in 2000 (Figure 4). A multiple regression analysis comparing chick growth trajectories in 2000 and 2001 showed significantly higher growth in 2001 (Table 2). The significant interaction term in Table 2 is a test of similarity of slopes of the regression lines. In 2000, average chick mass lagged behind that of 2001 by 1.37 g/day of age. Increased use of both cicadas and alkali fly pupae in 2001, however, make it impossible to attribute the increased growth (or fledging success, which might have been higher as a result of increased growth) to one or the other or both.

Table 2. Diet effects on nestling mass (g). The regression model was highly significant, explaining 82% of variation in nestling mass. Only the linear portion of the growth trajectory (5-30 days of age) was examined in the model.

| Source | Coefficient | df | F-ratio | P |
|-------------------------|-------------|----|---------|--------|
| Intercept | 67.32 | | | |
| Year | 7.61 | 1 | 0.63 | 0.4272 |
| Chick age | 20.32 | 1 | 1504 | 0.0000 |
| Year by age interaction | -1.37 | 1 | 6.87 | 0.0091 |

Optimal Diet and Reproduction

This study was largely motivated by an interest in whether the continuing meromixis in the lake was contributing to poor gull productivity from 1996 to 1999. Specifically, the fact that alkali flies appear to be a superior food resource in terms of energy content, combined with a rising lake level during these years that should result in an increase in the population density of alkali flies (D. Herbst, personal communication), begged the question of why California Gulls did not reproduce more successfully.

Optimal foraging theory has proved a valuable tool for understanding the foraging choices made by animals in their natural environment (Stephens and Krebs 1986, Krebs and Kacelnick 1991). Numerous field studies (e.g., references in Krebs and Davies 1991) have provided empirical support for the two major predictions of optimal diet theory relative to prey selectivity – that prey choice is largely determined by the relative profitability of different prey and the predation risk associated with foraging for different prey. Profitability is measured by net energy intake per unit time (factoring in traveling time to foraging areas, foraging costs, digestibility, etc.). For adult California Gulls, predation risk is probably very low in general and when foraging on most of the prey types considered here. Individuals feeding on garbage may be at higher risk because it involves foraging in areas of higher human density.

Energy content per prey item strongly affects profitability, particularly if the foraging strategy is no more costly for one type of prey than for the alternative. Although we do not yet have estimates of the energy content of each adult cicada, it will certainly be an order of magnitude greater than either a single shrimp or a single alkali fly larva or pupa. In addition, cicadas likely provide a broader range of nutrients, including protein, fat and amino acids, than alkali flies and brine shrimp. It is not surprising that cicadas are preferred in years when their populations are high.

Accessibility of prey is a second important component of profitability. Gulls foraged for shrimp both close to the nesting colony and at distant locations, whereas they harvested alkali and long-legged flies primarily along the shoreline of the lake, 2 to 20 km from the colony. Gulls captured cicadas in sagebrush habitats and piñon-juniper woodland at even further distances. Shrimp not infrequently occurred in extremely dense concentrations in the vicinity of the nesting islets. These dense concentrations can form when columns of warm water rise from the solar heating of submerged tufa boulders, from current gyres, and possibly due to other physical phenomena in Mono Lake (R. Jellison, personal communication, PHW personal observation). Dense concentrations occur also at freshwater springs emerging from the lake bottom, although most of these were rather distant from the Negit Islets. Gulls were able to increase their foraging efficiency on shrimp by exploiting these dense concentrations, where they captured 20 or more shrimp with each 'peck' (unpublished data). In addition, as the summer progressed, copulating pairs of shrimp, and sometimes females with two or three males attached, became common in the water column. The searching behavior of gulls feeding on shrimp suggested that they might preferentially target such groupings, where they would be able to consume multiple individuals with one peck. The ready accessibility of shrimp, however, does not explain why this prey was used much less in 2001 than in 2000, given there were no great differences in shrimp densities between the two years (R. Jellison, personal communication; PHW unpublished data).

Weather conditions, particularly wind speed and direction, may have a very important impact on foraging efficiency for various prey. Shrimp were exploited much less intensively during periods of moderate to high winds (PHW unpublished data), possibly because rough waters reduced visibility for the foraging gulls. Occasionally during windy periods, gulls would concentrate on the lee side of islets where they fed on shrimp, but the overall number pursuing this strategy appeared to be small. Given the general tendency for winds to pick up in the afternoon, this may explain the increased exploitation of alternate prey during the afternoon in 2000 (see Figure 4). On occasional calm afternoons, particularly late in the 2000 breeding season, gulls foraged conspicuously on shrimp around the nesting islets.

Wind may also play an important role in *increasing* the availability of alkali fly pupae and possibly larvae. These fly larvae occur within and on top of lake-bottom sediments in shallow water and on the stems of submerged plant material. In addition, since the larvae are capable of swimming, they also may occur at low densities almost anywhere in the water column. Larvae pupate under water on the sides of tufa boulders, stems of submerged plants, and any other structure submerged in shallow water. California Gulls are known to feed on these prey items *in situ* by picking larvae and pupae from off the substrate and stirring up the sediments to dislodge larvae (Winkler et al. 1977, Hite et al. 2000). However, we did not observe large numbers of adults foraging in this manner in either year, suggesting that gulls may be relatively inefficient at capturing prey in these locations. Rather, we sporadically observed gulls feeding in large numbers along the shore, where strong wave action had deposited dislodged pupae (and possibly larvae). Similarly, on mornings after an afternoon or night of very strong winds, gulls actively exploited 'drift lines' of detritus floating on the lake surface. These ribbons of material included many pupae as well as balls of algae on which alkali fly larvae (and brine shrimp) seemed to be feeding. In 2001, dislodged alkali fly pupae were very commonly seen dispersed across large areas of the water surface, sometimes in very dense concentrations. It is not clear what specific weather conditions caused these concentrations, but they were much more noticeable in 2001 and may explain the heavy use of alkali fly pupae in 2001.

Wind direction appeared to be most clearly linked to foraging decisions in the case of long-legged fly larvae. These larvae occurred at extremely high densities a few centimeters under the surface of moist sand. In 2000 this species was most notable on the north and northeast shore, but in 2001 we sampled high densities at many locations along the Black Point shoreline, while densities were quite low on the northeast shore. We observed gulls scraping away sand to access these larvae, but they foraged most intensively on this prey on days with very strong winds coming obliquely or perpendicularly to the shore. Strong wave action along the shore dislodged huge numbers of larvae and then deposited them on the sand surface with each outgoing wave. Tens of thousands of gulls were observed feeding along the splash-line on numerous occasions. Relatively little is known about the population dynamics and distribution of this species of long-legged fly, and their potential importance in the diet of California Gulls was not recognized until 1999 (Hite, et al. 2000).

CONCLUSION

The relative importance of brine shrimp, alkali flies, and long-legged flies for successful reproduction by California Gulls is of particular interest because of conservation issues pertaining to land use in the Mono Lake watershed, water depth and chemistry, and overall ecosystem health. These three species represent the major food resource not only for the gulls, but also for grebes, phalaropes and numerous other waterbirds that use the basin during their southward migrations in summer and fall.

Prey selection by California Gulls is almost certainly a function of the relative profitability of alternative prey species, which will shift with prey population density and availability. Causative factors behind the high year-to-year variation in reproductive success in this California Gull colony remain elusive. The decisions of whether to breed and how many eggs to lay are made well before any of the three major prey species are available in the lake in appreciable numbers. During the occasional year when cicadas are abundant, gull nestling survival may be particularly high, but this is not a general explanation for variation in reproduction. Early mild springs, which accelerate the growth of prey populations within the Mono Lake ecosystem, may be critical during meromictic episodes. Based on only two years of detailed study, it appears that the relative importance of brine shrimp versus alkali flies may be determined ultimately by weather conditions that affect availability. Further studies of the foraging ecology of the birds in years of different limnological conditions would be especially informative.

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