Appendix I. Natural History of the Mono Lake Alkali Fly

This appendix presents a discussion of the life history of the Mono Lake alkali fly and the physical and biological constraints that determine the fly's abundance and distribution in Mono Lake.

CLASSIFICATION AND TAXONOMY

The Mono Lake alkali fly (*Ephydra hians* Say) was first described and classified by Say in 1830 as belonging to the shore and brine fly family Ephydridae, in the true fly order Diptera. Brine flies (*Ephydrids*) are often the most abundant benthic and shore inhabitants of saline aquatic habitats throughout the world (Herbst 1986).

The genus *Ephydra* inhabits extreme environments such as acidic thermal springs, alkaline saline lakes, tidal splash pools, and coastal marshes, but individual species often are adapted to particular habitat types (Herbst 1990a). For example, *Ephydra thermophilia* is present only in acidic hot springs in Yellowstone National Park, while *Ephydra cinerea* is found in the Great Salt Lake in Utah (Herbst 1986). The Mono Lake alkali fly, as its common name implies, is specifically adapted to alkaline habitats. The species inhabits many other alkaline saline lakes and ponds in North America (Herbst 1990b).

LIFE HISTORY

The Mono Lake alkali fly has a typical insect life cycle, developing from egg to larva before pupating and metamorphosing into an adult reproducing insect (refer to Figure 3E-3 in Chapter 3E, "Aquatic Productivity"). The life cycle begins as a mated female fly crawls underwater to lay her eggs individually on benthic algal mats or substrate close to shore. The eggs remain on the bottom mainly because they are heavier than Mono Lake water, although the female fly may further assist by tucking her eggs into the algal mat. The opalescent, non-sticky eggs are football-shaped and are approximately 0.6-1.0 mm long and about 0.2 mm wide (Herbst pers. comm.). Hatching success depends on salinity and temperature. The eggs hatch in 1-3 days into tiny larvae (first instars) (Herbst 1986).

The larvae undergo a series of distinct development phases (categorized as first, second, and third instars) and shed, or molt, the old skin (cuticle) between phases. Average Mono Lake alkali fly instar dry weight and size increase exponentially: first instars weigh 0.02 mg and are 1.0-3.5 mm long, second instars weigh 0.20 mg and are 3.5-5.5 mm long, and third instars weigh approximately 2.9 mg and are 5.5-12.0 mm long (Herbst 1990b, Herbst pers. comm.). Larval development ranges from 4 weeks to more than 5 months, depending on temperature, salinity, and food quantity and quality. Laboratory studies show that the growth and development at 20°C usually require 4 days for first instars, 7 days for second instars, and 14 days for third instars (Herbst pers. comm.) (refer to Figure 3E-4 in Chapter 3E, "Aquatic Productivity"). In Mono Lake, where water temperatures are often lower than 20°C, development times may be longer.

When ready to pupate, the mature larva attaches itself by means of clamp-like clawed caudal prolegs to a protected underside of a rock, where it is relatively safe from dislodgment by turbulent water. The larva encases itself in a puparium, where the nonfeeding, inactive pupa undergoes complete structural change and emerges as an adult alkali fly within 1-3 weeks, depending on temperature (Herbst 1986). At 20°C, pupation time is 13 days. The pupae range in length from 8 to 10 mm and average 1.95 mg dry weight. The puparium with the pupa fills with air during pupation and will float if dislodged.

When the adult Mono Lake alkali fly emerges from the puparium, it ascends to the water surface enclosed in an air bubble developed in the puparium. It spends the remainder of its life along the lake shore grazing on algal and detrital food sources and procreating (Herbst 1986, Herbst pers. comm.). Normal adult life span is 10-14 days, but overwintering adults may survive for months. Food is essential to successful reproduction, and adult flies are capable of submerging to gain access to high-quality benthic algae. Mating of the densely aggregated adults seems to be random with no precopulatory behavioral displays (Herbst 1986). Fecund female flies produce a daily average of approximately 10 eggs over a period of 2 weeks (Herbst 1992). The females submerge to deposit their eggs in the benthic algal mats, thus completing the life cycle.

Length of adult flies in Mono Lake ranges from 4.2 to 6.3 mm and averages 4.8 mm (Herbst 1990b). Adults from Mono Lake are consistently smaller than adult flies of the same species found in Abert Lake (Oregon), Pyramid Lake (Nevada), and Carson Sink Ponds (Nevada), which are saline inland waters with lower salinities than Mono Lake (Herbst 1990b). Laboratory rearing of alkali flies from different geographic locations indicates that body size is determined by both environmental and genetic components (Herbst 1990b).

Pupation and metamorphosis are high energy-consuming processes. The Mono Lake alkali fly reaches its highest caloric content as a third instar and early pupa; mature larvae contain 12.4 calories per individual, whereas pupae and adults contain only 11.2 and 7.2 calories per individual, respectively (Herbst 1986). Dry weight of the emerging adult is only approximately 1.3 mg, less than half the weight of the pupating larva. Larvae must reach a certain body weight and caloric content to ensure successful pupation and emergence (Herbst 1986, 1990b). Pupal mortality increases rapidly at pupal widths (dorso-ventral width between 3rd and 4th prolegs) below 1.7 mm, and pupae have little chance of survival at widths below 1.5 mm (Figure I-1) (Herbst pers. comm.).

Mono Lake alkali fly have few predators or competitors, and their numbers are limited mainly by food availability and physical constraints. Dislodgment of larvae and pupae brought on by storm-generated waves or currents are probably the main cause of mortality. Larvae and pupae use clawed prolegs to cling to hard surfaces to prevent being swept away to the middle of the lake or the shore, where they are exposed to starvation, predation, or parasitism (Herbst 1986).

EFFECTS OF ENVIRONMENTAL FACTORS ON DEVELOPMENT, SURVIVAL, AND REPRODUCTION

Temperature

Ambient temperature strongly affects temporal and spatial patterns of abundance of the Mono Lake alkali fly. Temperature is a major regulator of many life cycle processes of the fly, such as hatching, growth, development, pupation, metamorphosis, and egg laying.

Low ambient temperatures slow metabolic processes and increase development time and mortality. If temperatures drop below a certain threshold, development ceases altogether (Herbst 1988). Inactive, nonfeeding lifestages involving much structural development, such as the pupal and egg lifestages, are especially sensitive to low temperatures. Pupae cannot develop or survive long at water temperatures below 5°C (refer to Figure 3E-5 in Chapter 3E, "Aquatic Productivity") (Herbst 1988). Because winter temperatures in Mono Lake regularly drop below 5°C, pupae presumably suffer high winter mortalities. Eggs also perish at these ambient temperatures, but eggs are not generally exposed to cold water because adult flies do not produce eggs during winter. All larval instars can survive the near zero temperatures, however, and overwintering populations consist mainly of slowly growing second and third instars (Herbst 1988, 1990a).

Increasing water temperatures in spring (March-April) cause rapid growth and development of the overwintering larvae and increase rates of development and survival of the pupae. Development time of pupae in the laboratory decreased more than five-fold as temperature was raised from 10°C to 25°C (Figure I-2). As a result of increasing rates of growth and development, the alkali fly population increases exponentially during spring (refer to Figure 3E-6 in Chapter 3E, "Aquatic Productivity") (Herbst 1986). The population remains abundant through summer, until declining temperatures and shortened photo-period in autumn cause adult flies to cease laying eggs (Herbst 1988). Pupal densities are highest in early autumn (August-September). Population density drops rapidly in October when cooling temperatures cause high mortalities of all lifestages.

Body size of developing larvae and adult alkali flies exhibit seasonal cycles. The flies are largest in early spring and smallest in autumn (Figure I-3) (Herbst 1988). These seasonal variations in body size may be due to temperature-induced changes in fly metabolism or to seasonality of food quality (Herbst

1986). Large flies have less lipid reserves than smaller flies, however, so fly caloric value does not vary much seasonally.

The growing season available to the Mono Lake alkali fly is short due to the lake's high-altitude location and cool ambient temperature. However, the fly develops and reproduces rapidly, producing 1-3 generations in a season (Herbst 1988).

Alkali fly larvae and pupae are most abundant in water less than 3 feet deep and are rarely found below the thermocline, where temperatures are too cold for growth and development (Herbst and Bradley 1990). Littoral temperatures exhibit greater extremes than pelagic temperatures because shallow depths respond more quickly to heating and cooling. Selected littoral-benthic areas may freeze in winter and heat up to 40°C in summer (Herbst 1986, Herbst pers. comm.). Diel temperature fluctuations also are higher in shallow water than in the middle of the lake. Selected shallow areas of Mono Lake, such as Black Point Tufa Shoals, are more sheltered from wind and waves, resulting in higher water temperatures and a longer growing season.

Salinity

High salinities osmotically desiccate aquatic organisms because body fluids are less saline than the surrounding saltwater. The osmoregulatory mechanisms employed by the egg are unknown (NAS 1987). The larva maintains osmotic homeostasis by excreting salt through specialized organs in addition to using unknown mechanisms, whereas the developing pupa is protected from osmotic desiccation by the puparium (Herbst 1986).

The alkali fly is well adapted to high salinities, but the bioenergetic costs of osmotic regulation reduce the total energy available for growth and development (Herbst 1986). High salinities have a marked negative effect on larval growth and development rates, larval survivorship, and pupation success (Figures I-4 and I-5) (Herbst 1986, Bradley 1991). Hatching success and pupal weight also are negatively affected. At salinities above 150 grams per liter (g/l) the detrimental effects of osmotic stress become insurmountable (Herbst 1986). The early instars are particularly sensitive to high salinities (Herbst 1990b).

High salinity further affects the alkali fly by reducing algal primary productivity and, possibly, quality (Herbst 1992). As food availability declines, alkali fly growth and development rates decrease correspondingly, resulting in smaller pupae and adults, higher mortality, and less reproductive success (Herbst 1986, 1992). Increased energy must be spent on foraging, and it becomes more difficult for the larvae to meet the high osmoregulatory costs (Herbst 1990b).

Alkalinity

As in most alkaline saline lakes, alkalinity at Mono Lake is caused primarily by large concentrations of carbonate and bicarbonate ions (Herbst 1986). The carbonate and bicarbonate ions make up a constant 40% of the total dissolved solids of Mono Lake water, so alkalinity is linearly related to salinity. Although lakes exist worldwide supporting insect communities at salinities much higher than those found at Mono Lake, none is as alkaline (NAS 1987).

The combination of high salinity and high alkalinity is very difficult for most species to adapt to, yet Mono Lake alkali fly larvae survive better in alkaline salt water than in non-alkaline salt water of the same osmotic concentration (Herbst 1986). The larvae have a very unusual physiological adaptation for dealing with high concentrations of carbonate and bicarbonate ions accumulating in their blood. The lime gland, a kidney-like gland that in other insects commonly removes nitrogen wastes, in Mono lake alkali fly larvae also is used partially to remove carbonate ions from the blood. Within specialized lime gland tubules, excess carbonate ions are precipitated with calcium, forming calcium carbonate or limestone, which is stored inside the lime gland until metamorphosis occurs (Herbst pers. comm.). Larvae probably have a dietary need for calcium, as Mono Lake has extremely low calcium concentrations (Herbst pers. comm.). In Mono Lake, most calcium is bound as calcium carbonate and other minerals because carbonate and bicarbonate concentrations in the lake are so high. Tufa formations consist mostly of precipitated calcium carbonate.

Substrate

Mono Lake's shoreline is open and windswept. Storm-generated waves and undertows easily sweep away larvae and pupae not firmly attached to or sheltered by rocks. Once adrift in the lake or cast ashore, the larvae and pupae are likely victims of predators, desiccation, and parasitism. Wave action also shifts benthic sands and muds, potentially burying larvae and pupae. To survive these conditions, the alkali fly must have access to rocky surfaces or vegetation to which it can cling, especially during pupation.

The alkali fly's benthic-littoral habitat can be classified, based on attachment potential, as consisting of soft or hard substrate types (refer to Table 3E-1 and Figure 3E-8 in Chapter 3E, "Aquatic Productivity"). Mud, sand, and gravel are included in the soft substrate category, with mud predominant. Littoral sands and occasional gravels encircle Mono Lake above elevations of approximately 6,365 feet (Stine 1992). Tributary creeks are the main sources of littoral deposits of silt, sands, and gravels, but shoreline erosion also contributes some material. Benthic algal and detrital mats covering mud and sands flourish chiefly where the shoreline is somewhat sheltered from wind and waves. Although numerous larvae forage in the algal and detrital mats, soft substrate offers less shelter from waves and no firm attachment sites.

Densities of alkali fly larvae and pupae are much higher on hard substrates than on soft substrates (refer to Table 3E-2 in Chapter 3E, "Aquatic Productivity"). Soft substrate close to tufa has been found to be much more densely populated than soft substrate far removed from tufa areas (Little et al. 1989). Possible explanations of the higher densities near tufa include greater recruitment, reduced wave action, more accumulated detritus, and the presence of more nutritious food (Little et al. 1989).

Hard substrate types consist of tufa-covered pumice blocks, free-standing tufa, beachrock, bedrock, and mudstone. Mudstone is the most extensive of the hard substrates in terms of total acreage (refer to Table 3E-1 in Chapter 3E, "Aquatic Productivity"), but is considered a poor-quality hard substrate habitat because its surface is relatively soft and does not contain sheltering micro-crevices (Herbst pers. comm.). Most of Paoha Island consists of compacted and uplifted mudstone, as do the Paoha Islets and submerged slump-blocks to the north, east, and west of Paoha Island.

Scattered tufa-covered pumice blocks are the second most extensive hard substrate. The tufa-covered blocks are good habitat for the Mono Lake alkali fly larvae and pupae because their roughly textured surfaces provide good foothold and shelter from waves. Most pumice blocks are more than 3 feet across and are found up to an elevation of 6,390 feet in drifts mainly in northern and western portions of Mono Lake.

The pumice blocks are evidence of a volcanic eruption occurring when lake elevation was 6,390 feet. The eruption pitched the blocks into Mono Lake, and southeasterly winds and currents carried the blocks, which were buoyant due to enclosed gas bubbles, to the northern and western shores where they slowly became waterlogged and sank. The pumice blocks vary in size and areal density (Stine 1992).

Tufa-coated bedrock of volcanic origin is found on the Negit islets, on several points on Paoha Island, and along earthquake faults on the lake floor (Stine 1992). It is the third most abundant type of hard substrate in terms of total acreage and provides good habitat for the Mono Lake alkali fly. Because of the steepness of the bedrock areas, only a small portion is within the littoral zone (CORI 1988).

Scattered solitary tufa towers, continuous tufa bulwarks, and other free-standing tufa types constitute a small but important hard substrate habitat type. These tufa substrates occur primarily on the southern portion of the lake at elevations ranging from 6,300 to 6,400 feet and consist of calcite and aragonite (two forms of calcium carbonate) and other mineral deposits precipitated where fresh spring water from lake bottom orifices mixed with saline lake water (Stine 1992). Some tufa originates from the mineral, gaylussite (Herbst and Bradley 1990). Tufa forms slowly everywhere on the lake bottom, and submerged hard objects such as vegetation often become encrusted with tufa over time. Tufa formation rates are much more rapid where springs supply a constant influx of calcium ions, which is the limiting ingredient for tufa in Mono Lake.

Tufa of all types is the most suitable habitat for aquatic lifestages of the Mono Lake alkali fly. Field studies found third instar larvae and pupae in far greater densities on tufa than on any other hard or soft substrate (Little et al. 1989, Herbst 1992). The preference of alkali fly larvae and pupae for tufa has several plausible explanations. Tufa provides superior attachment sites because of its rough surface. Vertical towers have deeper crevices than any other substrate, sheltering larvae and pupae from waves and bird predators (Little et al. 1989). Towers are elevated above the lake bottom, protecting early lifestages from burial or abrasion by shifting bottom sands (Little et al. 1989). Tufa also serves as a growth site for algae.

Beachrock is a hard substrate habitat consisting of tufa-cemented sands, gravels, and cobbles, found mainly on the deltas of Mill and Lee Vining Creeks and other smaller tributaries. Beachrock formed when calcium containing fresh water mixed with carbonate rich lake water, resulting in calcium carbonate precipitating and cementing rocks and gravels together. Today much of the beach rock habitat is covered with littoral sands. Although beachrock provides good habitat for the Mono Lake alkali fly, it is of little importance because of its limited distribution (Little et al. 1989).

Submerged vegetation such as grasses and bushes also can provide good attachment sites for larvae and pupae. Density of larvae and pupae in areas of submerged vegetation is about half of that on tufa (Herbst 1990a). Vegetation can persist for up to 10 years before deteriorating (Herbst 1990b).

Food

The feeding niche of the Mono Lake alkali fly can best be described as that of a scraper-gatherer, herbivore-detritivore (Herbst 1986). Throughout all lifestages, food sources consist of benthic algae composed mainly of diatoms (especially *Nitzschia frustrulum*), filamentous green algae (especially *Ctenocladus circinnatus*), blue-green algae (especially *Oscillatoria*) and perhaps various bacteria and protozoa associated with detritus (Herbst 1986). No food is required during the egg and pupa lifestages, but food is essential for the larvae and adult fly. The adult fly is capable of submerging to gain access to high-quality benthic algae.

Reduced access to food or poor nutritional value of food results in high mortality, slow growth, prolonged development time, smaller size at maturity, and reduced reproductive success in the alkali fly (Herbst 1986). Dietary studies indicate that various lifestages thrive on food high in diatoms and blue-green algae, and that the green alga, *Ctenocladus*, is of less nutritional value to the alkali fly (Herbst 1986). No research has been conducted to investigate the importance of bacteria and protozoa in the diet.

Food may well be a limiting factor for the alkali fly, especially on crowded preferred habitat such as tufa. Pupal and adult body size decrease from spring through autumn (Figure I-3), possibly due to limited food resources resulting from an increasing fly population during this time period (Herbst 1986).

Physical factors affecting food availability during summer are primarily depth and nutrient supply (Herbst and Bradley 1989). Benthic algae standing crop decreases with depth, as light penetration decreases, so shallow waters have better food availability for the Mono Lake alkali fly. Low ammonium concentrations limit production of planktonic algae in spring and summer (see Chapter 3E, "Aquatic Productivity") and probably also may limit production of benthic algae (Herbst and Bradley 1989). Some Mono Lake benthic algae are nitrogen fixers and therefore contribute nitrogen to the aquatic ecosystem (Herbst pers. comm.).

Interspecific Competition, Diseases, and Predation

The Mono Lake alkali fly faces no serious competition from other species and is by far the most abundant macro-invertebrate present in the benthic-littoral habitat. Potential insect predators and competitors of the fly cannot survive in Mono Lake because salinity and alkalinity are too high. The high salinity and alkalinity also reduce parasitism and diseases.

Under low salinity conditions, mortality of the alkali fly from predators and parasites can be quite high. Beetles, damselfly larvae, and tabanid and dolichopodid larvae prey on alkali fly larvae in saline lakes with lower salinities, such as Walker and Pyramid Lakes in Nevada (Herbst 1986).

In Lake Abert, Oregon, 60-70% of alkali fly pupae dislodged and swept ashore in heaps (windrows) were parasitized by a small wasp, *Urolepis rufipes* (Herbst 1986). Adult flies are preyed on by tiger beetles, damselflies, robber flies, and other predaceous terrestrial insects, in addition to birds.

Birds, primarily gulls, phalaropes, and grebes, are the primary predators of the Mono Lake alkali fly. As discussed earlier, the lifestage with the greatest caloric value per individual is the mature third instar, followed by the pupa, and it is not surprising that these lifestages are the preferred prey for birds. Pupae and third instars also are the most accessible lifestages for birds, because large quantities are continually dislodged by waves and either swept out to the middle of the lake by wind and currents (classified as drift) or washed ashore in windrows. In either case, the pupae and larvae are fairly helpless, exposed, and easy to detect because of their size. Some birds eat adult flies congregated on the shore.

Nutritional value of larvae or pupae in drift and especially windrows declines rapidly with time because they quickly become desiccated, parasitized, and decomposed. Birds have constant access to freshly dislodged larvae and pupae during most of the summer because drift and windrows are continuously generated. Surveys of open water drift indicate that about 1 metric ton of larvae and pupae can be found floating on the lake in summer (Herbst 1992).

The seasonal distribution of drift follows that of the alkali fly productivity (Figure I-6) (Herbst 1992). Drift is uncommon in winter, increases in spring through summer, peaks in August, then sharply declines as temperatures drop in autumn (Herbst 1992). Windrow abundance presumably follows the same seasonal pattern as drift. August was the month when Kuzedika Paiute Indians historically gathered pupae and larvae for food at Mono Lake by seining the nearshore water. This harvest constituted an important part of the Kuzedika's diet.

Drift and windrows are not uniformly distributed in Mono lake. Drift is concentrated where currents converge or upwelling occurs, facilitating foraging by birds. The highest larval and pupal densities observed in drift samples were 10-20 individuals per square meter. Some water birds can further concentrate food by paddling around in circles, which creates upwelling currents.

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