Seasonal and Diurnal Variation in the Diets of California Gull Nestlings at Mono Lake, California from 2000 to 2002

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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, 2001, and 2002. We observed ninety-four 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, 0.64 times/hour in 2001, and 0.78 times/hour in 2002 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 2002 and cicadas (*Okanagana cruentifera*) and alkali flies (*Ephydra hians*) in 2001. In 2000 and 2002, 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 all three 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.

The overall difference of diets fed to nestlings in 2001 compared to the other two years may be due to a cicada outbreak in that year, which provided foraging adults large numbers of a very profitable prey source. This greater reliance on alkali flies compared to brine shrimp may also reflect windier conditions throughout the 2001 season. Wind decreases the profitability of foraging on shrimp (while it may actually increase the profitability of foraging on flies), decreasing the prevalence of brine shrimp feeds in 2001 compared to 2000 and 2002.

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 chick growth in the three years of this study showed significantly faster growth and larger final body size in 2001 than in either 2000 or 2002. Growth did not differ between 2000 and 2002. 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 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 to 2002, 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; Hite et al. 2002; 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 Jellison1998). 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.

From 2000 to 2002, 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 5500 nest-hours of observation, including over 4500 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 (38^0N, 119^0W). 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 being measured 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 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 and 2002) 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 or longer focal watches at the colony to obtain detailed observations of the diets of 58 nestlings from 33 nests in 2000, 47 nestlings from 28 nests in 2001, and 48 nestlings from 33 nests in 2002. 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. In 2002, we observed nests without regard for when measuring would take place, and observations continued until the beginning of August even though many chicks had already fledged.

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 from conspecifics and sometimes by type of prey. We collected 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 trip.

In addition to diet data we also recorded general information on weather, ranking wind speed from low to moderate to high, during each observation.

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

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 grew 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.

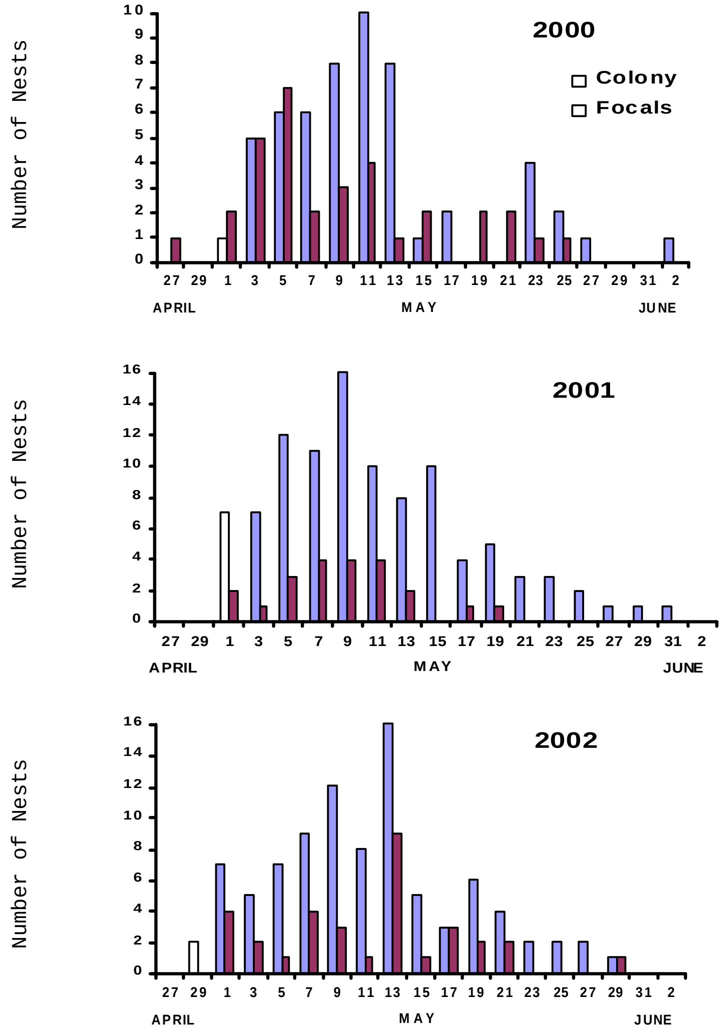

Figure 1. The seasonal distribution of laying dates for focal nests (red, or dark colored, bars) and a sample from the colony at large (blue, or light colored, bars) for 2000, 2001, and 2002. Laying dates are grouped into two-day intervals with labels along the abscissa indicating the start of the interval.

Table 1. Analysis of variance of sex and time of day influence on feeding rates (n = 2767 focal samples in 94 nests) in all three years of the study. 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	Sum-of-Squares	df	F-ratio	P
YEAR	0.084	1	2.721	0.10
CHICK AGE	4.504	1	146.142	< 0.01
DAYBLOCK	0.044	1	1.426	0.23
SEX	0.266	1	8.620	< 0.01
SEX*DAYBLOCK	0.125	1	4.048	0.04

Seasonal variation in the mean feeding rate by males and females was remarkably small in both years. A linear decrease (Figure 2, upper portion) in feeding rate as the season progressed (and chicks got older, see Table 1) was due entirely to an increasing number of visits to the nests in which the parent did not feed the brood. When these bouts are omitted from the analysis, feeding rates remained remarkably constant through the entire season (Figure 2, lower portion). 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.

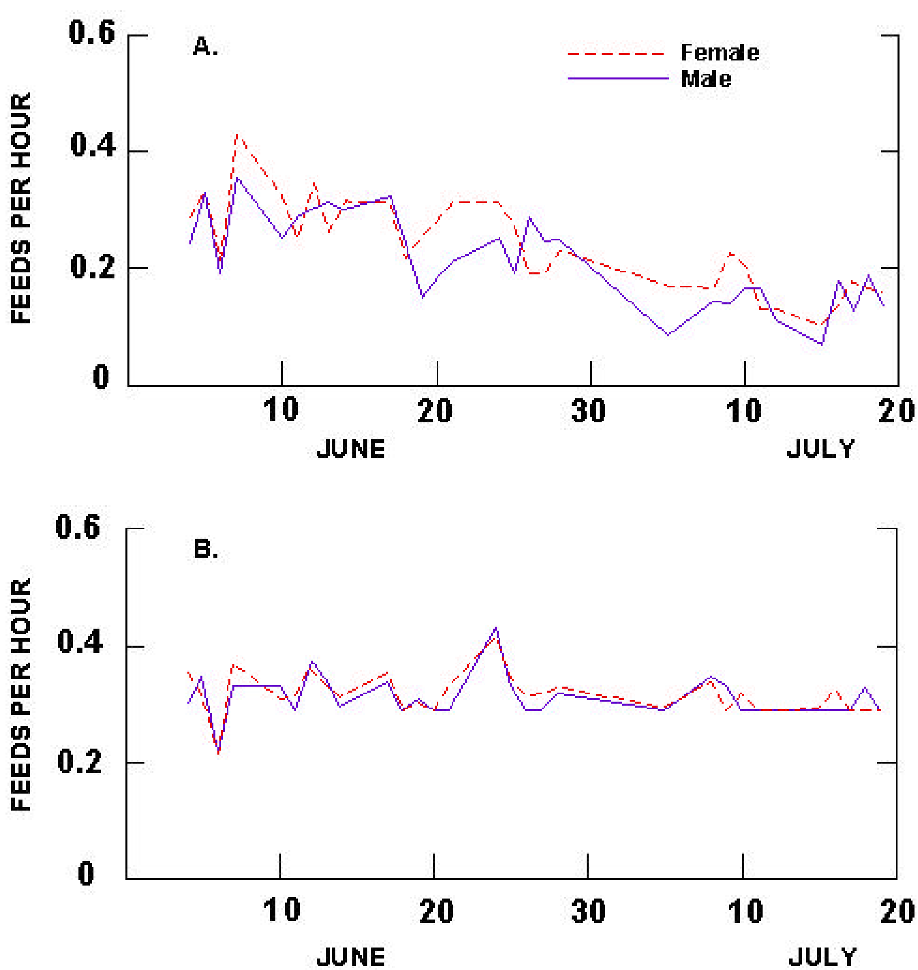

Figure 2. Seasonal variation in mean hourly feeding rates by female and male gulls in 2000. Panel A: mean rates include returns by parents during which no feeds were made to the brood. Panel B: mean rates include only feeding bouts with at least one regurgitation to the brood.

General Diet and Diel Patterns

The relative proportions of prey types fed to nestlings in 2002 returned to proportions similar to those in 2000 (Figure 3). In these two years, brine shrimp were the most common prey type fed to nestlings, followed by alkali flies. In 2001, a season of exceptionally high levels of cicada exploitation (corresponding to a cicada outbreak in the sagebrush and pinyon-juniper woodlands surrounding Mono Lake), the relative utilization of brine shrimp and alkali flies the inverse of that in 2000 and 2002, with heavier focus on alkali flies than brine shrimp.

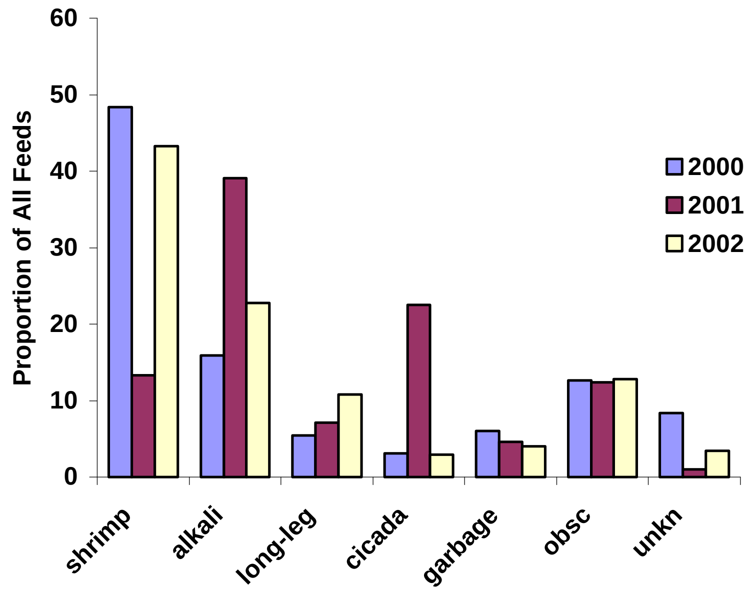

Figure 3. Relative frequency of prey types from feeding bouts throughout the nesting season. Shrimp = *Artemia monica*; alkali = larvae, pupae and adult *Ephydra hians*; long-leg = *Hydrophorus plumbeus*; cicada = *Okanagana cruentifera*; garbage = fish, fish parts, and food remains discarded in area land-fills, 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 2002, prey selection by males and females was quite similar in the morning, 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. In most respects, this pattern of provisioning was very similar to that in 2000. In 2001, brine shrimp were more commonly fed in the morning than in the afternoon by both sexes, but they made up a much smaller proportion of morning feeds as compared to the other two years. Alkali flies and cicadas dominated prey choices in 2001 in both morning and afternoon. Afternoon prey selection, as in 2000 and 2002, tended to be more evenly distributed among prey types, with strong differences in selectivity between sexes. In all three years, garbage was more likely to be fed by males than females.

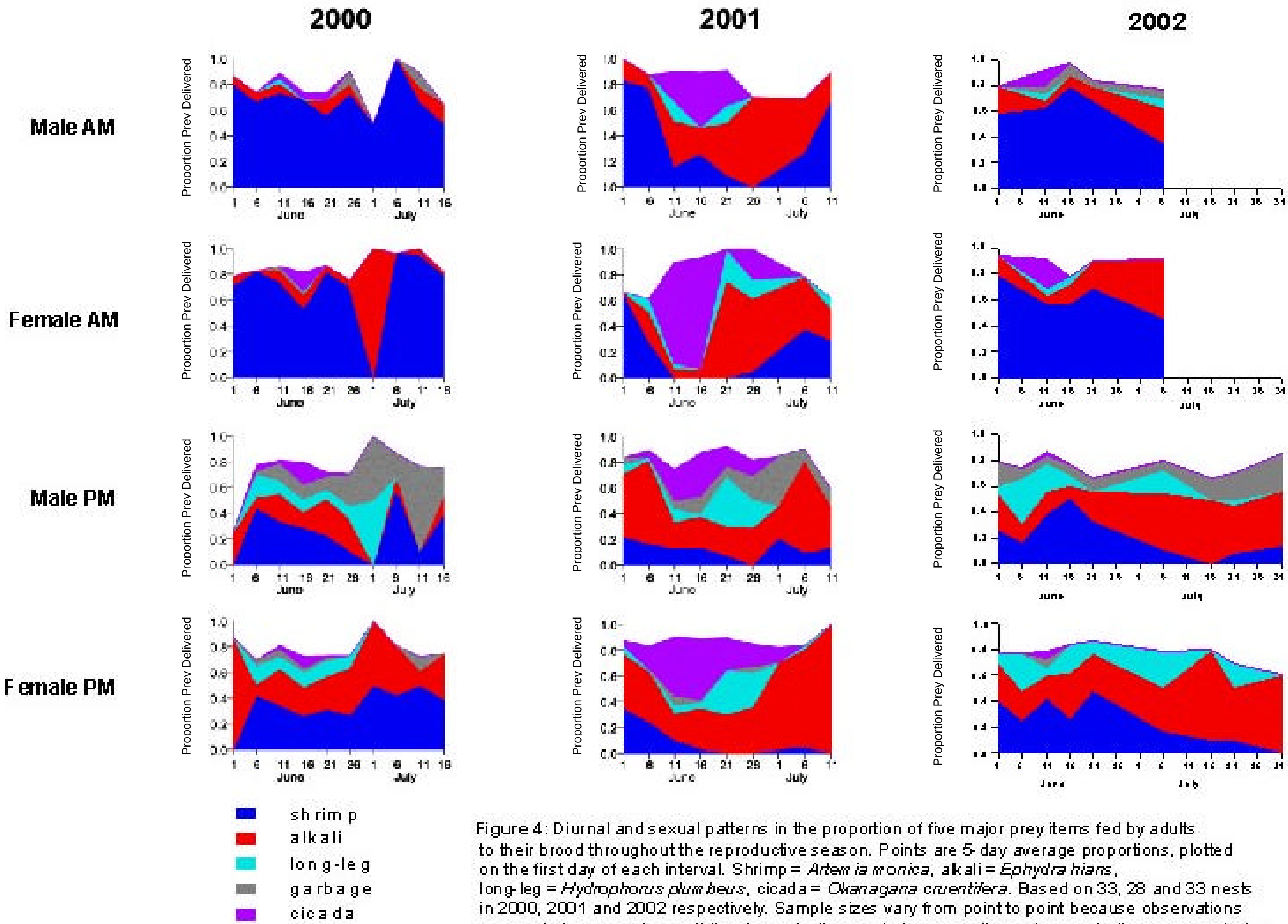

Figure 4: Diurnal and sexual patterns in the proportion of five major prey items fed by adults to their brood throughout the reproductive season. Points are 5-day average proportions, plotted on the first day of each interval. Shrimp = *Artemia monica*, alkali = *Ephydra hians*, long-leg = *Hydrophorus plumbeus*, cicada = *Okanagana cruentifera*. Based on 33, 28 and 33 nests in 2000, 2001 and 2002 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.

In 2002, observations of provisioning patterns continued until 2 August, far longer than in 2000 or 2001 (Figure 4). These late season observations were only conducted in the afternoon, however, limiting conclusions because we know diets vary between morning and afternoon. Diel variation notwithstanding, comparing changes in diet between early and late season within afternoon observations is still useful in understanding changes in provisioning patterns as the season neared its close. In Figure 5, the proportion of all feeds in the early season compared to the late season are shown using all diet data from 2002 (upper portion) as well as using only afternoon diet data in the early season as well the late.

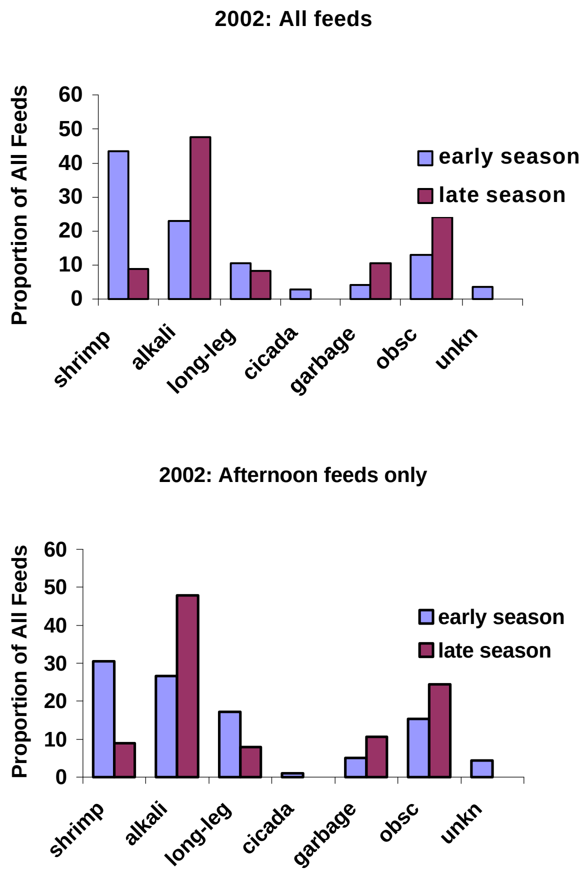

Figure 5. Relative frequency of prey types from feeding bouts in 2002 comparing early and late season feeds. 'Early season' includes all feeding observations from 6/1 to 7/17. 'Late season' is from 7/18 to 8/2. The lower graph is the same as the upper graph except that only afternoon data are included in the early season feeds to control for having only collected afternoon data in the late season. Prey types are the same as those in Figure 3.

In the late season, the amount of brine shrimp provisioned decreased to almost nothing, even when we excluded morning feeds. This was true for both sexes (Figure 4). The proportion of alkali flies rose dramatically, again even when we excluded morning feeds. Females were more likely than males to provide long-legged flies in the late season, and while provisioning levels for both sexes remained similar to the early season, they trailed off to zero at the end. Cicada use was limited primarily to a two-week period in June, and no cicadas were present in late season diets. Provisioning of garbage by females remained extremely low throughout the season, but by males it greatly increased in the late season.

Long-legged flies were more common in afternoon feeds in all three years, and were exploited at similar levels by males and females. Greater utilization of this prey source in the afternoon may in part be due to the greater likelihood of windy conditions in the afternoon compared to the morning, which offer gulls a unique foraging opportunity with respect to long-legged fly larvae (discussed in greater detail below).

The bloody cicada, *Okanagana cruentifer*, 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. In 2000 and 2002, gulls fed on cicadas for a two to three week period from early to late June, after which they disappeared from the diet. In 2001, this period was more extended, lasting into early July, after which they again disappeared from the diet before observations were concluded. In 2001, cicada feeds did not vary between time of day but did vary between sexes, with females more likely than males to feed cicadas to their chicks. In 2000, cicada feeds did not vary between sexes or between time of day, while in 2002 they did not vary between sex but did vary between time of day, with cicadas more likely in the morning than the afternoon.

The overall similarity of prey preferences in 2000 and 2002, and their marked differences from 2001, suggest that the former may be the typical provisioning pattern for California Gulls at Mono Lake. The low relative utilization of brine shrimp compared to alkali flies in 2001 may be in part related to heavy exploitation of cicadas. Diets in 2000 and 2002 differ most notably in the ratio of shrimp to alkali flies, decreasing from roughly 3:1 to 2:1.

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 (i.e. 'garbage' in Figure 4). Instead of being related to sex, the differences in apparent diet between day and night that Jehl and Mahoney (1983) report probably reflects differences in the composition of morning versus afternoon provisions fed to chicks by both sexes (Figure 4).

Diet and Chick Age

Chick growth follows a sinusoidal pattern, progressing slowly at first, increasing during a linear growth phase when energy demand is highest, and leveling off asymptotically as they approach adult size. Chick energy demands change as they develop, and adults may vary prey choices accordingly to meet these needs. These changing patterns of prey choice in response to chick age are not apparent in Figure 4, which summarizes diets for nests that hatched over a month-long period. Therefore, it is also useful to plot prey choice as a function of chick age (Figure 6). Due to the fact that no morning observations were conducted during the late season, all observations of chicks more than 50 days old were conducted in the afternoon. Comparing diets by age is not by itself a perfect way to look at the data – it does not take into account temporal phenomena like weather or the limited window when cicadas were available – but it is useful, especially when used in concert with a temporal analysis like Figure 4.

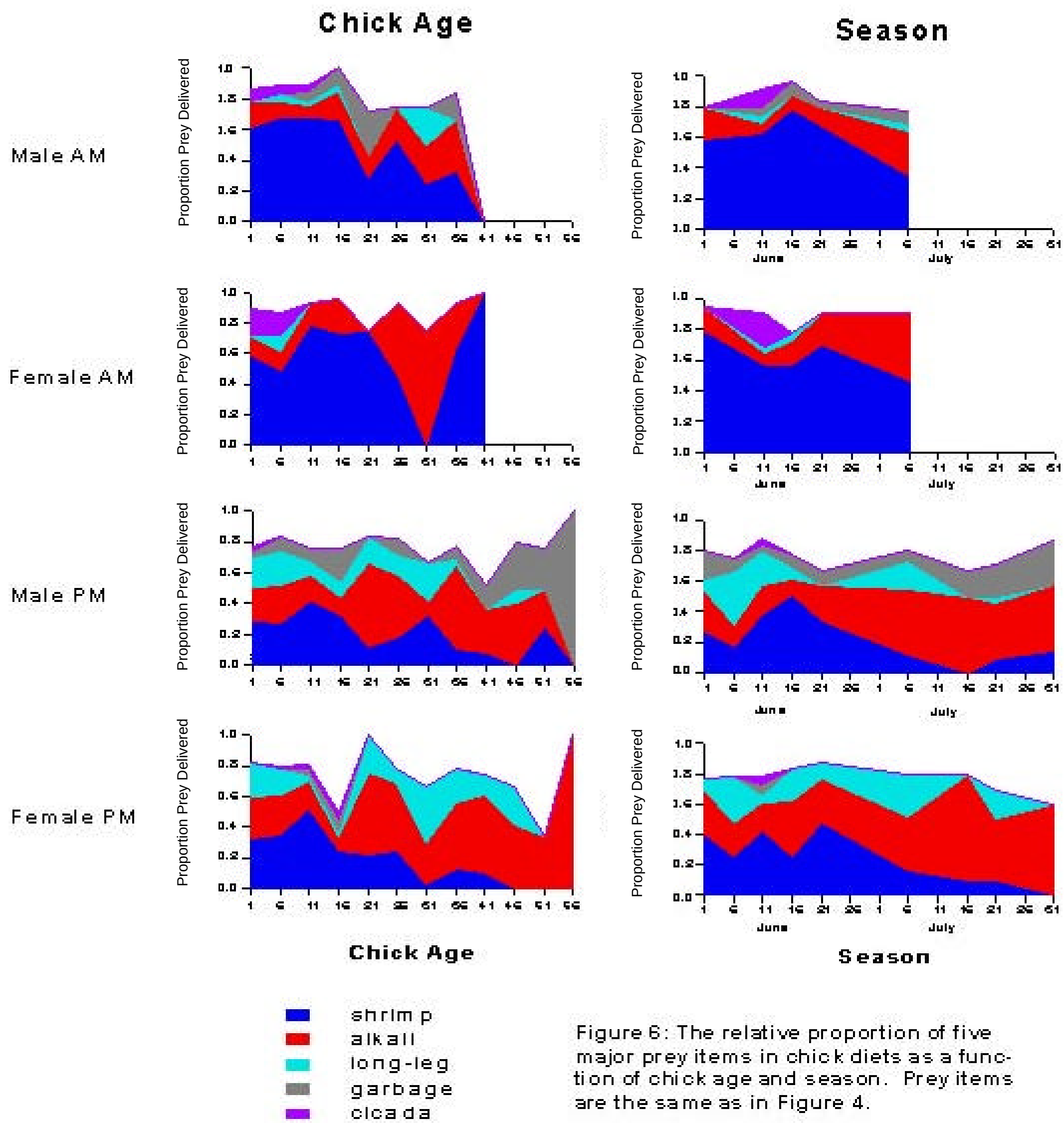

Figure 6: The relative proportion of five major prey items in chick diets as a function of chick age and season. Prey items are the same as in Figure 4.

Young chicks (up to five days old) received all major prey types, though garbage was only fed to a single nest of chicks this age. Brine shrimp started as the most common prey type delivered by both males and females until chicks were about 20 days old, though the amount of brine shrimp in the diet began decreasing when chicks were between 10 and 15 days old. The proportion of the diet made up of alkali flies jumped from 20% of the diet to 40% of the diet shortly after the chicks reached two weeks of age and remained at roughly that level from then until fledging. Long-legged flies were fed throughout chick development by both males and females. They remained at relatively constant levels until chicks were about 50 days old, after which they disappeared from the diet. While cicadas were not fed to chicks more than 20 days old, this was due to the disappearance of cicadas from all chicks' diets by late June (probably in response to declines in cicada availability) and not because they represent a poor food source for older chicks. Indeed, parents need to deliver more nutrition per visit as chicks grow older, and cicadas would likely be an ideal food source to older chicks if they remained available later into the season. The age class that received more cicadas than any other was chicks less than 5 days old, a fact that is very surprising considering the difficulty some of these small chicks seemed to have with swallowing even a single cicada. As mentioned above, females fed almost no garbage to their young in 2002, but garbage feeds by males greatly increased to chicks more than 45 days old and eventually became the only food fed to the oldest of the chicks.

Looking simply at how many alkali flies were fed to chicks hides variations in use of the three different life stages (Figure 7). In 2002, larvae made up the least portion of the diet that was alkali flies, and they were not fed to older chicks. Pupae were fed at a relatively constant rate both through the season and across chick age. Their representation amount increased both later in the season and in older chicks. Adult flies did not appear appreciably in chick diets until late June, and were likewise not fed much to chicks under two weeks of age.

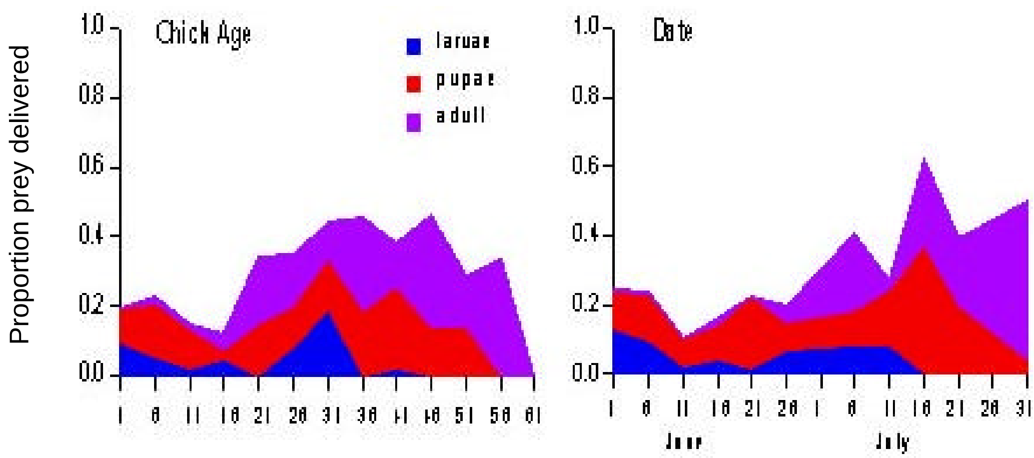

Figure 7. The relative proportions of the three life stages of alkali flies in chick diets, as a function of chick age or season. Data not separated by sex or time of day as in Figures 4 and 6. Points are 5-day average proportions, plotted on the first day of each interval.

Shrimp vs. Alkali Flies

In 2000 and 2002, 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 three 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 8), 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 8) 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). Lake-wide, 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.

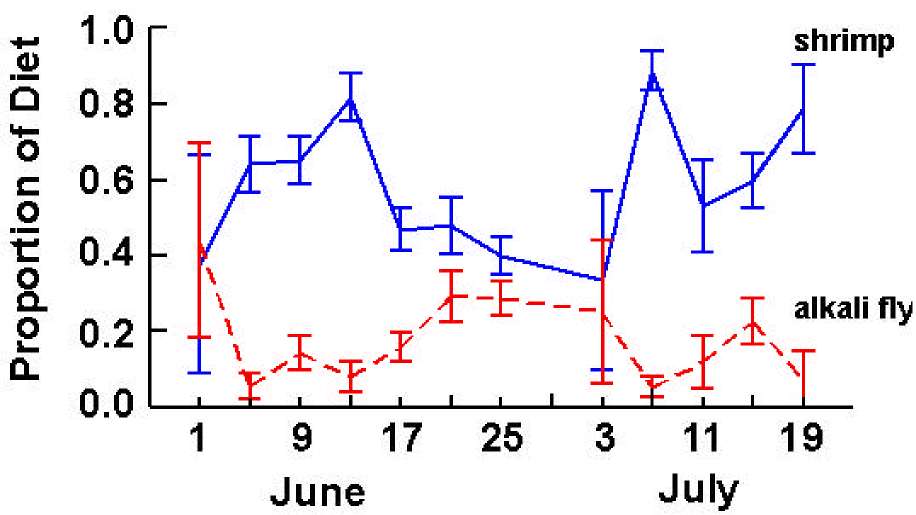

Figure 8. Proportion of brine shrimp and alkali flies in chick diets throughout the 2000 nesting season. Four-day means and SE are plotted (axis labels represent first day of the 4-day time period). "Alkali fly" here includes larvae, pupae, and adult stages. Means include only feeding bouts that included 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 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. 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 9). 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).

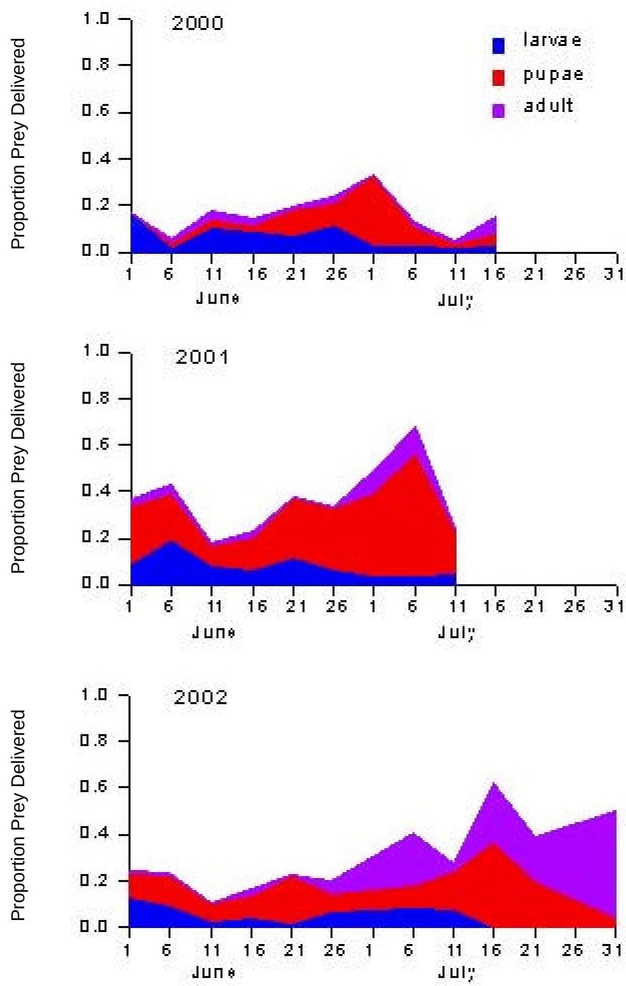

Figure 9. The relative proportion of the three alkali fly life-stages in chick diets in each of the three years of this study. Points are 5-day average proportions, plotted on the first day of each interval.

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.

A general linear model analysis comparing chick growth trajectories in 2000, 2001, and 2002 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 2001, chick growth was accelerated compared to that in 2000 or 2002, which were largely similar (Figure 10). Increased growth in 2001 is probably related to the increased use of alkali flies and/or cicadas in 2001, but it is impossible to tell the individual effects of these two prey types on chick growth.

Table 2. Annual and age variations in nestling mass (g). The regression model was highly significant, explaining 83% of variation in nestling mass. Only the linear portion of the growth trajectory (5-30 days of age) was examined in the model.

Source	Coeff	Std Coeff	Tolerance	t	p (2 tail)
Intercept	-1639.891	0.000	.	-1.768	0.078
Year	0.820	0.084	0.159	1.768	0.078
Chick age	6.786	150.480	0.000	2.899	0.004
Year by age interaction	-0.003	-149.560	0.000	-2.881	0.004

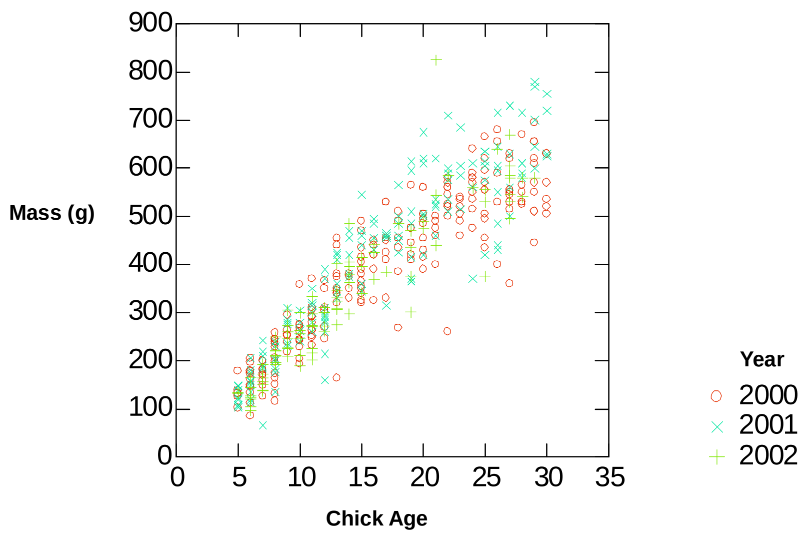

Figure 10. Chick growth in all three years of the study.

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 even though capture effort compared to other prey items is probably higher.

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 greater distances. Shrimp often 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 from 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, thus capturing multiple individuals with each peck. However, as there were no great differences in shrimp densities between the three years of this study, shrimp density alone does not explain why this prey was used much less in 2001 than in 2000 or 2002 (R. Jellison, personal communication; PHW & JMH 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 & JMH 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 (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 patterns may also explain the increased use of alkali flies compared to brine shrimp in 2001 compared to 2000 and 2002. Average wind speed during focal observations was roughly equal in 2000 and 2002, in both the morning and the afternoon. However, average wind speed in 2001 in both the morning and the afternoon was much higher than the other two years (Figure 11). Given that far fewer gulls have been observed foraging for shrimp during windy conditions, the greater prevalence of windy days in 2001 may explain the relatively low use of brine shrimp in that year

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 and 2002 this species was most notable on the north and northeast shore, but in 2001 we also sampled high densities at many locations along the Black Point shoreline. We observed gulls scraping away sand to access these larvae, but they foraged most intensively on this prey on days with very strong on-shore winds. 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).

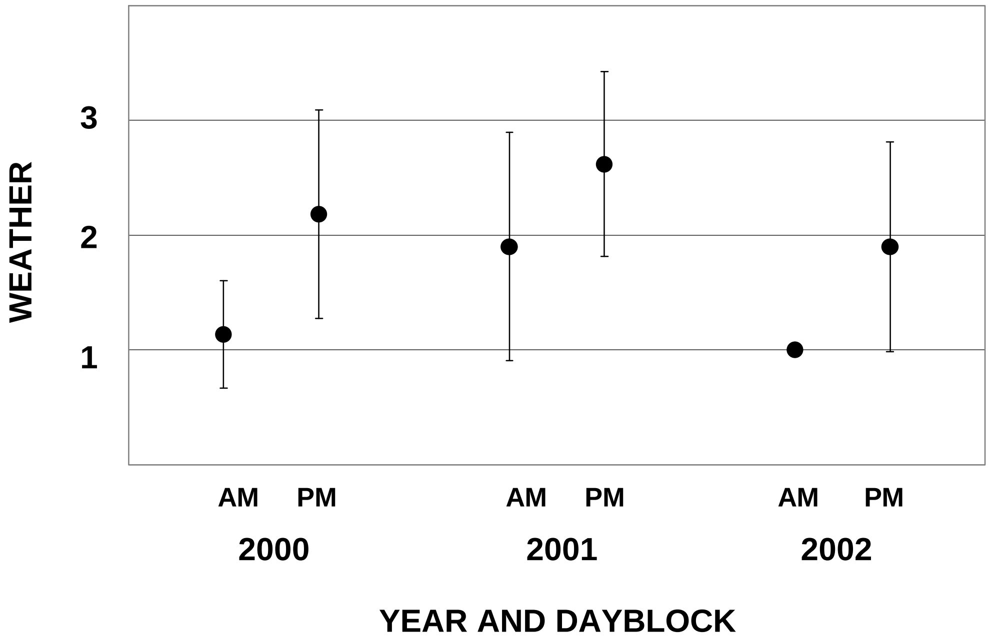

Figure 11. Average wind speed during focal observations in the morning and afternoon of all three years. Each focal observation was ranked as either a **1** (no/light wind), **2** (moderate wind), or **3** (heavy wind).

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 shifts 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 three 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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