Appendix C. California Gulls at Mono Lake since 1900: Population Trends, Survivorship, and Reproduction Success

POPULATIONS FROM 1900 TO 1940

Jehl et al. (1984, 1988) and Winkler and Shuford (1988) summarized the available information on Mono Lake's nesting California gulls since 1900 (Table C-1). These authors reviewed most of the same references contained in the incomplete historical record. They disagreed, however, on the reliability and interpretation of historical population estimates, especially the possible inferences regarding changes in the size and distribution of the gull colony in this century.

Dixon (1916) was apparently the first ornithologist to make quantitative censuses of the nesting gulls at Mono Lake. He estimated 1,000 pairs (about 2,000 adults) nesting along two long obsidian-like ridges on the north side of Paoha Island (Table C-1). Dixon (1916) also visited Negit Island but did not make reference to gulls nesting there. Based on Dixon's field notes, Grinnell and Storer (1924) characterized California gulls as "common in summer on Mono Lake, nesting on Paoha Island".

Dawson (1923) spent several days observing nesting California gulls on Paoha Island and estimated 250 pairs at the Lagoon Colony and about 600 pairs at the Black Rocks Colony (these colonies also were surveyed by Dixon [1916]) for a total of about 850 pairs (1,700 adults) (Table C-1). Dawson (1923) also visited the main colony on Negit Island, the largest at the lake at that time, but he did not estimate the number of gulls nesting there. He also observed an uncounted number of gulls nesting on the "outlying rock", which Jehl et al. (1984) identified as Little Tahiti Islet. Nichols (1938) reported that the Mono Lake colony was confined to Negit Island, and he estimated the total population at 3,000 adults.

Grinnell recorded a secondhand account of 60,000 nesting gulls at Mono Lake in his 1937 field notes (Table C-1). These notes also were reviewed by Winkler and Shuford (1988), who believed the secondhand nature of the account reduced its reliability because it was not based on Grinnell's personal observations. These authors, however, considered Grinnell's notes evidence that a sizeable colony probably nested at Mono Lake in the late 1930s.

Despite the few direct counts of the prediversion gull colony, the available observations provide evidence that at least a few thousand nesting gulls were present on Negit Island or Paoha Island before 1940 (Table C-1). Although it is much larger than Negit Island, Paoha Island was probably used less frequently by nesting gulls during this century because of the intermittent presence of humans, domestic goats, and coyotes (Jehl et al. 1984, McPherson pers. comm.).

POPULATIONS FROM 1941 TO 1975

The first postdiversion estimates of the California gull colony were made by Young (1952), who reported approximately 1,500 nesting birds restricted to about 3 acres on the northeast side of Negit Island (Table C-2). Young (1952), observing that his counts were lower than those of Dawson (1923), Grinnell and Storer (1924), and Nichols (1938) (Table C-2), believed that the population was declining. Young's (1952) comparisons of his estimates with those of Dawson (1923) have little meaning, however, because Dawson did not attempt to count the most populous colony on Negit Island.

Johnston (1956) conducted detailed studies of the reproductive physiology of California gulls at Negit Island, the only colony in the early 1950s. He did not attempt to make systematic censuses of their population, and his rough estimates ranged from 3,000 to 10,000 nesting adults during 1952 and 1953. Similarly, Johnston (1956) questioned Young's (1952) interpretation of gull population trends and indicated that it was unwise to speculate about the numbers in this colony until annual census data were available to replace the sporadic and perhaps inaccurate records that existed at that time.

Although Dawson (1923) reported an uncounted number of gulls on the "outlying rocks" of Negit Island in 1919, most of the highest Negit Islets emerged from the lake in the 1930s and these were mainly pinnacles. Not until the early 1960s did substantial areas of substrate suitable for nesting gulls become available (Stine 1992). The Negit Islets were apparently first colonized by large numbers of nesting gulls during the early or mid-1960s, but apparently no systematic counts of the California gull colony were made during this decade (Table C-2). Jurek (1972) made a rough estimate of 10,000 gulls in the vicinity of the colonies at Negit Island and the Negit Islets and estimated "uncounted thousands around the lake". He considered his estimate of 1,200 adults at Negit Island conservative because many birds were not visible, and he did not make a complete count there. Nesting gulls on the Negit Islets may have outnumbered those on Negit Island, but they were not counted (Jurek 1972).

Jurek (1973) estimated that 42,500 adult gulls were present during an aerial survey of Mono Lake in late August 1973. In most years, nesting California gulls depart from Mono Lake by early August, and Jurek's (1973) high count indicates an unusual influx of fall migrants, delayed breeding that year (Jehl et al. 1984), or possibly an overestimate.

Stallcup and Greenberg (1974) estimated 20,000-30,000 adult gulls at Mono Lake but their count was made from a mainland vantage point more than 4 miles from the nesting colony where most nesting gulls were not visible (Table C-2). Mangan (1974) also estimated about 20,000-30,000 breeding gulls, but he did not make separate counts of Negit Island and the Negit Islets. In 1975, however, Mangan

(1975) and Heindel (1975) estimated only about 2,000 adult gulls on Negit Island; none appeared to be nesting on the Negit Islets (Table C-2).

POPULATIONS FROM 1976 TO 1988

Winkler et al. (1977) made the first attempts to census the lake's entire gull population from the ground and estimated about 51,000 nesting adults in early July 1976 (Table C-3). During this census, about two-thirds of the nesting birds were on Negit Island and about one-third were on the Negit Islets. With a total of more than 50,000 nesting gulls, the Mono Lake colony was one of the two largest in the world and supported about 20% of the global population and 95% of the California nesting population of this species (Winkler 1983a, Dennis M. Power Associates 1980). The world's largest concentration of nesting California gulls occurs at the Great Salt Lake, which supported a population of about 75,000-80,000 adults during most of the 1980s (Paul et al. 1990) and currently holds about 130,000 nesting gulls (Jehl pers. comm.).

The Mono Lake colony was not censused in 1977 or 1978, but Winkler estimated that the gull population was roughly constant from 1976 to 1978 because the density of nesting gulls and their distribution appeared to be similar in those years (Winkler and Shuford 1988). During this period, the breeding population was estimated at 40,000-50,000 adults and the population used both Negit Island and the Negit Islets (Winkler 1980a, 1983b). Negit Island was first land bridged to the mainland around November 1977. Because of concerns about the potential impacts of coyotes and other terrestrial predators on nesting gulls, government agencies blasted a channel between Negit Island and the mainland in 1978 (Winkler 1980b, Winkler and Shuford 1988).

In July 1979, nesting gulls were first observed on the Paoha Islets. About one-quarter of the lake's population nested there that year (Jehl 1991a; Court Testimony, Vol. XIII) (Table C-3). Efforts to protect Negit Island, including blasting channels and erecting predator fences, were unsuccessful, and canids (probably coyotes) crossed the land bridge, causing abandonment of the Negit Island colony and reducing the number of successfully reproducing gulls (Winkler 1980b, 1983b). In 1980, the number of nesting gulls remained about the same as 1979 and the proportions of the total population nesting on the Negit and Paoha Islets remained about the same (Winkler 1987, Winkler and Shuford 1988).

During 1981-1982, Mono Lake dropped to its lowest historical elevation of 6,372 feet (NAS 1987, CORI 1988). The major difference between the census results in the 2 years was the absence of reproduction on Twain and Java Islets in 1982 because of land-bridging to the mainland at the beginning of the year. Twain Islet was the most densely populated islet from 1979 until 1981, and Twain and Java Islets had supported an average of 40% of lakewide breeding population during that period (Winkler 1983b).

In 1983, long-term gull studies were initiated on the Paoha Islets by the Hubbs-Sea World Research Institute (HSWRI) (Jehl 1983) and on the Negit Islets by the Point Reyes Bird Observatory

(PRBO) (Shuford et al. 1984). These research teams shared information and had more comprehensive coverage of the entire Mono Lake gull population, which improved the overall estimates of breeding adults and their reproductive success. Since 1983, the size of Mono Lake's gull colony has been estimated by counting the total number of occupied nests on each island and islet and multiplying by two adults per nest (Jehl 1983, 1984b; Shuford et al. 1984).

Between 1983 and 1988, the estimated number of adult gulls nesting at Mono Lake ranged between about 44,000 and 50,000 (Table C-3). Negit Island was recolonized by nesting gulls in 1985 after resident coyotes were trapped and removed from the island (Shuford and Page 1985, Winkler and Shuford 1988). A few gulls also nested on Duck Islet (a peninsula of Paoha Island at lake elevations below 6,379.5 feet) in 1986 but not in subsequent years after it again became a peninsula (Table C-3). Numbers of nesting gulls on Negit Island increased every year between 1985 and 1989, but at their maximum of about 5,500 adults (in 1989), they represented only about 12% of Mono Lake's nesting population. During 1983-1988, the majority of gulls nested on the Negit Islets, and almost one-half of the lake's population was on Twain Islet; other Negit Islets that supported more than 1,000 nesting gulls in any year included Little Tahiti, Little Norway, Steamboat, Java, Spot, and Tie (Dierks 1990, 1991).

About one-third of Mono Lake's gull population nested on the Paoha Islets in 1983, but from 1984 through 1988 the Paoha Islets never supported more than about 15% of the total population (Table C-3). During these years, Coyote Islet consistently supported more than 1,000 nesting gulls; Anderson, Browne, and portions of McPherson Islet supported 500 or more birds in most years (Jehl 1989). Other Paoha Islets, including Brewer, Hoffman, Gull, Smith, Conway, Dawson, Whitney, Channel, Obsidian, and Winkler, were used intermittently by nesting gulls because rapidly changing lake levels and related erosional forces made them unavailable in many years (Jehl 1989).

Despite rapid changes in the lake's level and the distribution of potential nesting habitat during 1983-1988, Mono Lake's adult gull population remained relatively stable (i.e., between about 44,000 and 50,000 birds) during this period.

POPULATIONS FROM 1989 THROUGH 1992

Coyotes were present on Negit Island and Pancake Islet in 1989, limiting gull reproduction at those sites. Gulls nested without disturbance, however, on other islets and most were on the Negit Islets with Twain, Java, and Little Tahiti supporting the largest populations. More than 5,000 gulls also nested in small colonies on the outer "white rocks" areas on the eastern and southern shoreline of Negit Island (Dierks 1990). Similarly, more than 5,000 gulls nested on the Paoha Islets in 1989 (Jehl 1989).

In 1990, the number of nesting gulls was estimated at 61,500, the highest recorded at Mono Lake by that time (Dierks 1991, Jehl 1991b). The number of nesting gulls on the Paoha Islets almost doubled from an estimated 2,682 in 1989 to 5,145 in 1990 (Jehl 1991b). Similarly, numbers of breeding gulls on most of the Negit Islets increased markedly from an estimated 16,641 in 1989 to 22,765 in 1990.

Gull numbers on Negit Island increased only slightly in 1990 compared to the previous year; Negit Island and Pancake Islet were the only two islands that were visited by coyotes that year (Dierks 1991). Pancake Islet was reinvaded by coyotes and other mainland predators in 1990; it supported 651 nests (down from 1,395 nests in 1989) in late May, when coyote tracks were first observed on that islet that year. In early July, Pancake Islet was totally abandoned; damaged eggshells also showed signs of canid predation, suggesting that coyotes had completely disrupted gull nesting (Dierks 1991).

In 1991, an estimated 43,520 adult gulls nested at Mono Lake and the Negit Islets and Negit Island supported 80% of the lake's breeding gulls. As in previous years, Twain Islet supported about one-half the nesting gulls at Mono Lake; Little Tahiti, Java, and Steamboat Islets also provided habitat for more than 1,000 adults. More than 1,500 gulls attempted nesting on land-bridged Negit Island, but they all abandoned the island by late May (see "Predation" below). Pancake Islet was connected to the mainland in 1991 and was not used by nesting gulls (Dierks and Shuford 1992). Approximately 8,884 gulls nested on the Paoha Islets in 1991; as in recent years, the largest colonies were on Browne, Coyote, and McPherson Islets (Jehl 1991b).

In 1992, the gull colony exceeded its 1990 high and an estimated 64,976 breeding adults were recorded at Mono Lake (Table C-3). More than 70% of the nesting gulls were on the Negit Islets; Twain Islet supported 31,792 adults, which represented almost 50% of the lake's breeding gulls that year (Shuford pers. comm.). Other Negit Islets supporting large numbers of nesting gulls included Little Tahiti (7,620), Little Norway (946), Steamboat (1,724), Java (2,080), and Spot (660) (Dierks and Shuford 1992).

Only four nests were found on Negit Island in 1992, and none was successful. The land bridge offered coyotes and other mainland predators easy access to the island and probably reduced its attractiveness to nesting gulls. Evidence of coyotes (i.e., fresh tracks and several recently preyed upon chick corpses) was found on Java Islet for the first time since 1982. Probably as a result of coyote predation, chicks on Java Islet had a low postbanding survival (percent of chicks banded in early July that fledged) and the rates on various Negit Islets were: Java (78%), Steamboat (95%), Krakatoa (90%), Little Norway (88%), Spot (88%), Little Tahiti (90%), and Twain (90%) (Shuford pers. comm.).

The Paoha Islets had unprecedented numbers of nesting gulls in 1992, when an estimated 18,566 adults were reported (Table C-3). This total represented more than 28% of the lake's population and included nearly twice as many breeding adults as were reported in 1990, the next highest yearly count. One pair of gulls tried unsuccessfully to nest on Paoha Island during the 1992 breeding season (Jehl pers. comm.).

REPRODUCTIVE SUCCESS FROM 1976 THROUGH 1992

Four techniques have been used to estimate gull reproductive success at Mono Lake, including the fenced plot, islet-by-islet, Lincoln index, and cooperative interagency census methods (Winkler 1983a, 1987). Only the fenced plot and islet-by-islet methods, however, have been widely used to report lakewide reproductive success since 1983 (Shuford pers. comm.). The fenced plot method involves direct counts of chicks in enclosures. This method is usually more accurate than the other techniques; however, the only long-term data set available using this method is from the Negit Islets (Shuford pers. comm.). The islet-by-islet method relies on the best estimates of reproductive success from each of the islands and islets derived from one of the three other methods mentioned above.

The first method used to estimate lakewide reproductive success, later known as the cooperative interagency census, was begun by Winkler in 1976 (Winkler 1983a). This technique employed censuses of chicks from a boat and had the advantages of rapid, lakewide coverage of the breeding colony and minimal disturbance of nesting birds (Winkler 1987). The main limitation of these censuses was the inability of observers to detect all chicks on islets of differing size and relief, which resulted in underestimates of the breeding adults and fledglings. Cooperative interagency counts were continued through 1987, however, to provide continuity with Winkler's (1983a) estimates of the number of fledged young that were derived using this method (Shuford pers. comm.). Shuford (1986) compared his estimates of fledging success in 1983-1986, which were derived from several largely independent methods of censusing, and found that they generated similar values.

Regardless of which method is used to derive the data, reproductive success is calculated by dividing the estimated number of fledged young in the entire colony by the number of breeding adults. The number of breeding adults early in the nesting season (e.g., the third week in May) is the most meaningful index of the adult breeding population (Winkler 1987). Late-season estimates (e.g., early July) of adult populations do not account for adults that initiated nesting but abandoned the effort (Winkler 1987). Thus, the fledging success per adult when applied to the entire colony is somewhat inflated because the total number of fledglings produced should be attributed to a smaller number of adults.

Based on reinterpretation of data originally presented by Winkler et al. (1977), fledging success of the Mono Lake gull colony was estimated at 0.52 in 1976 (Shuford pers. comm.). Systematic censuses of the gull colony were not conducted in 1977 and 1978, and no estimates of reproductive success are available for those years (Table C-3).

In 1979, mainland predators (probably coyotes) invaded Negit Island for the first time, and reproductive success for the Mono Lake colony was about half its calculated value in 1976 (Table C-3). Predators caused total reproductive failure on Negit Island that year but did not destroy the entire Mono Lake colony because many other gulls nested on the Negit and Paoha Islets (Winkler pers. comm.).

Winkler (1987) and Winkler and Shuford (1988) estimated the colony at relatively constant population sizes (i.e., between 40,000 and 50,000) from 1979 until 1982 but observed major differences in reproductive success in those years. In 1980, fledging success almost doubled compared to 1979, but 1981 and 1982 had the lowest reproductive success on record (Table C-3). High temperatures and possibly reduced food supplies were hypothesized to have caused high chick mortalities in 1981 (Winkler 1987). Twain and Java Islets were land bridged to the mainland late in 1981, and nesting gulls abandoned them in 1982. Total chick production in 1982 was about 43% lower than it had been the previous year. When adult gulls abandoned their nesting habitat on Twain and Java Islets, some of them apparently began preying on gull eggs from nests on other islets; some adult gulls whose nests had been destroyed also became "marauders" and probably increased overall nest predation even further (Winkler pers. comm.).

In winter 1982 and 1983, the elevation of Mono Lake increased by more than 8 feet due to extremely high runoff. In this period of lakewide changes, gull reproductive success increased from the values observed in the 1981 and 1982 breeding seasons (Table C-3). Lake levels continued to rise in 1984, but gull reproductive success decreased from the previous year. From 1985 until 1988, the lake's elevation remained above 6,378 feet and gull reproductive success was higher than that observed in the early 1980s (Table C-3).

Despite the presence of coyotes on Negit Island and Pancake Islet late in the season, gulls continued to reproduce successfully at Mono Lake in 1989 (Dierks 1990, Jehl 1989). Overall, reproductive success was high compared to the late 1970s and early 1980s (Table C-3). In 1990, the gull colony had the highest fledging success on record (Dierks 1991, Jehl 1991b). Lakewide reproductive success in 1991 declined from the previous year, and the three small colonies on Negit Island failed completely (see "Predation" below).

In 1992, fledging success was higher than in any previous year except 1990 (Table C-3). No clear explanation was apparent for the high fledging success reported at Mono Lake in 1992. Jehl and Shuford (pers. comms.) suspected it could have been due to the warm spring weather and an early brine shrimp hatch.

SURVIVORSHIP

Winkler (1987) analyzed 136 recoveries of gulls banded at Mono Lake between 1938 and 1985; the final pool included only records of birds that fledged and departed Mono Lake and that were recovered in reasonably fresh condition. In the past 20 years, sophisticated methods have been developed for estimating survival rates from band recovery data (Brownie et al. 1985). These new methods assume that large numbers of birds have been banded in all age classes in the same year and permit estimations of the age-specific survival and recovery rates of a larger population.

Unfortunately, the Mono Lake sample of band recoveries contained only one individual that had been banded as an adult; thus, it was not possible to use the new methods to estimate the age-specific survival rate of this population (Winkler 1987). A precise estimate of the adult and juvenile survival rates for the entire world population of this species was impossible using the new methods because fewer than 100 gulls banded as adults have been recovered dead in all the years of banding.

Due to the lack of adequate band recovery data, Winkler (1987) considered the distribution of the ages at death of all birds in the recovered sample, regardless of the year in which they were banded. By assuming that the interannual variation in survival rates was negligible, the population size was approximately stable, and the recovered sample was a random sample of the larger population, Winkler (1987) calculated a survival rate by estimating the rate at which the sizes of successive age classes dwindle. The mean survival rate over all age classes using these methods was 0.57.

Winkler (1987) also estimated survivorship of Mono Lake gulls by observing a population of color-banded adult gulls on Little Tahiti Islet from 1980 until 1982. By counting the number of marked gulls returning each year, he estimated the adult survival rate at 0.79. Winkler (1987) examined sources of bias to determine which value (e.g., 0.57 or 0.79) was the best estimate of gull survivorship. The estimate derived from the age structure assumed a relatively stable population, despite the fact that it was growing at an annual rate of about 5% from the early 1900s until the mid-1970s (Jehl et al. 1984). Population growth would have the effect of overrepresenting younger age classes in the sample but would be unlikely to affect the representation of older age classes.

Another source of bias in the life table analysis is the problem of band losses, which underrepresent older age classes and decrease their apparent survival rate (Winkler 1987). Recognizing the problems inherent in either approach to estimating survivorship, Winkler (1987) tentatively recommended survival rates of about 0.8 for adults and 0.6 for juveniles.

ESTIMATION OF POPULATION GROWTH RATE

Winkler (1987) used the estimates of survival rates and fecundity described in the preceding sections to produce a life table for the Mono Lake gull colony. The fecundity of this colony has been studied only since 1979, and even during this relatively short time fledging success has varied significantly (Table C-3). The life table must include a "typical" estimate of the number of fledglings produced per female in the population = m_x.

The Mono Lake colony has an unusually low clutch size, averaging only two eggs, which limits its potential production of offspring (Winkler 1985). Winkler (1987) used the 4 previous years of record (i.e., 1983 through 1986) and calculated that an individual on average produced only about 0.3325 offspring per reproductive season (sum of fledged chicks [61,201] divided by sum of adults early in the breeding season [184,078]). Fledging success has varied each year at Mono Lake, and average fecundity generally has increased in this colony since Winkler's (1987) analysis was conducted (Table C-3).

Given the uncertainties in the estimations of both fecundity and survivorship, Winkler (1987) presented his life table as a series of five options that depended on the initial assumptions. For each option, he tabulated the assumed survivorship and fecundity rates and calculated an overall population growth rate. A stable population would have a population growth rate of 1.0, and populations with growth rates less than 1.0 are shrinking; no population will persist for a long period with a growth rate of less than 1.0 without being constantly replenished by immigrants from other populations. Population growth rates for Winkler's (1987) five options ranged from a low of 0.661 to a high of 0.905, suggesting that the Mono Lake gull population was not sustaining itself with local recruits from the population.

Winkler (1987) also calculated the population growth rate of the population for a wide variety of survival rates and fecundities to determine how much these variables must be changed in order to predict a stable or increasing population. The results of these simulations suggest that the Mono Lake gull population will decline in the future (unless it is presently being supplemented by immigrants from other sites), or the values used for fecundity and survivorship are grossly underestimated (Winkler 1987).

Murray (1988) reviewed Winkler's (1987) life tables and concluded that an adequate analysis would require quality data on age-specific mortality and fecundity. Murray (1988) questioned the use of 0.3325 as an average annual fecundity value because it was calculated using the cooperative interagency census method. He recalculated fecundity rates using data gathered by other methods and concluded that the fenced plot method was the most reliable and yielded the highest m_x value (0.3953); those derived by the islet-by-islet method were closer to the fenced plots than they were to the interagency counts in 2 of 3 sample years. Murray also pointed out that Jehl and Stewart (1988) estimated 0.85 chicks per pair at nine fenced plots on the Paoha Islets in 1987; this converts to 0.445 chicks per adult, which may be a more realistic value of $m_{x.}$

Murray (1988) also questioned other aspects of Winkler's (1987) life table analysis, including the assumption of an 8-year life expectancy, the failure to include the effects of immigration in the model, and the calculations of finite rates of population increase. Winkler (1987) used an 8-year life expectancy because it was the oldest band recovery available, but this may be an unrealistically short life span for a bird of this size (Murray 1988). A life table that does not account for the effects of immigration underestimates the population's annual rate of growth. Finally, the range of values calculated by Winkler (1987) (i.e., 0.661 to 0.905) indicates a decline of between 34% and 10% for the Mono Lake gull colony. As presented by Winkler (1987), the population data from 1983 to 1986 indicated a slight increase, and Murray calculated on the basis of population size a value at 1.0318, representing an increase of about 3% per year.

Winkler's (1987) life table analysis and Murray's (1988) commentary received extensive discussion in court (Dodge, Goldsmith, Moskovitz, Court Testimony 1991, Vol. XXVII). Despite the attention these analyses have received in the literature and in court, important data are lacking for appropriate use of life tables to evaluate population changes of Mono Lake's gull colony. The lack of convincing data on age-specific survival and fecundity rates derived from marked populations of known age prevents the calculation of finite rates of population increase for this population. Even if such data existed, it may not be possible to calculate an average fecundity rate because fledging success is highly dependent on the incidence of land bridging and the subsequent invasions of coyotes and other mainland predators into formerly secure nesting islands.

If life tables are used to analyze population trends of the Mono Lake colony in the future, they should include fecundity and survivorship data derived from long-term studies (e.g., more than 10 years) to account for year-to-year variations that appear to be inherent in this population. If possible, such analyses also should consider the effects of immigration in overall population growth (Winkler pers. comm.).

FACTORS AFFECTING REPRODUCTIVE SUCCESS

The present status of gull nesting at Mono Lake is a complex interplay between several factors. Winkler (1987) described six factors that potentially could have major effects on the breeding productivity of gulls at Mono Lake, including predation, weather, parasites, food supply, nesting density, and habitat quality.

Predation

Predation and disturbance by great horned owls are known to have caused total reproductive failure on several small Paoha Islets and parts of larger islets in 1983 and 1984 (Jehl 1983, 1984b, 1991a; Court Testimony, Vol. XIII, p. 12; Court Testimony, Vol. XIV, pp. 4-7). Similarly, golden eagles and prairie falcons also prey on gulls at Mono Lake, but these avian predators typically visit colonies infrequently and are unlikely to reduce overall nesting success of large colonies (Jehl and Chase 1987, Winkler 1987). Although numerous examples exist of birds of prey disrupting gull nesting efforts, these predators appear to have had a negligible effect on the overall reproductive success of the Mono Lake colony or the entire nesting populations on large islets (Shuford 1985, Dierks 1990).

In contrast, mainland predators such as coyotes have had a major impact on the reproductive success of nesting gulls at Mono Lake, and studies from other areas have shown that canids can destroy nesting efforts if they gain access to gull colonies (Kadlec 1971). In 1979, coyotes crossed the land bridge to Negit Island and probably caused a complete nesting failure there. In 1982, Negit Island had already been abandoned and the coyotes crossed new land bridges to Twain and Java Islets and probably caused these colonies to fail (Winkler 1983b; Winkler and Shuford 1988; Jehl 1991a; Court Testimony, Vol. XIII, p. 12). In 1990, coyotes also were implicated in the abandonment of Pancake Islet (Dierks 1991). Gulls have made limited efforts to colonize Paoha Island in recent years (Jehl pers. comm.) and have failed, probably because several coyotes are resident on this island.

During April 23 and May 18-20, 1991, high coyote activity was observed on Negit Island, including fresh canid prints near two of three nesting groups and a sighting of an adult (Dierks and Shuford 1992). Nesting gulls abandoned Negit Island in late May (Shivik pers. comm.), and nests examined on July 10 contained eggs or downy carcasses of downy young, but not carcasses of feathered chicks (Dierks and Shuford 1992). The continued presence of coyotes on the island was suggested as the most likely reason for the abandonment by nesting gulls in 1991 (Dierks and Shuford 1992, Jehl pers. comm.). The presence of several decapitated adults, however, indicated that resident great horned owls probably also preyed on nesting adults (Jehl pers. comm.).

Twelve coyotes were fitted with radio collars in 1991 and monitored during the entire gull breeding season, including during winter gull arrival (October 20, 1990 to April 23, 1991), nesting and chick rearing (April 23 to July 26, 1991), and fledging and dispersal (July 26 to September 19, 1991) periods (Shivik and Crabtree 1992). Of the marked coyotes, three transient and one territorial individual visited the vicinity of Negit Island, primarily during the gull fledging and dispersal period (Shivik and Crabtree 1992). At least six adult coyotes (including marked and unmarked individuals) visited the island during the course of the study.

The high coyote activity in April and May corresponded with an abrupt decline in the number of crossings by marked individuals over the land bridge. Two or three coyotes resided on the island from April 23 until July 15 and probably excluded other coyotes during this period. A resident female was captured on Negit Island on July 3, and she remained on the island until July 15 before departing for the mainland. Coyote activity was evident on Negit Island for an additional 2 months after the gull abandonment occurred, suggesting that food supplies other than gulls could lead coyotes to take up residence there. Evidence of den digging suggested that coyotes also attempted to breed on the island (Shivik and Crabtree 1992).

Shivik and Crabtree (1992) found that coyotes in the study area ate many species of animals and adapted their diets to consume various available food sources. Rabbits were the primary prey ingested by coyotes during the winter gull arrival period and the fledging and dispersal period, and gulls were the primary food source during the nesting and chick rearing period. It should be noted, however, that gull biomass observed in scats does not directly translate to a predation rate; though gulls were known to have been killed by coyotes, some gulls may have been a scavenged food source.

Shivik and Crabtree (1992) found three adult gulls that were suspected of being eaten by coyotes, one of which showed direct evidence of being killed by a canid (e.g., canine punctures and subcutaneous hemorrhaging). Two eggs were found on Negit Island that appeared to have been eaten by coyotes (i.e., neat, incisor-like damage to an empty shell).

Egg shell fragments were found in six of 50 coyote scats collected on Negit Island from late April until early September (Shivik and Crabtree 1992). These eggs were not identified to species, but the following evidence suggests they were from gulls: no coyote activity was observed near artificial nests (stocked with chicken eggs) set out on Negit Island, nests of territorial passerines in the study area would be difficult to find, and gull nests are clumped in colonies permitting access to many nests simultaneously. Shivik (pers. comm.) concluded, however, that data from marked coyotes and direct observations of predation events would be required to clearly identify the cause of abandonment by Negit Island's nesting gulls in 1991.

Most predation events probably occur at night when humans are least likely to observe them. For example, Emlen et al. (1966) observed that nocturnal visits by a raccoon were indirectly responsible for extensive egg and chick mortality at a colony of ring-billed gulls in Michigan. The raccoon caused very little nest destruction but incited panic flights, which caused breeding adults to leave their nests for up to 4 hours and eventually to abandon the nesting area. Thus, coyotes at Mono Lake need not prey on a large number of gulls to have a disruptive effect on nesting efforts.

Observations made in previous breeding seasons also suggest that coyotes played a role in the abandonment of the Negit Island nesting populations in 1991 (Dierks 1990, 1991; Dierks and Shuford 1992). After gulls recolonized Negit Island in 1985, the first coyotes were not observed until 1989. In 1990, coyotes were again evident during the breeding season; Negit Island was the only large island that did not experience a large gull population increase that year. Dierks (1991) considered coyote predation to be a factor in the low reproductive success on Negit Island in 1989 and 1990. In 1991, the initial breeding population was lower than in 1990, and the island was abandoned relatively early in the breeding season. In light of predator-induced abandonment of Negit Island in 1979, Java and Twain Islets in 1982, Pancake Islet in 1990, and low fledgling survival on Java Islet in 1992, it is probable that coyotes also caused the abandonment of Negit Island in 1991.

Coyotes do not require a physical land bridge to gain entry to a nesting island. Murphy (pers. comm. in Shivik and Crabtree 1992) observed a coyote swimming between Negit and Paoha Islands in 1990, and he watched an individual swimming as far as 20 meters to reach Negit Island in 1991. Similarly, a water depth of 1 foot over the imminent land bridges to Negit Island and Pancake Islet (at lake elevations of about 6,376.5 feet) and Java and Twain Islets (at lake elevations of about 6,373.5 feet) was insufficient to prevent coyote crossings in 1979 and 1982, respectively (Winkler 1987). Coyotes have been resident on Paoha Island for years, however, and have apparently not crossed the relatively narrow channels (e.g., less than 100 yards wide) to the closest Paoha islets (Jehl pers. comm.).

In studies of canid behavior elsewhere, Getz and Smith (1989) found that distances of 60-150 meters (200-500 feet) and water depths of 0.6-1 meter (2-3 feet) were required to reduce canid predation of waterfowl nests. Likewise, Giroux (1981) recommended a distance of at least 170 meters (560 feet) and a depth of approximately 0.7 meter (2.3 feet) to ensure a reliable deterrent to coyote crossings of open water.

Weather

Heat stress may have caused the extremely high rate of chick mortality observed in 1981 (Jehl and Jehl 1982, Mahoney and Jehl 1982). Winkler (1983b) hypothesized that a combination of heat stress and food shortages may have been responsible. Heat stress may also have been a factor in the low reproductive success observed in 1984 (Shuford et al. 1985), and Winkler (1983a) also found statistically significant correlations between chick mortalities and high temperatures.

Jehl (1983) reported a high rate of gull chick mortality on low-lying portions of the Paoha Islets following heavy storms; he observed that high waves washed chicks away or drenched them with saltwater, causing death from exposure. Storm-induced mortality was negligible on the rocky, steep-sided Negit Islets during 1983 (Shuford et al. 1984). Because most gulls nest on high, rocky areas where they are protected from waves and high winds (e.g., Negit Islets or higher terraces of the Paoha Islets), severe storms are unlikely to have major effects on gull reproductive success at Mono Lake.

Parasites

A tick species (*Argas monolakensis*) unique to Mono Lake (Schwan et al. 1992) carries the Kemerovo group virus and was first discovered under gull nests at Mono Lake in 1966 (Johnson and Casals 1972). High levels of tick infestation have subsequently been reported on California gull adults and chicks (Schwan and Winkler 1984). Ticks have been reported on Mono Lake gulls and correlations have been noted between chick mortalities and levels of tick infestation (Shuford et al. 1984; Shuford 1985, 1986; Dierks 1990). However, no specific documentation indicates whether ticks (or the virus they carry) have had a major effect on the reproductive success of the Mono Lake gull population in any year (Shuford 1985, Dierks 1991).

Food Supply

Invertebrate prey at Mono Lake, including alkali flies and brine shrimp, has accounted for more than 50% (by volume) of gull chick diets in all sampling years since 1976 (Winkler 1983a, 1983b; Mahoney and Jehl 1982; Jehl 1984b; Shuford et al. 1985; Shuford 1985, 1986; Strauss 1987; Dierks 1988, 1990, 1991). For example, in a recent PRBO study the food items that had been fed to chicks just before capture were brine shrimp (57.4%), alkali flies (36.7%), fish (3.2%), and human garbage (2.7%) (Dierks 1991). Studies from Great Salt Lake (Winkler 1983a, 1987), however, indicate that brine shrimp are the least preferred food for gulls. Studies of foraging behavior at Mono Lake suggested that gulls primarily foraged at nearby dumps (e.g., within 30 miles of the lake) in early spring, but switched to natural food as soon as it became available (Jehl 1985).

Preliminary studies of the foraging ecology of juvenile California gulls at Mono Lake in July and August 1991 suggested that submerged tufa shoals are an important feeding habitat (Elphick and Rubega pers. comms.). These observers suggest that more than 50% of all feeding attempts by juvenile gulls in this habitat were either on emerging alkali flies or floating pupae. Furthermore, foraging success rates were high because emerging adult and pupal forms of the alkali fly are relatively inactive and easy to capture at the water surface. A high proportion of juvenile gulls frequent inshore areas while foraging, and it seems likely that these areas represent an important source of concentrated food. Elphick and Rubega (pers. comms.) suggest that alkali flies may contribute significantly to the survival of postfledgling gulls and may constitute gull's preferred prey during this period.

Dietary studies of California gulls are incomplete, but studies of invertebrate prey organisms indicate that alkali flies have a higher caloric value and lipid content than brine shrimp (Herbst et al. 1984) and represent the most nutritionally important food source at Mono Lake. Boula (1986) and Boula and Jarvis (1984) found that alkali flies were the most important food source to migratory water birds at Abert Lake, Oregon. Similarly, Rubega (1992) found that red-necked phalaropes required alkali flies in their diet at Mono Lake and that they could not survive in laboratory trials when offered an exclusive diet of brine shrimp. These studies do not discuss the nutritional requirements of California gulls, but it is likely that the high lipid content and caloric value of alkali flies are important to developing juvenile gulls.

During 1981, many chick deaths occurred late in the season; Winkler (1987) suggested that heat stress and possibly food shortages may have limited gull reproductive success. In 1982, the lake remained at low levels and brine shrimp densities were extremely low during spring and early summer. In this period, the gulls appeared to take other prey such as cicadas (*Okanagana gibbera*, *O. cruentifera*, and *O. occidentalis*), which are infrequently abundant in Mono Basin (Winkler 1983b). Brine shrimp densities recovered by July 1982, and gulls resumed foraging on brine shrimp as their primary food source. Recovery of brine shrimp numbers this late in the nesting season, however, was of limited value to the majority of gull chicks that had already passed through the most energy-demanding period of their growth (Winkler pers. comm.). Thus, at the lowest historical lake level (6,372 feet), brine shrimp appeared to be sufficiently abundant, at least after early summer, to sustain the nesting gulls. Cicadas also were extremely abundant that year and supplemented the food supply during this period of low brine shrimp abundance (Winkler pers. comm.).

Nesting Substrate

Jehl (1984b) and Jehl et al. (1984) characterized the preferred gull nesting habitat at Mono Lake as open, rough terrain on relatively flat terraces that are protected from the highest waves. Jehl (pers. comm.) noted that gulls on the Paoha Islets will first occupy areas of rough or rugose substrate (e.g., tufa-encrusted areas, logs, and small boulders), which occur both on and above the wave-cut platforms. Once these areas are occupied, the nesting birds will begin using nonrugose substrates (e.g., open sandy areas). With few exceptions, nesting gulls will not occupy any areas on wave-cut platforms less than 8-12 inches above the water surface or on the windward sides of the islets. They also will not occupy the steep wave-cut slopes of these islets.

Jehl (1991a; Court Testimony, Vol. XIII, pp. 3-7) stated that gulls do not select nesting habitats with regard to temperature or shade. He noted that California gull colonies at other nesting sites avoid thick, high brush that may impair lateral visibility, and that the historical colony on Negit Island was an anomalous situation. Further, he feels that there is little relationship between vegetative density and reproductive success and stated that nesting gulls tend to select open areas first (Jehl 1991a; Court Testimony, Vol. XII, pp. 76-79).

Based on observations of gulls in other portions of their range, such as the Great Salt Lake, Winkler (pers. comm.) believes that gulls colonizing a site for the first time will always prefer open nesting sites because they feel safer there. He does not regard open nesting sites as preferable in all circumstances, especially during hot years on islands that are safe from predators. He feels that gulls selected greasewood habitats on Negit Island prior to 1979 either because they gradually moved there from open areas as they gained a sense of security or because when gulls first started nesting in the area little open habitat was available. The gulls probably avoid greasewood habitats now because, like gulls everywhere that have experienced predation due to recent land bridging, they avoid habitats with limited visibility.

Until 1979, Negit Island was one of the only stable nesting islands for California gulls in their entire range (the other major site is Gunnison Island at Great Salt Lake where they nest in brush) (Winkler pers. comm.). Since 1979, Negit Island has been no more reliably predator-free than in most other places that this species nests, and it is not reasonable to expect them to immediately recolonize this area after recent land bridging events. If the Negit Island land bridge had never formed, Winkler (pers. comm.) would have expected the gulls to nest at higher numbers in greasewood habitats than in any other area at Mono Lake. He also predicted that they would have higher nesting productivity at Negit Island greasewood habitats, especially during hot years.

Shuford believes California gulls have a hierarchical method of habitat choice (Shuford 1991a; Court Testimony, Vol. XIV, pp. 12-18). The first factor is the selection of a nesting island that is free of ground predators. Once on the island, Shuford testified that gulls select shoreline nest sites if appropriate nesting substrates are available because these sites are typically cooler and more easily defended from other gulls. The disadvantage of shoreline nest sites is that they are more vulnerable to destruction from high waves. Preferred nesting substrates appear to be rough surfaces (e.g., rocks, tufa crust, shrubs, or logs), and the gulls avoid sandy beaches lacking surface debris, even if they are near the shoreline. Habitat relief probably provides several benefits, including visual screening from adjacent, territorial gulls and predators and shade for chicks. Shade may be important during hot years (such as 1981) when adults leave their chicks for long periods late in the nesting season (Winkler 1987).

In addition to nesting in greasewood scrub habitats on Negit Island before it was land bridged, California gulls have been observed nesting in scrub habitats elsewhere in their range, including at Honey Lake Wildlife Area and at portions of the Great Salt Lake (Shuford pers. comm.). Similarly, Pugesek and Diem's (1983) studies of nesting California gulls in Wyoming suggested that older gulls preferred to nest in sites with shrub shelter at the center of the colony. In their 2-year study, however, they found no significant differences in reproductive success between gulls of the same age nesting in shrubby and nonshrubby habitats. They cautioned that because their study had a short duration it may not have revealed the advantages of shrubby sites that might be apparent during infrequent or intermittent heat waves. The selection of shrubby sites by older gulls suggests that these areas may provide a long-term reproductive advantage.

In most years, California gulls at Mono Lake, and apparently at the Great Salt Lake (Paul et al. 1990), appear to be highly adaptable in their choice of nesting substrates and can reproduce successfully in both greasewood and open, unvegetated substrates. Reproductive success in these two habitats at Mono Lake, however, has not been compared over a period of years because recent land bridging has not permitted long-term studies of the Negit Island population. Recent nesting success on islands without extensive shrubs (Dierks 1990, 1991; Jehl 1989, 1991a) does not provide sufficient evidence to conclude gulls never benefit from nesting in shaded habitats.

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