FORAGING SNOWY PLOVERS AND THE DISTRIBUTION OF THEIR ARTHROPOD PREY AT MONO LAKE

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FORAGING ECOLOGY OF SNOWY PLOVERS AND THE DISTRIBUTION OF THEIR ARTHROPOD PREY AT MONO LAKE, CALIFORNIA

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ABSTRACT

The distribution, diet and feeding success of Snowy Plovers (Charadrius alexandrinus) foraging along the northeast shore of Mono Lake, California, were studied during the summer in 1980 and 1981; arthropod prey distribution and natural history were studied in 1981. Censuses of foraging plovers were made along 4.5 km of the lakeshore and along a 4.5 km long, nearby seep to determine the relative importance of these two feeding locations. Plover diet was determined by observing feeding birds, and by collecting feces and analyzing their contents. Arthropod abundance and distribution were assessed in 1981 by placing pitfall traps in feeding locations and other microhabitats within an area used by nesting plovers.

The prey resource for the Snowy Plover consists of a variety of ground-dwelling arthropods, primarily flies and beetles. Fifty-seven species (75,370 individuals) were collected from 73 pitfall traps placed in five major microhabitats. A mean of about 24 species were captured from each of 12 sampling sites. The most abundant species were Araneae (Dictynidae: Dictyna sp.), Collembola (Poduridae: indet. sp.), Hemiptera (Saldidae: Saldula

arenicola), Coleoptera (Carabidae: *Bembidion ephippigerum*; Staphylinidae: *Bledius* sp.; Anthicidae: *Tanarthrus inyo*), and Diptera (Dolichopodidae: *Thinophilus spinipes*; Ephydridae: *Ephydra hians*, *Mosillus bidentatus*, *Ptilomyia alkalinella*.

The region within 25 m of the water at the lakeshore and a 1 km section of the seeps had the highest numbers of arthropods according to the pitfall trap results. *Ephydra hians* and *Bembidion ephippigerum* were two of the most abundant, suitably-sized prey species in these two areas. *Ephydra hians* larvae and pupae reached very high densities in certain regions of the seeps. *Bembidion ephippigerum* is apparently active both day and night. Low numbers of arthropods were captured from pitfall traps placed on the dry alkali flats and gravel ridges. Three species of dolichopodid flies (*Thinophilus spinipes*, *T. latimanus*, and *Hydatostega plumbea*) collected during this study are new records for California.

The population of foraging Snowy Plovers that I studied consisted of approximately 53 birds in 1980 and 100 birds in 1981. Very little foraging was observed where most plovers nested: the alkali flats and gravel ridges. Plovers did most foraging at neutral feeding grounds that were up to 1.5 km from some nesting territories. More plovers foraged along the lakeshore than at the seeps during both years, but this difference was only significant in 1981. In 1981 four times as many plovers used the lakeshore as the seeps. Plovers were generally well-spaced while foraging, but there was no evidence that feeding territories were maintained. Significantly more males than females were encountered on lakeshore censuses in 1980 and 1981, and at the seeps in 1980.

The exoskeletal fragments of 12 arthropod species (6 dipterans; 4 coleopterans; 1 hemipteran; 1 branchiopod crustacean) were identified in plover feces. The main prey were Ephydra hians and Bembidion ephippigerum; 91% of the feces contained the fragments of one of these two species. Adult E. hians and B. ephippigerum appear to be the main prey taken at the lakeshore, but E. hians larvae are probably the main prey taken at the seeps. At the lakeshore plovers appear to take E. hians, B. ephippigerum and Tanarthrus inyo in proportion to the relative abundance of each species as determined by pitfall traps.

When plovers were actively feeding they made about 5-7 prey capture attempts per minute. A higher percentage of prey capture attempts were successful when plovers foraged for Ephydra hians larvae than when they foraged for adult flies. About twice as many larvae were captured as adult flies in a typical foraging bout.

Substrate moisture and shoreline detritus apparently affect the distribution and abundance of arthropods at Mono Lake; arthropod abundance, in turn, influences the foraging locations of Snowy Plovers. Plovers foraged where prey were most abundant. The impact of water diversions from the Mono Lake Basin on Snowy Plovers and their arthropod food supply is briefly discussed.

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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

A view of the study area at Mono Lake looking to the southwest from the gravel ridges.

INTRODUCTION

This report summarizes the results of a study conducted at Mono Lake, California, in 1980 and 1981 of foraging Snowy Plovers (*Charadrius alexandrinus nivosus*) and their arthropod prey. The purpose of this study was to investigate the distribution, diet and foraging behavior of Snowy Plovers breeding on the northeast shore of the lake. The relationship between the plovers' choice of feeding areas and the abundance of their arthropod prey was also examined. Visual observations of foraging birds and the analysis of fecal material was used to determine their diet. The distribution, microhabitat preference, and relative abundance of arthropods was investigated primarily by using pitfall traps.

The Snowy Plover is a small shorebird in the family Charadriidae. It has one of the most cosmopolitan ranges of any shorebird and populations breed on continents and islands throughout the world (Palmer 1967). Nesting populations in California are found along coastal sandy beaches and on sparsely vegetated or barren flats adjacent to shallow lakes, mostly east of the Sierra Nevada and Cascade Mountain ranges (Page and Stenzel 1981). In 1976 Snowy

Plovers were discovered nesting at Mono Lake (Winkler et al. 1977). The results from a recent survey of the plover's breeding distribution and status have shown that the population at Mono Lake (384 adults in 1978) is the second largest in California and comprises 10% of the state population (Henderson and Page 1981).

The breeding biology of the Snowy Plover has been the focus of studies at Mono Lake by Gary Page and Lynne Stenzel of the Point Reyes Bird Observatory. This research centered on breeding productivity, nest dispersion patterns and the impact of nest predators on breeding success (Page et al. 1983). Part of this study was to determine if Snowy Plovers maintained feeding territories.

It is difficult to assess adequately the food supply of insectivorous birds. Morse (1970) states that few studies present accurate estimates of how much prey is available in the habitat and how much is taken. Gibb's (1960, 1966) studies of parids feeding on insect larvae in pine plantations are among the most detailed of any investigations of insectivorous birds and their prey. The heterogeneous nature of most habitats used by insectivorous birds and the patchy occurrence of insect populations are factors that make the measurement of this prey resource so difficult. Nonetheless, many workers have attempted to measure prey populations in studies comparing territory size and resource abundance in insectivorous birds (Stenger

1958, Schoener 1968, Cody and Cody 1972, Wiens 1973, Seastedt and MacLean 1979).

Numerous studies have investigated the marine invertebrate diet and foraging ecology of shorebirds on the wintering grounds. Grinnell et al. (1918), Bent (1929), Palmer (1967), Hale (1980) and Johnsgard (1981) provide information on the general diet of plovers. The information on the Killdeer (Charadrius vociferus) (Bryant 1914, Grinnell et al. 1918) indicates that insects make up most of their diet year-round. Page and Stenzel (MS) investigated the winter diet of the Semipalmated Plover (Charadrius semipalmatus) and the Black-bellied Plover (Pluvialis squatarola), and found annelid worms, small crustaceans and dipteran larvae to be their main prey. Strauch and Able (1979) made a detailed study of three plovers (Charadrius semipalmatus, C. Collaris and C. wilsonia) in Panama. Duffy et al. (1981) studied Semipalmated Plovers and other shorebirds on their wintering grounds in Peru. The diet of the Semipalmated and the Golden Plover (Pluvialis dominica) was studied on their breeding grounds by Baker (1977). In most cases, when plovers feed in estuarine or coastal sandy beach habitats they take small marine invertebrates, but at inland locations insects are their major prey.

On the nesting grounds most shorebirds are insectivores, yet little quantitative information exists on the diet and food availability during this season (Hale 1979, 1980). Exceptions are the studies by Pitelka and his students of Calidris sandpipers nesting on the tundra at Point Barrow, Alaska (Pitelka 1959, Holmes 1966, Holmes and Pitelka 1968, Holmes 1970, MacLean and Pitelka 1971).

Cramp and Simmons (1983) summarized a variety of information on the diet of the European race of the Snowy Plover (C. a. alexandrinus) breeding in inland areas of the western Palearctic region and report that they take mainly flies and beetles. Little is known of the diet or feeding ecology of Snowy Plovers in North America. On the Great Salt Plains in Oklahoma, Snowy Plovers were observed feeding on the brine fly Ephydra hians (Diptera: Ephydridae), Bledius (Coleoptera: Staphylinidae), and a variety of lepidopterans, grasshoppers and large beetles blown onto the flats from the surrounding vegetation (Ortenberger and Bird 1933, Purdue 1976, Groves and Knopf 1982). Groves and Knopf (1982) also found Snowy Plovers feeding on localized and abundant water boatmen (Hemiptera). On salt evaporating ponds in south San Francisco Bay and San Diego Bay plovers feed extensively on brine flies (Ephydridae) (Page and Stenzel 1981, pers. obs.). At a coastal sandy beach location in central California (Limantour Spit, Marin County), oligochaetes, polychaetes, and small crustaceans were the primary prey items in stomach-pumped samples of three Snowy Plovers (Page and Stenzel, unpubl. data). Fisher (1893:25-26) visited Owens Lake, Inyo County, California, in early June 1891 and made the following observations of Snowy Plovers foraging on brine flies:

> it fed extensively, if not exclusively, on a species of small fly (Ephydra hians Say), which was found in immense masses near the edge of the lake. Many of these swarms of flies were four and five layers deep and covered an area of 15 or 20 square feet. Some idea can be formed of the inexhaustible supply of food which these insects furnish for birds when it is known that colonies of equal size occurred at close intervals in suitable localities all around the lake, which has a shore line of between 40 and 50 miles.

In 1980 Snowy Plovers were observed feeding on brine flies along the shallow creeks that now flow onto the dry lakebed of Owens Lake (pers. obs.).

A number of methods have been used by previous workers to study the diet of shorebirds. Most have involved collecting birds and examining stomach contents (e.g. Reeder 1951, Holmes 1966, Recher 1966, White and Harris 1966, Brooks 1967, Bengston and Svensson 1968, Holmes and Pitelka 1968, Goss-Custard 1969, Prater 1972, Baker 1977, Strauch and Able 1979, Rundle 1982). Other researchers have determined diet by visually identifying prey items as they are taken by foraging birds (Baker and Baker 1973, Goss-Custard and Jones 1976, Stenzel et al. 1976, Morrell et al. 1979). The use of prey remains at the nest site (Morrell et al. 1979), regurgitated pellets

(Hibbert-Ware and Rutledge 1944, Goss-Custard and Jones 1976, Stenzel et al. 1976, Harris 1979) and fecal material (Feare 1966, Goss-Custard et al. 1977, Duffy et al. 1981) are some methods used to assess shorebird diet that did not involve sacrificing any birds. Feces have also been used to examine the diet of other types of birds: Hawaiian Goose (*Nesochen sandvicensis*) (Baldwin 1947), House Martin (*Delichon urbica*) (Bryant 1973), wagtails (*Motacilla* spp.) (Davies 1976) Sand Martin (*Riparia riparia*) (Waugh 1979), and the Dartford Warbler (*Sylvia undata*) (Bibby 1979). Hartley (1948) and Rundle (1982) have criticized the use of fecal material to determine diet; but, if the species under investigation is rare or endangered (Baldwin 1947, Bibby 1979) or if local populations are small, this is nevertheless a useful technique. Stenzel et al. (1976) emphasized that if they had collected specimens for stomach analysis rather than using other methods to determine diet, they would have removed the equivalent of 75% of the Long-billed Curlews (*Numenius americanus*) and 21% of the Willets (*Catoptrophorus semipalmatus*) from the local population. Furthermore, if collecting would disrupt other aspects of a study then alternative methods of determining diet are needed (Davies 1976, Jehl 1979).

The only information on the shoreline arthropods at Mono Lake is provided by Herbst (1977) who collected at seven lakeshore sites in July and August 1976. In the present study pitfall traps were the primary technique used to investigate the arthropods along the northeast shore of the lake. Pitfall traps have been widely used to sample populations of ground-dwelling arthropods (Greenslade 1964, Gist and Crossley 1973, Uetz and Unzicker 1976, Luff 1975, Baars 1979, Curtis 1980). Although several investigators have pointed out problems with pitfall traps (Greenslade 1964, Southwood 1978), they are considered to be an adequate method for determining the relative abundance of arthropods when the habitat is flat and fairly homogeneous.

STUDY AREA

Mono Lake lies in a closed basin at the eastern base of the Sierra Nevada, about 16 km east of Yosemite National Park. The lake currently sits at an elevation of approximately 1940 m above sea level and measures 15 by 20 km. The lake level, however, is falling an average of 0.46 m a year (P. Vorster, pers. comm.) as a result of the diversion of tributary streams by the City of Los Angeles. The lake is very saline and alkaline due to high concentrations of chlorides, carbonates and sulfates (Dana et al. 1977). In August 1980 the total dissolved solid concentration was 90,000 mg/liter (L.A. Dept. of Water and Power, *fide* P. Vorster). Just two species of macroscopic aquatic invertebrates live in the lake, the brine shrimp

(*Artemia monica*) and the brine fly (*Ephydra hians*), but they occur in extraordinary numbers.

During the spring and summer the climate of the Mono Basin is typically dry and hot. Daytime temperatures sometimes surpass 32°C, but at night temperatures often drop below freezing (Page et al. 1979). Wind speeds above 50 km/hr are not infrequent and wind direction is generally from the south. Alkali dust storms along the north and east shore are common. Although thunderstorms occur regularly in the early afternoon in August, precipitation rarely reaches the ground.

The study area, on the northeast shore of the lake, spans 4.5 km in a northwest-southeast direction and 1.5 km in a northeast-southwest direction (Fig. 1). Much of the study area consists of lakebottom sediments that have only been exposed since 1941 when water diversions began. The terrain comprises mostly broad alkali flats with little topographic relief. Three or four rolling gravel ridges, running parallel to the lakeshore, rise 5-15 m above the flats along the northern edge of the study area. The area is barren of vegetation except for scattered greasewood bushes (*Sarcobatus vermiculatus*) and a sparse cover of salt grass (*Distichlis spicata*) on the gravel ridges. The gravel ridges and other low ridges 0.1-0.5 m high on the alkali flats represent old shorelines where the water level remained stable for a period of time. The three most prominent ridges, High Ridge (HR), Upper Drift Ridge (UDR) and Drift Ridge (DR) were 1400 m, 1100 m and 750 m respectively from the water's edge in 1978 (Fig. 1). These distances increase by 30 to 100 m a year (in years of average precipitation) as a result of the receding lakeshore.

Above UDR the gravel ridge substrate consists of sand sprinkled with small dark-colored basalt pebbles. Scattered driftwood occurs along UDR and DR. Below UDR and extending to within about 100 m of the water's edge the substrate consists of sand mixed with alkali. Loose drifted sand covers this alkali-sand crust in places, and the crust often forms a puckery layer 1-3 cm above a lower layer of moist sand. Bright green-colored algae grows on top of the moist sand when it is shaded by the alkali crust. Within approximately 150 m of the water's edge seepage begins to saturate the substrate. Here a thin layer of wet or dry alkali often covers a moist mixture of brown clay or silt and decomposing organic material. In places this substrate is so saturated with water that walking through it is accomplished only with great difficulty. Other areas along shore are dry and firm due to accumulations of small white tufa pebbles (tufa is calcium carbonate) or sand. Windrows of brine fly pupal cases, feathers, and decomposing brine shrimp appear along the shore after periods of strong winds. Tufa towers up to 1.5 m high dot parts of the shoreline and project above the lake's surface.

Underground water percolates to the surface along the south edge of DR where it forms shallow puddles of brine up to 200 m wide. This region is called the DR seeps (Fig. 1). Salts crystallize into a crust over some of the puddles and halophytic bacteria often turns the water pink. The upper edge of the seeps closest to the row of stakes marking Drift Ridge is composed of firm moist sand. The seeps contracted slightly as the season progressed, but when rain fell (an uncommon event) they temporarily enlarged if precipitation was sufficient. After rains even the alkali flats remained damp for several days. The alkali just below UDR was consistently damp although no puddles of brine developed.

Water bubbles onto the alkali from several fresh-water springs (0.5-1.5 m diameter) saturating small areas of flat that often supported growths of red algae. A deep pool measuring 10 by 15 m is located in the southeast corner of the study area. The springs fluctuated slightly in size through the season and from one year to the next. Groundwater originating in the Bodie Hills north of the lake appears to be the source for the springs and seeps along the northeast shore. The total dissolved solids of some of the springs and seeps ranges from 900-2200 mg/liter (P. Datzman, letter).

Snowy Plovers nest on the alkali flats and gravel ridges throughout the study area. This area supports the densest concentration of nesting plovers at Mono Lake (Page et al. 1979). Other birds found nesting were an occasional American Avocet (Recurvirostra americana) and a few pairs of Horned Larks (Eremophila alpestris). At least one pair of Violet-green Swallows (Tachycineta thalassina) nested in a small tufa tower along shore in 1981.

Several hundred California Gulls (Larus californicus) regularly forage along shore and at the Drift Ridge seeps; they drink and bathe at the larger springs. Up to 20,000 pairs of gulls nest on islets in the lake. Beginning as early as mid-June large numbers of southbound migrant shorebirds arrived in the study area and congregated along the lakeshore where they roosted and fed.

METHODS

Two seasons of fieldwork lasting a total of six months were spent on this study, from 3 June to 6 September 1980 and from 20 May to 15 August 1981. The study area was visited four to five days a week to observe and census foraging Snowy Plovers, to collect arthropods, and to carry out other fieldwork. I worked mostly between 06:30 and 13:00 or between 15:30 and 20:30 since mid-day air temperatures made fieldwork very difficult. Fieldwork was occasionally postponed or halted due to alkali dust storms.

A grid of 0.3 m high stakes was placed in the study area to provide reference points for describing the locations of plovers and for locating pitfall traps. This grid consisted of four rows of stakes. One row ran along the current lakeshore (LS) and the others along HR, UDR and DR, roughly parallel to the current lakeshore (Fig. 1). Along DR, which approximately bisects the study area, stakes were spaced exactly 100 m apart and numbered consecutively. Stakes in the other rows were placed so that they were in line with a mountain peak visible on the southern horizon and with the stake of the corresponding number on DR. Consecutively numbered stakes in rows other than on DR were therefore not exactly 100 m apart, but varied in spacing from 90-110 m. The locations of plovers, pitfall traps and other objects described in this report are indicated by a number following the lakeshore or ridge abbreviation. This number represents distance in kilometers east of the western boundary of the study area. For example, LS 3.5 indicates the location 3.5 km east of the west boundary of the study area along the lakeshore.

In 1980 arthropods were collected using several techniques, including net sweeping, sticky traps (resin-covered microscope slides) and pitfall traps. Some arthropods were simply collected by hand.

Pitfall traps were the main arthropod sampling technique used in this study and the results presented are based almost entirely on data gathered from June to August 1981. The pitfall trap consisted of two six-ounce plastic drinking cups (diameter = 7 cm), one set inside the other, buried flush with the surface of the substrate. When a trap was first placed in the ground the substrate was carefully smoothed so that no gaps or pits existed around the edge. The upper cup was filled with antifreeze (propylene glycol) to a level 2 cm above the bottom. Arthropods walking along the ground reached the lip of the trap, fell in and were poisoned. Antifreeze is an excellent killing agent for use in hot, arid climates because it does not evaporate. Antifreeze also preserves the poisoned arthropods and prevents them from decomposing. A square piece of hardware cloth was anchored over the top of each cup to prevent plover chicks from falling in. The mesh size of the hardware cloth (1 cm^2) was large enough for almost all arthropods to pass through easily, although some may have avoided capture by walking on the cloth over the cup. Trap location was marked by placing a 30 cm high, blue-flagged stake next to each cup.

A total of 73 pitfall traps were set in the five major microhabitats in the study area: lakeshore (37 traps), Drift Ridge seeps (8), damp alkali (8), dry alkali (12), and gravel ridges (8). In each microhabitat, except at the lakeshore, every trap location contained a pair of pitfall traps spaced 10 m apart (Fig. 1). The DR seeps, damp alkali and gravel ridges were each sampled at four locations. The dry alkali was sampled at six locations. Some trap locations were later grouped (dry alkali: east, west and north sites; DR seeps: east and west) based on similarities of their capture results. At the lakeshore traps were placed between LS 0 and LS 3.5. In most cases a single trap was placed every 100 m along shore, in one of five concentric zones that were parallel to the shore. Zone 1 was 1-5 m, zone 2 was 5-10 m, zone 3 was 10-25 m, zone 4 was 25-50 m, and zone 5 was 50-150 m from the water's edge. Four lakeshore locations (LS 0.5, LS 1.5, LS 2.5, and LS 3.5) each contained two traps spaced 10 m apart. The traps at LS zone 1 were placed within 1-2 m of the water's edge when this was possible. In most cases few results were obtained from these traps either because wind-driven waves flooded them (22 traps) or, because water pressure in saturated substrates forced them up and tipped them over (3 traps). Traps placed within 1-2 m of the water remained effective only if the elevation of the substrate was at least 5 cm higher than the level of the lake and the substrate was not fully saturated.

Prior to 1941 the lake level rose during the summer months due to snow-melt carried into Mono from tributary streams (Gaines 1981). The lake level now declines in the summer because the evaporation rate greatly exceeds freshwater inflow. The evaporation rate reaches a peak in July (Mason 1965 fide Loeffler 1977). In the study area the lake level declined steadily from June through August and in 1981 the shoreline receded over 1.5 m a day in certain locations. This caused an increase in the trap-to-water distance between consecutive collections. Since the arthropod capture rate was clearly related to a trap's proximity to water it became necessary to determine the distance from trap to water during each exposure period. This distance was either measured by pacing or was estimated visually. To analyze the arthropod capture data a mean exposure-period distance was calculated for each lakeshore trap by averaging the two distances measured during consecutive trap collections. For example, a trap that was 3 m from the water on 10 July and 15 m from the water on 20 July was considered to be an average of 9 m from the water during the 10-20 July exposure period.

It was not possible to place traps in the saturated soil at the DR seeps because over a period of several days the water pressure forced them out of the substrate. Data from seven traps were not used because of this. Traps were set in the moist sand as close to the standing water in the seeps as possible. At the gravel ridges wind-blown sand and pebbles partially filled many of the traps, but the antifreeze level was still sufficient to poison arthropods up to the time of collection in all but two of them.

Two traps on the dry alkali became completely filled with wind-blown alkali dust and two others disappeared, perhaps pulled from the substrate by coyotes (Canis latrans) or ravens (Corvus corax).

Arthropods were collected from the traps on average every 11 days between 4 June and 14 August 1981, for a total of 371 collections. Arthropods were removed from a trap by pouring the antifreeze from the upper cup through a fine-mesh (1 mm^2) soil sieve. The arthropods retained on the surface of the sieve were placed in a plastic vial using fine-point forceps. The antifreeze was poured back into the cup which was then reset into the lower cup. The lower cup remained in the ground so that the surrounding substrate was not disturbed during trap collections. Arthropods were later identified, divided into groups and counted. Many of the insects were keyed to family, using Usinger (1956), Cole (1969), and Borror and DeLong (1970). Several entomologists (see Acknowledgements) were provided with specimens of the more common arthropods that were collected and they identified many of them to species.

The time period between pitfall trap collections is termed the "trap exposure period." The trap exposure period for all traps varied from six to 32 days ($\bar{x}$ = 11 days). Arthropod abundance in this report is expressed as the number captured per trap-day. A trap exposed for 24 hours, for example, represents one trap-day; four traps exposed for 10 days represents 40 trap-days. This method allows the comparison of results from traps exposed for different exposure periods. The trapping effort among the microhabitats is shown in Appendix 1.

Mosillus bidentatus, an ephydrid fly, appeared to be common and widely dispersed yet only small numbers were captured in the pitfall traps. An additional method was devised to assess the relative abundance of this species. Based on the strong attraction of these flies to urine-soaked soil, a bait consisting of one part ammonia and two parts water was developed. Standard amounts of this bait were sprayed from a squeeze bottle onto 26 cm^2 areas surrounded by 30 cm diameter circles. *Mosillus bidentatus* flies approached the bait almost immediately, flying in low to the ground and settling inside the 30 cm diameter circle; they did not usually land directly on the bait-soaked substrate. A "*Mosillus* count" was made by counting the maximum number of flies within the circle in a two-minute period beginning immediately after the bait was sprayed. When more than 100 flies were inside the circle at one time their numbers were estimated by counting in groups of ten. Counts were made at six locations along four transects running perpendicular to the lakeshore at stakes 0.5, 1.5, 2.5, and 3.5. Each transect extended from the gravel ridges north of High Ridge to the lakeshore and four microhabitats were sampled. At each sampling location two counts were made, spaced 25 m apart. A total of 152 "*Mosillus* counts" were made.

To assess the numbers of *Ephydra hians* pupae and larvae occurring in the DR seeps, 70 mud cores were taken between DR 2.0 and 4.0. Cores were taken by forcing either a tin can (diameter = 5.8 cm) or a plastic vial (diameter = 2.6 cm) three centimeters into the substrate. Pupae and larvae were removed and counted by washing the core with freshwater through a set of three soil sieves that differed in mesh size; the mesh size of the finest sieve was 1.5 mm^2.

With Page and Stenzel, I trapped and marked Snowy Plovers to allow individual recognition. A total of 66 were color-banded in 1978, 70 in 1980 and 15 in 1981. Twenty-two birds were captured at lakeshore feeding areas in April 1978, but the rest were captured at the nest. Birds were captured using 90 cm long by 40 cm wide strips of noose-covered hardware cloth. The slip-knot nooses were 4.0 cm in diameter and were made from three or eight pound fishing line. After frightening an incubating bird away, three or four strips were placed around the nest and anchored in place with wire stakes. We then retreated at least 200 m from the nest. Within 15 minutes the bird returned to its nest and became entangled when its legs were snared by the nooses. Each bird was removed from the trap and given a unique combination of colored leg bands:

two bicolored bands in 1978 and four unicolored bands in other years. All birds were given U.S. Fish and Wildlife Service bands. The birds were released within five minutes of capture after which they returned quickly to the nest.

Censuses of plovers were made between stakes 0 and 4.5 along the lakeshore and the DR seeps, the two major feeding locations in the study area (Fig. 1). These censuses indicate the size and distribution of the population feeding at these locations on a daily basis. Census results include actively foraging birds in addition to individuals that were roosting or simply standing at the time they were recorded. A census generally lasted three to five hours and, except for a few censuses, each was made by one person. Censuses were made using 9 X 35 binoculars and a 20 power spotting scope. A censuser walked slowly along the census route and stopped at least every 100 m to scan the surrounding terrain for several minutes. Birds were not usually approached closer than 50 m unless it was difficult to determine the colors of leg bands on marked individuals. Seventy censuses were made: 26 in 1980 (13 each at LS and DR) and 44 in 1981 (21 at LS and 23 at DR). I made 30 of the censuses; Page made 24 and Stenzel 22 of the censuses.

Bird movements along the lakeshore or the seeps during a census created minor problems that affected census results. As a result of these movements some birds were recorded more than once when they flew ahead of the censuser and realighted after an initial sighting. To reduce the likelihood of inflating census totals due to the repeat counting of certain birds, a correction factor was developed for each census. The correction factor varied from census to census and was based on the percentage of color-marked birds that were resighted along the census route. A correction factor of 10% (1 of 10 color-marked birds resighted once), for example, was used to reduce the total census figures by 10% for that particular census. The percentage of color-marked plovers that were resighted compared with the total number of color-marked birds that were observed is considered to reflect the movements made by all birds (marked and unmarked) during a census. It was not possible to correct for the opposite situation in which birds crouched out of sight or flew away unnoticed. The following information was recorded for every plover encountered during a census: age, sex, color-band combination, activity and location.

I made 23 timed observations of actively foraging plovers to measure the rate of food intake and to determine the success rate of predation on Ephydra hians adults as compared with larvae. These observations were made on five days between 23 June and 19 July 1981. Fifteen observations were made at the lakeshore and eight at the DR .

seeps. Observations were of single birds foraging continuously for at least one minute, but most observations lasted for at least six minutes. Observations were timed with a stopwatch and the total observation time was 167 minutes. Plovers could often be approached to within 50 m and with a spotting scope it was almost always possible to identify at least two of their major prey items (E. hians adults and larvae) and to determine if a prey capture attempt was successful. Prey capture was determined by observing a plover grab a prey item or by noting the swallowing motion that immediately followed prey capture. I defined a prey capture attempt as a fast, direct movement toward a prey item followed by a lunge with the bill. A small Panasonic tape recorder was used to record information so that I was able to watch foraging bouts continuously. The following information was recorded: age and sex of bird, prey item, number of prey capture attempts, number of successful prey captures, number of defecations, time, and location.

Visual observations were generally only adequate for determining predation on the conspicuous Ephydra hians adults and larvae. Most other prey were either too small or too widely-dispersed to determine visually if they were taken by plovers. The overall variety and relative abundance of prey included in the plovers' diet was determined by collecting feces. Fecal analysis is a good method for analyzing diet if the number of potential arthropod prey species in the habitat is not great, and if arthropod distribution and relative abundance is known. Feces are fairly easy to collect and an actively feeding plover defecates approximately every eight minutes. Birds do not possess digestive enzymes capable of breaking down insect exoskeleton (R. Tullis, pers. comm.), so prey fragments, though often tiny, can be identified after passing through a bird's intestinal tract.

Sixty-eight fresh fecal samples were collected from feeding plovers. Thirty-one fecal samples were collected in 1980 and 37 in 1981. Six samples were collected in May, 21 in June, 29 in July and six each in August and September. Feces were collected from 28 males, 8 females, four juveniles, seven chicks, and 21 unsexed adults. Six samples were from chicks captured for banding at Warm Springs (2 km east of the study area). All samples were from five microhabitats in the study area except for seven collected at Warm Springs.

Fecal samples were collected by walking to the spot where a bird defecated and searching the ground. Feces were carefully scraped off the substrate with a knife blade to avoid including any of the underlying soil and each sample was placed in a glass vial filled with alcohol. Feces were not collected during plover censuses or during timed feeding observations since several minutes were usually required to locate a fecal sample and this often caused the bird to alter its behavior or leave the area. Fresh feces were moist and distinctively shaped so they were easily distinguished from old feces. A fecal sample was not collected if I could not be certain that it was deposited by the plover under observation, a situation that developed when large numbers of migratory Wilson's Phalaropes (*Phalaropus tricolor*), Least (*Calidris minutilla*) and Western Sandpipers (*C. mauri*) used the lakeshore.

Feces were teased apart in a petri dish using fine-point forceps and a probe, and the remains were viewed with a 20-power dissecting microscope. Preserved arthropods from the study area were used for identifying the prey remains. A species was listed as occurring in the feces only if enough remains were present to make a firm identification. A fly species was listed as an item in the feces only if a wing fragment, for example, possessed a diagnostic venation pattern.

RESULTS

Arthropods

Arthropod Distribution and Abundance

The most numerous arthropods along the northeast shore of Mono Lake were flies, beetles, shore bugs, collembolans and spiders. Most of the arthropods were widely scattered and inconspicuous. Although much of the study area appeared lifeless, close inspection of the substrate revealed that many species were common and some occurred in large numbers. Arthropods became obvious at the immediate lakeshore or where shallow water sat on the substrate. A total of 75,370 arthropods were captured in pitfall traps placed in the study area. Over 57 species of arthropods were captured with Diptera and Coleoptera predominating. The sizes of 11 common species are given in Table 1. The following were the most abundant species:

Araneae

Dictyna (sp. indet.)

Collembola

Poduridae (sp. indet.)

Hemiptera

Saldula arenicola

Coleoptera

Bembidion ephippigerum
Tanarthrus inyo
Bledius (sp. indet.)

Diptera

Thinophilus spinipes
Ephydra hians
Ptilomyia alkalinella
Mosillus bidentatus

The mean number of each species captured per day at the pitfall sampling sites is shown in Tables 2-13. The number of individuals of a given species captured during a pitfall exposure period is a function of several factors: the overall abundance of a species, its movement patterns and trap encounter behavior, and weather conditions. Since the first two conditions vary among species the numbers of individuals captured do not have the same significance from one species to another. The pitfall traps therefore represent relative estimates of arthropod abundance and activity rather than absolute measures of abundance (MacLean and Pitelka 1971, Southwood 1978). The pitfall traps yielded consistent results and they appear to reflect accurately the relative abundance and habitat distribution of arthropods along Mono's shore.

The pitfall capture rate varied considerably among the different sampling sites (Fig. 2). Collembolans were much more abundant than other species at three sites, but because they are too small to be potential Snowy Plover prey they are not considered in this discussion of overall arthropod abundance. The lakeshore zone 1 pitfall traps had the highest capture rate of any sampling site with a mean rate of almost 55 arthropods per trap-day. At the lakeshore the numbers of arthropods decreased with increasing distance from the water (Fig. 2). The capture rate at LS zone 5 was only 12% that of LS zone 1.

The second most important microhabitat for arthropods was the DR seeps. The two regions of the seeps (east and west) appeared to differ in arthropod abundance: the mean capture rate at the east site was almost twice as high as the west site. The eastern region of the seeps was much wetter than the western region.

The damp alkali sampling sites below UDR had a capture rate that was slightly higher than the DR seeps west site. The east and west dry alkali sites differed considerably in the numbers of arthropods collected. The west site had a mean capture rate that was five times that of the east site. The dry alkali north site had a mean capture rate similar to that of the dry alkali east site. The gravel ridge microhabitat had the lowest arthropod abundance of any sampling location. The complete lack of moisture at this microhabitat apparently excludes most species and those captured were generally nocturnal. In general, the moisture content of the substrate appears to be a major factor influencing arthropod abundance.

Species richness among microhabitats varied from 35 species at the damp alkali site (Table 12) to 16 species at the dry alkali east site (Table 8). About 24 species per site were collected from the 12 sampling sites. A large percentage of the species total from each site consisted of very rare species represented by five or fewer individuals. Over 35% of the species taken at 11 sites consisted of very rare species (Tables 2-13). The dry alkali north site had the highest percentage of very rare species (66%) and the DR seeps east site had the lowest percentage (22%).

Density or absolute abundance was determined only for *Ephydra hians* larvae and pupae; therefore, no information is presented on the biomass of the arthropod populations.

A list of the common arthropods along the northeast shore, with their relative abundance and habitat preferences, is given in Appendix 2. Some arthropods were not captured in the pitfall traps, but were observed in small numbers in the study area. These species are listed in Appendix 3.

Arthropod Species Accounts and Natural History

Diptera

Eight species of flies from four families were captured in the pitfall traps. At least seven additional species were observed or captured by hand (Appendix 3). The Ephydridae (4 species) and Dolichopodidae (2 species) contributed the most species, whereas one species each of anthomyiid and ceratopoginid fly were collected.

The brine fly *Ephydra hians* is one of the most abundant arthropods at Mono Lake. Aldrich (1912) and Wirth (1970) give general accounts of the biology of *E. hians*. They are found around shallow saline and alkaline lakes throughout western North America (Wirth 1970). At Mono Lake aspects of their biology have been described briefly yet vividly by Mark Twain (1876) in *Roughing It* (pp. 265-269). Herbst (1977, 1980) found them to be one of the most abundant insects along Mono's shore and investigated their physiological ecology and salinity tolerance.

Ephydra hians was the most conspicuous arthropod in the study area and at times dense congregations blackened segments of the lakeshore and the DR seeps. Large numbers were observed skating on the lake's surface or flying parallel to shore close to the water. They were common to extremely abundant on saturated substrates composed of detrital material covered with either a film of water or a thin layer of algae. Masses of densely-packed flies called fly mats developed at favored locations. The maximum mat density was estimated at 80,000 individuals/m^2 and at times mats completely obscured the underlying substrate. An average-sized mat covered 0.25 m^2, but on occasion they exceeded 1.0 m^2 in size.

A fly mat did not remain in the same location for very long, but instead advanced slowly across the substrate changing shape as it moved. This resulted when flies at one edge of the mat flew over and landed in front of those flies in the lead, creating a conveyor-belt kind of movement. When the location of a mat was marked it was found that it had dispersed or moved to a new area within several hours. When foraging birds, however, charged through a fly mat the flies rose in a low cloud but resettled again within seconds. Fly mat formation was very sporadic; stretches of shoreline or portions of the DR seeps where mats were abundant on one day were devoid of mats the next. Mats at the DR seeps were very conspicuous in June and September, but were nonexistent in July.

Ephydra hians was the most abundant arthropod at lakeshore zone 1 where it comprised over one-third of the total number of arthropods captured in the pitfall traps (Table 2). Within the lakeshore microhabitat the capture rate of *E. hians* generally decreased with increasing distance from the water (Fig. 3). At LS zone 5 they were the fourth most abundant arthropod (Table 6). They were common along the DR seeps between DR 2.0 and 3.5. At the DR seeps east site, however, they only accounted for 2.2% of the total in the traps (Table 11). Visual observations made during plover censuses and at other times along the DR seeps indicate that they are much more abundant there than the pitfall data suggest. Their low capture rate may be because the pitfall traps were not placed in the very wet substrate that this species preferred. The damp alkali, dry alkali, and gravel ridge sites had very low numbers of *E. hians*.

The pitfall trap data from two sites where substantial numbers of *Ephydra hians* were captured (LS zone 1) and where trapping effort was prolonged (LS zone 3; see Appendix 1) were used to examine seasonal population fluctuations. Although the data are quite variable they still suggest that seasonal fluctuations in capture rate occurred

(Fig. 4). The increase in numbers in mid-June for LS zone 3 was followed by a decline into late June. Numbers then increased sharply in early July at both LS zones 1 and 3. The very high increase at LS zone 1 is due partly to the addition of eight traps placed in new locations on 30 June. Whether these fluctuations along the lakeshore are due to population cycles or to a redistribution of the population is difficult to determine since brine fly populations are patchy by nature.

Adult *E. hians* feed by pressing their proboscides against the substrate where they obtain algae and detritus. D. Herbst (pers. comm.) found diatoms in the stomachs of *E. hians* he dissected. Diatoms are an abundant member of the lake's phytoplankton community (Lovejoy and Dana 1977).

In typical feeding posture *E. hians* was observed to hold its head down with the abdomen raised. The abdomen was oriented in response to the angle and height of the sun. In the morning when the sun was low in the sky the body was held horizontally, but as the sun climbed the abdomen was "aimed" towards it and tracked its course through the day. This apparent thermo-regulatory behavior probably serves to reduce water loss by preventing overheating. Less body surface is exposed to the sun when *E. hians* assumes this posture. This interesting behavior was especially noticeable when a cloud momentarily obscured the sun, casting a shadow over the lakeshore. During this brief period the flies immediately lowered their abdomens. After the cloud had passed all abdomens were raised again and pointed at the sun. Herbst (1977) also noted this behavior at Mono Lake.

Ephydra hians eggs are deposited in the detritus along the lakeshore, on small submerged tufa towers offshore (Herbst 1977), and at the DR seeps. The larvae develop into 7 mm long stages that feed on detritus and algae. The larvae metamorphose into pupae enclosed within a reddish-brown pupal case. Larval and pupal brine flies were abundant in the moist sand at the DR seeps between DR 2.0 and DR 4.0, although very uncommon west of there. Certain areas of the eastern part of the seeps had very high densities of pupae and larvae (Table 14). Core samples taken on 5 August 1981 contained no E. hians, but rather the pupae and larvae of a smaller ephydrid, probably Lamproscatella salinaria. Adult E. hians were very scarce along the seeps at this time, but L. salinaria was common. Populations of immature E. hians were not measured at the lakeshore.

The second most abundant arthropod at the lakeshore zone 1 was Thinophilus spinipes, a dolichopodid fly (Table 2). Dolichopodids are predators that typically occur along the edges of streams or lakes (Robinson and Vockeroth 1981). Their abundance at the lakeshore is indicated by two traps exposed for six days in early June which captured 952 individuals. Relatively few T. spinipes were captured in other lakeshore zones (Fig. 3) and the only other area where they were common was the DR seeps east. Thinophilus spinipes numbers peaked at a mean of almost 80 per trap-day in early June (Fig. 5), one of the highest capture rates for any arthropod during the study. After mid-June only very small numbers were captured along the lakeshore. A similar pattern occurred at the DR seeps east site (Fig. 5). This is the first record of T. spinipes for California (Foote et al. 1965, R. Hurley, pers. comm.).

Large numbers of Thinophilus spinipes were seen copulating on the damp alkali below UDR where larvae were also found, and freshly-emerged adults with unexpanded wings were common there (about $5/m^2$) in late May 1981. Larvae and freshly-emerged adults were found at the lakeshore in early July 1980. On one occasion an adult was observed eating an adult Ephydra hians.

Members of Mosillus bidentatus, another species in the Ephydridae, are shiny black, have a rounded appearance and are about half the size of Ephydra hians (Table 1). They occur throughout western North America (Wirth 1965). They were inconspicuous most of the time in all microhabitats except at the lakeshore where they occasionally became so numerous that they formed black bands over regions of rich detritus. At these times they were much more abundant than *E. hians*. Herbst (1977) also suggested that *M. bidentatus* (which he referred to as an unidentified chloropid species) may be more abundant than *E. hians* at times. *Mosillus bidentatus* normally numbered about 150/m along shore. The pitfall trap data shows them to be approximately five times as abundant at LS zone 3 (Table 4) as they are at LS zone 1 (Table 2). These results coincide with visual observations since more were seen congregating along detrital lines 10-20 m away from shore rather than right next to the water. The ammonia baiting method complements the pitfall data and visual observations. This method shows *M. bidentatus* to be most abundant within 60 m of the lakeshore and least abundant on the gravel ridges (Table 15). Higher numbers responded to baiting on the dry alkali between DR and UDR than at the DR seeps (Table 15). The data on *M. bidentatus* are insufficient to discern any seasonal population fluctuations.

Mosillus bidentatus apparently responds to the ammonia attractant by olfaction since more flew to the bait from the downwind direction than from other directions. The ammonia attractant probably produces an odor similar to that of bird feces and this may explain *M. bidentatus*' attraction to it. Frequently they were seen crawling on fresh gull feces. These flies did not respond to baiting if wind speed was faster than 20 km/hr and baiting attempts during early morning hours when the air temperatures were low were not successful.

Ptilomyia alkalinella, another ephydrid, was one of the smallest insects encountered (Table 1). Cole (1969:p. 398) states that they "frequent the strange little alkaline lakes" in the Western Great Basin. They were common at LS zone 1 (Table 2) and at the DR seeps east site (Table 11), where they were the most abundant arthropod trapped. Numbers declined markedly at the DR seeps east site after trapping began in early June, rose in early July and declined again to almost zero by mid-August (Fig. 6).

Several other flies were also regular members of the arthropod fauna. *Lispe* (sp. indet.) is a large anthomyiid fly that was rare to fairly common at LS zones 1-3 (Tables 2-4), at the DR seeps east site (Table 11) and around the pool near LS 4.3. Larvae identified as those of *Lispe* were found in the substrate at the DR seeps and a female was observed laying eggs at the LS 4.3 pool. *Leptoconops kerteszi* (Ceratopogonidae), commonly called "no-see-'ems," were prevalent throughout the study area just after emergence. They are a major biting pest in the Mono Basin, as well as around alkaline and salt lakes in Utah (Cole 1969). Their orange larvae (1-2 mm in length) occurred in large numbers in the moist substrate at the damp alkali below UDR between stake 0 and 1. *Lamproscatella salinaria* was common at the lakeshore zones 1-4 (Tables 2-5) and at the DR seeps east site (Table 11). On 4 July 1980 the density of *L. salinaria* was approximately 100/m^2 on the damp alkali near UDR 0.3. Few were captured in this microhabitat, however (Table 12).

Thinophilus latimanus is a small dolichopodid and males have a distinctive black basal foretarsal segment. Specimens collected during this study represent the first records for California (Foote et al. 1965, M. Buegler and R. Hurley, pers. comm.) and are apparently the only ones collected since the typé specimen (a single male in 1925) was described from Colorado Springs, Colorado, by Van Duzee (1926). They were common at the damp alkali sites during the early part of the season where, for example, they numbered 10/m^2 on 23 May 1981 (Table 12). *T. latimanus* was also fairly common at the DR seeps east site (Table 11), but were absent almost entirely from the lakeshore.

Coleoptera

Beetles were not as conspicuous as flies, but nonetheless some species were very abundant, and a total of 11 species were captured. In order of decreasing abundance the six regularly captured species were:

Carabidae:	*Bembidion ephippigerum*
Anthicidae:	*Tanarthrus inyo*
Staphylinidae:	*Bledius* (sp. indet.)
	Carpelimus (sp. indet.)
Cicindelidae:	*Cicindela* (sp. indet.)
Histeridae:	unid. species

All beetles were ground-dwellers and except for *Cicindela* they were rarely seen flying.

Bembidion ephippigerum is a black and gold beetle that was common along shore on the surface, under driftwood and at other moist locations in the study area. Lindroth (1963) states that *B. ephippigerum* is found at the border of saline lakes with sparse or no vegetation. The insect collection at the California Academy of Sciences includes specimens from Mono Lake (J. Liebherr, pers. comm.). *B. ephippigerum* were found under the alkali crust and sometimes even under the pitfall traps. They are fast runners and moved about quickly on the ground in search of food. *Bembidion* beetles in general feed on dead or dying insects that drift ashore (Lindroth 1963).

Bembidion ephippigerum were one of the most abundant insects captured and a total of 12,086 individuals were collected from the pitfall traps. They were most abundant at LS zones 1-3, the DR seeps east site and the damp alkali site (Fig. 7). The damp alkali site had the highest capture rate with over 10 per trap-day (Table 12) and except for Collembola they were the most abundant species there.

The numbers of *Bembidion ephippigerum* fluctuated considerably through the season (Fig. 8). The two major peaks in abundance were in early June and from late June to mid-July. The initial declines may have been partially due to trapping out (called "digging in" in Southwood 1978). Trapping out is to be suspected if high initial capture rates are followed by much lower rates very soon after traps are exposed. This occurs because the local population becomes partially depleted of individuals due to the impact of trapping. In this case the decline is considered an artifact of the trapping method rather than a true population decline. The rise in numbers in late June at the DR seeps east and damp alkali sites probably represents a real increase in abundance. The parallel increase at LS zone 3 may have been due to additional pitfall traps that were exposed at this time. Numbers at the damp alkali and DR seeps east sites declined to almost zero by early August. At LS zone 3 B. ephippigerum was on the increase in early August (Fig. 8).

Larvae of Bembidion ephippigerum were captured at every site except the dry alkali west site. They were commonly seen crawling under debris or under the alkali crust. Their occurrence and abundance patterns coincide closely with that of adult B. ephippigerum.

Tanarthrus inyo is a small anthicid beetle that was common in all microhabitats except the gravel ridges (Fig. 7). Chandler (1975:p. 326) briefly describes the ecology of Tanarthrus beetles and states that this genus is "associated with saline and mud flats, often remnants of the great lakes of the Pliocene and Pleistocene periods." _Tanarthrus inyo_ ranges from Death Valley, California, to Harney Lake in Oregon (Chandler 1975). It is reddish-orange and superficially resembles a red ant. Specimens of _T. inyo_ collected at Mono Lake during this study may represent the first from Mono Lake, although this locality is well within their range (Chandler 1975).

The distribution pattern of _Tanarthrus inyo_ was opposite that of all other arthropods: they achieved their greatest abundancé on the dry alkali. At the dry alkali west site they were the most abundant species and constituted 95% of the total (Table 7). Thirty-one percent of all the _Tanarthrus inyo_ collected in the study area (12,075 individuals) were from the dry alkali west site. It is not clear why so few individuals were captured at the dry alkali east site as compared with the west site since the sites appeared to be similar. Some attribute of the traps may have resulted in the low capture rate at the east site.

At the dry alkali west site the numbers of _Tanarthrus inyo_ increased markedly in late June reaching a peak on 9 July (Fig. 9). Thereafter they declined through the end of the study period. The pattern at this site is very similar to that for _Bembidion ephippigerum_ at the damp alkali site (Fig. 8). The abundance of _T. inyo_ at LS zone 3 and the DR seeps west site show minor fluctuations through the season (Fig. 9), with increasing numbers through mid-August.

Tanarthrus inyo is a carnivorous scavenger feeding on dead wind-blown insects (Peterman 1973). During this study it was seen carrying dead *Ephydra hians* and feeding on Eared Grebe (*Podiceps nigricollis*) carcasses washed up along shore. Twenty-four *T. inyo* were seen feeding on the dried remains from two cracked, abandoned Snowy Plover eggs. Peterman (1973) reports that this beetle was so wary that it could not be approached closer than 2 m. This was not the case at Mono where it was easily captured by hand and, with no provocation, walked onto my clothing and bit my skin if I sat still.

Bledius (sp. indet.) is a brown staphylinid beetle with dull orange-colored elytra. It constructs vertical burrows approximately 8 cm deep and 3 cm in diameter in moist sand. Burrows were found along the lakeshore, at the damp alkali below UDR, and at the DR seeps. Some burrows were also found on the alkali flats south of DR where the underlying sand was moist. Burrow density ranged from $30/m^2$ to over $150/m^2$. The highest density was along the upper edge of the DR seeps, but it is doubtful that all burrows were currently active. Herbst (1977) reports an unidentified staphylinid beetle from Mono.

Although *Bledius* numbers were low when compared with *Tanarthrus inyo* and *Bembidion ephippigerum*, sufficient numbers were captured to suggest that trapping out did occur (Fig. 10). The increase at LS zone 1 in early July resulted from a number of new traps that were placed along shore.

Bledius were captured at all sites except the gravel ridges. The lakeshore zones contained the highest numbers and although burrows were numerous in certain regions along DR the capture rates there were low (Tables 10 and 11). *Bledius* were active at dusk when they walked rapidly about, but only once did I see them fly. When disturbed or handled they commonly curled the abdomen over their head as if to sting.

Carpelimus (sp. indet.) is a staphylinid beetle about half the size of *Bledius*. These two species were similar in their microhabitat preference, but *Carpelimus* was less common. Thousands of individuals took flight at dusk on 26 June 1981.

Cicindela (sp. indet.), a tiger beetle (Cicindelidae), was fairly common around the damp alkali below Upper Drift Ridge between stakes UDR 0 and UDR 2.0, but was much more abundant along shallow creeks to the west and east of the study area. Adults moved about rapidly, alternately running and flying along shore and at the springs where they preyed on insects. The damp alkali below UDR was the only region in the study area where *Cicindela* larvae were found.

An histerid beetle was captured at eight sites, with the largest numbers at the lakeshore. All histerid specimens appeared to be of the same species. A tiny staphylinid (body length = 1 mm) was captured in small numbers at six sites. Twenty-five Notoxis (sp. indet.), an anthicid beetle, were captured on the gravel ridges (Table 13). K. Hagan (pers. comm.) has collected Notoxis at Mono Lake.

Hemiptera

Saldula arenicola, the shore bug, was common and widespread in the study area, especially on moist and saturated substrates. At the DR seeps in late May 1981 the density of immature S. arenicola (nymphs) was about 15-21/m^2. They were most abundant at LS zones 1 and 2 (Tables 2 and 3), and at the DR seeps east site (Table 11). Their seasonal fluctuation (Fig. 11) is very similar to that of Bledius (Fig. 10) and is probably related to the same factors suggested for Bledius.

Collembola

Collembolans were the most numerous arthropods in the study area; over 29,000 were estimated from all the pitfall traps. All individuals appeared to be members of the family Poduridae. Collembola were most abundant on the damp alkali below UDR and on the dry alkali between DR and UDR (Fig. 2). Although they were probably resident on the damp alkali where most were captured, I suspect that many were blown into the traps by the wind.

Collembolan populations were at a maximum in early June when trapping started (Fig. 12), but declined precipitously in mid-June. After a slight increase towards the end of June (Fig. 12) they disappeared almost entirely by mid-July. It is very doubtful that trapping out was a factor in these observed population fluctuations since these tiny insects are so abundant. Due to their small size Collembola were counted in the pitfall traps as they floated on the surface rather than after pouring the antifreeze through the sieve, since most would have passed through the mesh. Collembolans are much too small to be the intentional prey of Snowy Plovers.

Hymenoptera

Small hymenopterans, chiefly chalcidoids, were fairly common along the lakeshore, while other hymenopterans, including red ants and various wasps and bees, occurred mainly on the gravel ridges.

Arachnida

At least six species of arachnids used the study area. The majority of this group was composed of spiders (four species). Dictyna (sp. indet.), a small light-brown dictynid spider, were by far the most abundant; over 2290 were captured. They were equally abundant in each of the lakeshore zones (Tables 2-6), which suggests that water or substrate moisture may not be an important microhabitat requirement. They were most numerous at the DR seeps east site (Table 11) and the lowest numbers were at the gravel ridges (Table 13). This occurrence pattern probably relates to prey abundance, though if this factor alone is considered then higher numbers would be expected at LS zone 1. Numbers remained fairly stable at the DR seeps east site until late July when they declined (Fig. 13).

Dictyna constructed jumbled webs on the ground using small sticks or other debris for attachment and support. Often the webs were anchored underneath the flaky alkali crust. One web held 25 Ephydra hians, 20 Ptilomyia alkalinella and five Thinophilus latimanus. Dictyna individuals may also catch prey "on the run" for they frequently walked about on the open alkali.

Salticid (at least two species) and lycosid spiders were not common but they were widespread and found in all microhabitats. No microhabitat preference could be discerned for these spiders. On the gravel ridges 33 sun spiders (Solpugida: [Eremobatidae]: Eremobates, sp. indet.) were caught. These large, cursorial predators were only active at night. Hydrachnid mites were fairly numerous on the gravel ridges (Table 13), where they were the second most abundant arthropod.

Nocturnal Activity of Arthropods

To assess the nocturnal activity of arthropods nine pitfall traps were set at 22:30 on 30 July 1981 and collected at 06:30 the following morning. Four traps that were placed in the dry alkali 500 m north of the lakeshore captured only six Bembidion ephippigerum, but five traps placed 3 m from the water at shore captured 85 B. ephippigerum, 6 Dictyna, 3 Ephydra hians, 2 Bledius and 1 Saldula arenicola. This suggests that at least some species are fairly active at night. Bembidion ephippigerum may be especially active. Many species of Carabidae, of which B. ephippigerum is a member, are nocturnal in their activities (Borror and White 1970).

If the nocturnal capture rate for Bembidion ephippigerum (85 individuals in 5 traps or 17/trap in 8 hours) is extrapolated to a 24-hour period then the rate becomes 51 per trap-day. This rate is higher than that for any other lakeshore trap, the maximum being 38.7 B. ephippigerum per trap-day for one trap 17 m from the water exposed between 17-23 June. This rate is not as high, however, as that for some traps placed at the damp alkali site.

The high nocturnal capture rate may indicate that some arthropods are even more active at night than during the day. Nocturnal activity must drop significantly when the temperature approaches freezing, as it does on many nights. The reasons for the high, short-term capture rate with traps exposed only at night may also be related to where the traps were placed: near water and in new trap locations. Traps placed close to water captured more arthropods than those placed in dry locations. Furthermore, trapping out could not occur since the trap-exposure period was very short and traps were all in new, previously untrapped locations. Also mesh covers were not used; their absence may have allowed more arthropods to fall in the traps.

Snowy Plovers

Distribution and Abundance of Foraging Snowy Plovers

Snowy Plover nests are widely scattered across the alkali flats and gravel ridges, and are typically spaced over 100 m apart. This wide spacing of nests reduces egg loss to predators, mainly the California Gull (Page et al 1983). In areas where most plovers nest (i.e., alkali flats and gravel ridges) the abundance of arthropods is low. Relatively few nest territories included portions of the seeps or lakeshore where arthropod prey were abundant. As a result, most plovers feed off the nest territory at suitable feeding locations sometimes exceeding 1.5 km from the nest.

Although the study area consists mostly of dry alkali flats and gravel ridges plovers were rarely observed foraging there. Most foraging occurs at moist substrates and in the study area the lakeshore and the DR seeps were the two major feeding locations. Throughout the season plovers foraged along the entire 4.5 km length of the lakeshore and along the DR seeps, especially between DR 1.8 and DR 4.5. Foraging birds occurred singly, spaced 50 m or more apart, or in loose-knit groups of about 2-5 individuals. At the lakeshore birds usually foraged within 5 m of the water's edge; many foraged within 0.5 m of the water or on flat, sandy islets just offshore. Sometimes plovers foraged 50-100 m away from the water, but more typically they used this region of drier substrate for roosting rather than for feeding. At the DR seeps foraging was generally confined to the moist or saturated sand within 100 m south of the stake row along the ridge. Areas at the seeps where salts crystallized into sheets and crusts were little used. The damp alkali below Upper Drift Ridge, between UDR 0 and UDR 1.0, was used by 5-15 plovers almost every day from 20-31 May 1981; this area dried considerably by late May and thereafter few plovers foraged in this location.

Families of plovers with young chicks sometimes foraged on the alkali flats, perhaps as a means of reducing encounters with California Gulls. California Gulls will eat plover chicks (pers. obs.) and gulls are common at the seeps and lakeshore. Adult male plovers with their chicks retreated toward the alkali flats away from these feeding areas when they were approached closer than about 250 m by a censuser. The flats may therefore be of some importance to plover families, but since families are so wary this is difficult to determine.

There is no evidence that plovers maintained feeding territories. Known, color-marked individuals were seen feeding at the DR seeps and at the lakeshore on the same day or along different sections of these two microhabitats on different days. Aggressive encounters between feeding birds were very uncommon unless male plovers were accompanying the chicks. In this case they did occasionally chase other plovers away. Cramp and Simmons (1983) report that Kentish Plovers (C. a. alexandrinus) in Europe also feed away from the nest territory on neutral grounds.

It appeared that plovers nesting in the study area did most of their feeding in the study area. Color-marked birds were rarely observed to the west or east of the study area. There was also a tendency for known, color-marked plovers to use the closest suitable feeding locations to their nest territory. Many foraged along sections of the DR seeps or lakeshore that were directly southeast (or occasionally northwest) from their nest. A bird with a nest at UDR 2, for example, used sections of the seeps or lakeshore between stakes 1.5 and 2.5 more than other locations.

During both years more plovers foraged along the lakeshore than at the DR seeps (Table 16). This difference was significant in 1981 (t test; $p < 0.05$), but not in 1980. In 1980 a mean of 28.8 plovers per census used the lakeshore. In 1981 the lakeshore mean was 79.3, significantly higher than in 1980 (t test; $p < 0.05$).

There was no significant difference (t test; $p > 0.05$) between the numbers of plovers using the DR seeps in 1980 and 1981 (Table 17). On 14 July 1981, 25 plovers foraged between DR 1.9 and 2.5, but a group of such size was uncommonly large.

Color-marked individuals were identified on 64 of 70 (91%) of the censuses. The number of color-marked birds on a census varied from a mean of 13% in 1980 at the lakeshore, to 20% there in 1981 (Table 18). The percent of resighted, color-marked individuals varied from zero (53 censuses) to 33% (two censuses). In 1980 a mean of 0.8% of all color-marked birds were resighted per census at the DR seeps and a mean of 7.2% were resighted at the lakeshore. In 1981 a mean of 0.8% were resighted during the DR seep censuses and 3.0% were resighted at the lakeshore. In general, bird movement was slight and no color-marked bird was resighted more than once on a census. Resightings of color-marked birds occurred mostly with males that were attending chicks. These males often behaved in an agitated manner and attempted to distract or lead the censuser away from the chicks. They did this by running rapidly ahead, calling, or by flying back and forth along the census route.

In 1980 and 1981 over twice as many males as females were encountered along the lakeshore (Table 16). Males were also more abundant than females at the seeps; this difference was significant in 1980 (t test; $p < 0.05$), but not in 1981 (Table 17). The reasons for this unequal sex ratio at feeding locations are explained partially by the nest attendance behavior of the plover. Although both sexes incubate and shade the eggs, the female attends the eggs more than the male during the day (J. S. and J. C. Warriner, pers. comm.). Therefore, during the times when censuses were conducted most females with active nests were in the nest territory. If not actually on the nest, the female must at least be very close by because eggs cannot be left unprotected for long. Direct sunlight can quickly destroy unshaded eggs (Bartholomew and Dawson 1979) and unprotected nests are vulnerable to predators. As a result, females with active nests are not likely to spend much time away from the nest territory during the day. Another reason for the unequal sex ratio at feeding areas is due to a real difference in the total numbers of males and females in the nesting population. According to Page and Stenzel (unpubl. data) males outnumber females by about 1.4 to 1.0 at Mono Lake.

There were no sections along the lakeshore where plovers were not encountered (Fig. 14). In 1980 most sightings of plovers on the lakeshore occurred in the area between LS 2 and LS 4.5 (Fig. 14). In 1981 plovers foraged more consistently between LS 2 and LS 2.8 than in other areas, and as in 1980, few plovers used the western part of the study area between LS 0 and LS 1.4. Sections around LS 3 and between LS 3.4 and LS 4.2 were used less than other sections (Fig. 14).

The occurrence pattern of plovers along the seeps is quite different from that at the lakeshore. A 1.8 km section between DR 0 and DR 1.8 was least used in both 1980 and 1981 (Fig. 15). This region has few brine fly larvae. During both years many plovers were found between DR 1.8 and DR 2.4. Many also occurred between DR 3.4 and DR 4.0 in 1980, and between DR 3.8 and DR 4.4 in 1981 (Fig. 15). In 1981 the region from DR 0 to DR 1.8 was used by a higher proportion of birds than in 1980.

The plovers' seasonal use of the lakeshore was similar in 1980 and 1981 (Figs. 16 and 17). In 1980 peak numbers occurred in mid-July and remained high at least through 2 August. The high count was 60 on 14 July. Low counts occurred in early and late June. In 1981 peak numbers also occurred in mid-July with 125 on 17 July (Fig. 17). The largest single flock consisted of 62 roosting birds at LS 2.7 on 15 August 1981. Another group of 43 plovers foraged along a 300 m section of the lakeshore on 2 August 1981. Lowest numbers were in late May in 1981 and numbers appeared to drop off again in late July and early August. The birds represented on censuses prior to late June are all probably locally nesting plovers. After mid-July it appears that southbound migrants begin arriving, probably from breeding areas to the north and east of Mono Lake.

At the DR seeps in 1980 the number of plovers was fairly stable between 6 June and mid-July (Fig. 18). They declined after mid-July and on 2 August only 6 plovers were counted. In 1981 numbers were higher from 20 May to 28 June than on subsequent censuses (Fig. 19). On 29 July no plovers were seen and in mid-August only one or two plovers used the seeps. It appears that plovers decline considerably at the seeps between late June and mid-July.

Diet

Flies and beetles constitute the major prey resource of the Snowy Plover at Mono Lake. *Ephydra hians* appears to be one of the plovers' most important prey items based on visual observations of feeding birds and investigation of fecal samples. Along shore, and less frequently at the DR seeps, plovers charged into fly mats or pursued scattered flies. *Ephydra hians* larvae appear to be the major prey at the DR seeps. Plovers probably also took other ephydrid larvae (*Lamproscatella salinaria* ?) from the seeps. On several occasions plovers waded into shallow water at the lakeshore and foraged for brine shrimp, but this was not commonly observed. On 27 July 1981, however, ten plovers foraging in the water all appeared to be taking shrimp.

Over six fly species and four beetle species were identified from fragments in plover feces (Table 19). Exoskeletal fragments of Ephydra hians (adults and larvae), and Bembidion ephippigerum occurred with the highest frequency of the fecal samples examined. Sixty-two of the samples (91%) contained the fragments of at least one of these three prey items. The remains of B. ephippigerum and E. hians were often found in the same sample. Most fecal samples contained fragments from at least two different prey items. Tanarthrus inyo exoskeletal fragments were found in 19% of the samples. Thinophilus spinipes and T. latimanus fragments were recovered from plovers feeding at the damp alkali in late May 1981, a time when these two species were common in this microhabitat. Three fecal samples containing T. latimanus fragments were recovered from plovers that were actively foraging for this species. Brine shrimp remains were found in three fecal samples collected at the lakeshore. Feces collected at the lakeshore contained the remains of a total of 13 arthropod species, a greater variety than from any other microhabitat. This high species variety may be partly a function of the number of samples collected there (51% of total) as compared with other microhabitats.

The exoskeletal characteristics used to identify fragments in the feces are shown in Table 20. Beetle elytra, fly wings and head capsules, and E. hians larval skins and air tube tips were the most useful fragments for identifying prey remains. A bias associated with this method of diet determination is that small or soft-bodied organisms will be under-represented in the record. These organisms are digested more completely than large, hard-bodied organisms (Hartley 1948, Swanson and Bartonek 1970, Custer and Pitelka 1976, Rundle 1982). Fragments that do persist will be difficult to spot because of their small size. An additional bias favors the detection of fragments from organisms that have distinctively patterned or colored exoskeletons. The beaded lines running the length of the elytra on Bembidion ephippigerum and the iridescent abdominal segments of Thinophilus are diagnostic characteristics of these insects and their fragments are much easier to discern than those from more nondescript species. The skins of E. hians larvae are of a white tissue-like material that was also easy to spot in feces. Small, uncommon arthropods with dull colors or exoskeletal patterns are therefore under-represented when fecal dissection is used to determine diet. Dictyna and Mosillus bidentatus are probably eaten by plovers, but determining this by fecal analysis is difficult or perhaps impossible for the reasons stated above.

No attempt has been made to quantify systematically the number of individual arthropods represented by fragments in a fecal sample since the degree of decomposition varied among samples and most fragments were very small. Nonetheless, almost every sample possessed some fragments that were identifiable, including some remains of soft-bodied prey which Rundle (1982) thought would not appear in feces. Only two samples were rejected because their remains were not identifiable. Both feces were old and were evidently not deposited by the plover under observation.

Some fecal samples contained extremely well-preserved body parts. One sample contained five intact *Ephydra hians* head capsules and two *E. hians* bodies with attached legs. Another contained the remains of at least eight *E. hians* larvae (16 sclerotized air tube tips: one pair per larvae). An intact *E. hians* pupa with a well-developed fly inside was found in one sample. Another contained 11 *Bembidion ephippigerum* femora representing two individuals. One from the damp alkali at UDR 0.6 had 46 *Thinophilus latimanus* tibiae representing at least eight flies. A sample from a small spring 400 m south of DR 2.5 contained five intact *Tanarthrus inyo* head capsules; two heads even had antennae attached. Many samples from the lakeshore contained shrimp eggs that were probably consumed accidentally by the plover. One sample from the lakeshore contained a single adult female brine shrimp with a paired egg case holding 50 eggs. Another sample was composed of 80% E. hians larval skins.

Plovers take some prey species in direct relation to the apparent abundance of those species in the environment. Ephydra hians and Bembidion ephippigerum, two of the most abundant arthropods at the lakeshore, were the two most frequently identified arthropods in the plovers' feces (Fig. 20). Ephydra hians larvae were another common prey item at the lakeshore, but I have no data on their abundance there. Tanarthrus inyo was less common at the lakeshore and correspondingly less common in the fecal samples.

The plovers prey on many of the common arthropods at the lakeshore (Table 21). The lack of feeding observations on Thinophilus spinipes and their absence in plover feces is probably explained by the ephemeral occurrence of T. spinipes along the lakeshore (Fig. 5). Plovers probably foraged for them, but I did not observe this and no feces were collected when T. spinipes were abundant. Mosillus bidentatus and Dictyna were also common (Tables 2-6 and 15), but they are small and nondescript, and therefore easily overlooked in fecal samples. Only three samples contained Saldula arenicola parts (Table 19). Adults and nymphs of S. arenicola are excellent jumpers and may be difficult for plovers to catch.

At the DR seeps plovers also foraged for most of the available prey (Table 22). Based on fecal sample dissection and observations of foraging birds it is clear that *Ephydra hians* larvae and (to a lesser extent) adults are the most important prey species for plovers in this microhabitat. The statement by Dana and Herbst (1977) that birds at Mono Lake do not feed on brine fly larvae is clearly contradicted by these results.

A number of other arthropods that occur in the study area (Tables 2-13) are rare, or are less than about 2.5 mm in length, and are probably not items in the plovers' diet.

Foraging Behavior and Success

Snowy Plovers are visual foragers that feed in the manner typical of most members of the Charadriidae (Pearson and Parker 1973). This foraging behavior can be described as "look-run-stop-peck." The foraging bird ran along in a halting, zig-zag fashion, stopping every 2-10 m to peck at a prey item. The speed at which the birds run depends on the abundance and behavior of their prey. Several other foraging methods were also used. At the lakeshore plovers pursued densely packed brine flies by charging open-mouthed into a mat, snapping at the flies that flew up around them. This feeding method has also been noted in Oklahoma (Purdue 1976) and in south San Francisco Bay (pers. obs.). It is an energy-intensive method that involves fast running and much head-twisting and bill-snapping. Another method was used by plovers foraging for _E. hians_ larvae in the mud at the DR seeps. At the seeps the plovers apparently cued in on the slight wiggling motions the larvae made just beneath the surface. The plover ran quickly to the site of this movement and probed the mud. If an initial probe was unsuccessful no further probing was made at that location, but instead the plover ran to another spot and repeated this behavior. They were not observed "foot-trembling" while foraging for larvae, a type of behavior described for this species and other _Charadrius_ plovers (refs. in Johnsgard 1981, Cramp and Simmons 1983). Brine fly pupae are motionless in the substrate. Since feeding plovers respond primarily to movements made by their prey they probably take pupae only rarely (Table 19).

Plovers often changed foraging techniques quickly. Adult brine flies or other insects were pursued one minute, larvae the next. Plovers did not feed continuously, but alternated periods of active foraging with periods of rest. A bout of active foraging lasted from 1-30 minutes. Often during the day plovers roosted at locations that were up to 200 m away from the lakeshore or DR seeps. I did not follow any single plover for more than about 30 min so I have no data on the amount of time an individual spends foraging during a day. They appeared to do more feeding during the early morning than at mid-day or late afternoon. Whether plovers forage at night is an unanswered question. Other species of plovers commonly feed at night (H. Cogswell, pers. comm.).

When plovers pursued *Ephydra hians* larvae they thrust the bill beneath the moist substrate and pulled the larva out and shook it quickly before swallowing. Shaking probably subdues the larva and flings off adhering droplets of saline water. Larvae handling time made prey capture easy to observe. Adult fly capture was less obvious, but was still easily observed because the plover usually snapped the bill two to three times, crushing the fly before swallowing it. Although *Bembidion ephippigerum* is very important in the diet, plovers were not actually observed preying on this beetle. The scattered distribution of *B. ephippigerum* as compared with that of the brine flies, makes visual confirmation of predation very difficult.

Plovers appeared to be less successful at taking *Ephydra hians* adults than they were at taking larvae (Table 23). Adult *E. hians* were captured at a mean rate of 2.4/min by actively foraging plovers, but fewer than half of their attempts to capture adults were successful. The foraging rate for adult flies was about five capture attempts per min. The fastest foraging rate I observed was 12 attempts per min (121 attempts in 10 min) for a plover repeatedly charging into brine fly mats. This plover captured 51 flies in the 10-min period. Data regarding the success rate of the "mat charging" versus the "hunt and peck" methods are insufficient to allow comparison of these two methods. The mean foraging rate for larvae was faster than for flies, but over twice as many larvae as adult flies were captured per min (Table 23). The fastest foraging rate for larvae was 11.3 attempts per min (113 attempts in 10 min). On 28 June 1980 a plover actually captured 25 larvae in two min. Larvae are fairly stationary in the substrate and may be easier to capture than adult flies which can escape by flying off. Although plovers are more successful at capturing *Ephydra hians* larvae than they are at capturing adults, the relative importance in the diet of larvae and adults is not known.

Competitive Foraging by Other Birds

A number of other species also foraged along the lakeshore and at the DR seeps. Some of these birds are potential competitors with the Snowy Plover. California Gulls were common at the lakeshore, and between 50 and 800 rested or foraged along the 4.5 km section of shore on a daily basis. In 1980 the mean of 12 gull censuses was 255 individuals (sd = 258) and in 1981 the mean of 18 censuses was 99 (sd = 87). Gulls were also common at the DR seeps, although numbers fluctuated considerably from day to day. They fed only between DR 1.8 and DR 4.0, and their occurrence marks fairly accurately the limits of the brine fly larvae in the seeps. In 1980 the peak count was 145 ($\bar{x}$ = 55; sd = 51; N = 12 censuses) and in 1981 the peak count was 250 ($\bar{x}$ = 66; sd = 55; N = 31 censuses). Gulls fed intensively on brine fly pupae at the seeps by paddling in the muddy substrate. The pupae were picked from the mud surface as they floated up. The gulls also captured emerging adults that were not yet able to fly. Of 31 fecal samples collected from gulls on 27 August 1980 at the seeps, 21 contained *Ephydra hians* pupal cases, 11 contained *E. hians* adult fragments and 4 samples had larval remains. If the gulls' diet at the seeps is primarily brine fly pupae they probably do not compete seriously with Snowy Plovers. At times plovers appeared to actively avoid gulls, but at other times the two species foraged side by side.

Other common to abundant species at the lakeshore were American Avocets, Western and Least Sandpipers, Wilson's Phalaropes, Violet-green Swallows and Horned Larks. The only other shorebirds at the DR seeps were small flocks (usually fewer than 10 individuals) of Killdeer, Long-billed Curlews, Western Sandpipers and Baird's Sandpipers (*Calidris bairdii*). Interactions between Snowy Plovers and the other shorebirds were rare.

DISCUSSION

Arthropod abundance and distribution at Mono Lake is strongly correlated with substrate moisture or proximity to water. The substrate at the immediate lakeshore (LS zones 1 and 2) and at the DR seeps is either moist or very close to water. At the lakeshore the overall pitfall capture rate for arthropods declines steadily with increasing trap distance from shore, paralleling the reduction in substrate moisture. Moist detritus may be the most important factor governing arthropod abundance. This detritus builds up along shore to over a meter thick in some places. It is composed of unicellular algae, dead or dying invertebrates, feathers, and even decomposing birds. A wrack line of brine fly pupal cases, stranded brine shrimp, and feathers is evident in places, especially after strong winds force water up on shore. This detritus along with live algae provides a food source for detritivorous and herbivorous insects, particularly brine flies. These primary consumers are in turn prey for carnivorous insects, spiders, and birds. Snowy Plovers and other waterbirds feeding on the arthropods along shore form the last link in this simple food chain. A similar food chain exists at the DR seeps, but algae are probably more important as an energy source than is detritus.

The large amount of detrital material along the north and east shores is probably a result of south winds that predominate in the spring and summer. These winds move across the lake and at times carry lake water 50 m or more onto the shore. Throughout this season a steady supply of nutrients and detritus is deposited along shore. On the other hand, along the south shore from Navy Beach to Simmon Springs, the substrate is mostly firm and sandy with very little detrital accumulation. On the two trips I made along this 8 km section of the south shore the overall abundance of arthropods (including Ephydra hians, Bembidion ephippigerum, Saldula arenicola and Dictyna) appeared to be much less than along the northeast shore. An all-lake Snowy Plover census conducted in 1978 (Page et al. 1979) recorded only 39 birds between Navy Beach and Simmon Springs (4.9/km), compared with 165 birds (25.4/km) along a section of the northeast shore (6.5 km) that included the study area. The accumulation of detritus (and therefore high arthropod numbers) may influence where plovers choose to nest at Mono Lake. Along the northeast shore nesting plovers are assured of a rich food supply close at hand.

The discovery that the brine fly Ephydra hians and the carabid beetle Bembidion ephippigerum are among the most abundant insects in the study area is not surprising. Brine flies of the genus Ephydra are abundant throughout the west in saline habitats and they are well known for their large populations at Great Salt Lake

(Wirth 1970, Collins 1980), at Mono Lake (Aldrich 1912, Herbst 1977) and around salt ponds in south San Francisco Bay (Wirth 1970). At least 162 species of Bembidion are found in Canada and Alaska alone, and most are strongly hygrophilous and common on shoreline substrates (Lindroth 1963).

Many other arthropods are common and occur in large numbers throughout the spring and summer along the northeast shore of Mono Lake. The discovery of so many species (57) in this seemingly barren habitat attests to the usefulness of pitfall traps for sampling ground-dwelling arthropods. The relative abundance of an arthropod species as determined by pitfall trapping is a function of at least three factors: absolute abundance, catchability and mobility. The first factor was estimated for the common species when possible by visual observations. In most cases these observations coincided well with the results obtained by pitfall trapping. If catchability and mobility can be quantified for a given species then correction factors can be calculated to adjust the pitfall capture data for a better estimate of relative abundance. Baars (1979) did this in his study of pitfalls and carabid beetles. When a pitfall trap is encountered, an individual arthropod can avoid capture by going around it; even after falling in, some individuals may be able to escape. Luff (1975) used six species of carabid beetles in controlled experiments to test pitfall trap efficiency and found that species varied in catchability and that traps caught about 75% of all the beetles that contacted their perimeter. No two species will be exactly equal in catchability or mobility. The species with the greater agility, stronger flying ability, or keener eyesight will be less catchable than another species. Flies are probably better able than beetles to escape traps once they have fallen in because they are better fliers.

Species that are less mobile will not encounter traps as frequently as more active species. For the five most common, strictly cursorial species in the present study (Bembidion ephippigerum, Tanarthrus inyo, Bledius sp., Saldula arenicola and Dictyna sp.), all except Bledius seem to be fairly similar in mobility. The other four species were seen frequently throughout the day running on the substrate, although it is not known whether they contact traps at the same rate. Bledius, on the other hand, was typically found in its burrow, especially during the hottest part of the day. It may stay close to its burrow and perhaps even has a home range or territory around the burrow. This would reduce its rate of capture and lower its estimated relative abundance compared with those species that wander freely.

The ephydrid Mosillus bidentatus was less catchable in the pitfalls than other flies and according to the pitfall data it does not appear to be very abundant. This is apparently because either it is not a particularly active forager or it is able to avoid capture when encountering a trap. The baiting method and visual observations, however, shows it to be quite common and among the most abundant of arthropods. Ephydra hians was widespread and common on most moist substrates and it was an especially active forager. This, in addition to its absolute abundance, is one reason why this species in particular had such a high pitfall capture rate. Detailed studies of arthropod foraging patterns and trap encounter behavior are needed before correction factors can be calculated to apply to the pitfall trap data.

All arthropods experienced some seasonal fluctuation in abundance, and most appeared to be declining by mid-August. Only Thinophilus spinipes and the collembolans, however, declined permanently in mid-season. The peak in numbers for both Bembidion ephippigerum and Tanarthrus inyo in early July may reflect an increase either in density or in mobility.

In his study of Mono's shoreline insects, Herbst (1977) discusses the microhabitats and shoreline zonation patterns of Ephydra hians, a "chloropid" fly (Ephydridae: Mosillus bidentatus), and Saldula arenicola. These were the three most abundant species that he noted. He found E. hians to be most abundant at the lakeshore on wet detrital mudflats next to the water; Mosillus bidentatus was most abundant near the lakeshore on sand and gravel substrates; and S. arenicola was encountered most often on the dry alkali sand flats. My findings agree with Herbst's for E. hians. M. bidentatus was also probably most abundant on sand-gravel substrates since this seemed to be the typical substrate where most were observed (10-60 m from shore). My results differ from Herbst's however, with the distribution of S. arenicola; it was rarely captured on dry alkali substrates or on any substrate that was away from water.

Herbst (1977) observed a total of 11 species along the lakeshore, one-third the number collected at lakeshore zones 1-5 in the present study. Herbst did not find Bembidion ephippigerum, Tanarthrus inyo, or Dictyna, all common species along the shore. This is probably because his lakeshore sampling was limited to 7 samples taken on 5 days, and he captured insects by hand or estimated densities visually rather than using trapping techniques.

The anthicid beetle Tanarthrus inyo is interesting because its distribution and abundance differed so strikingly from that of other arthropods. It is most abundant on the dry alkali where almost no other species occurred. Other arthropods must find it difficult to tolerate the conditions on the alkali or to find food there. The distribution pattern of T. inyo at Mono may not be typical of all areas where it occurs. At the Carson Sink in

Nevada it is absent from the dry alkali but common next to shallow ponds (Chandler 1975). There a different anthicid beetle, _Tanarthrus salinus_ was common on the flats and absent from water margins. Competitive interactions with other species of beetles may influence the microhabitat distribution of _T. inyo_. The distribution patterns of _T. inyo_ and _Bembidion ephippigerum_ at Mono are almost exactly opposite one another (except at lakeshore zones 2 and 3). It is not known if _B. ephippigerum_ occurs at the Carson Sink.

Papp (1978) furnishes some comparative information on beetles from a high Sierra site 16 km from Mono Lake at an elevation of 3200 m. His study site, however, was vegetated and therefore markedly different from the shoreline of Mono Lake. Papp recorded 37 species of beetles compared with 11 species collected in my study. No species were shared between his site and mine. Interestingly, a _Bembidion_ beetle (_B. quadrifoveolatum_) was one of the most common species in Papp's study area.

Shorebirds are mostly generalists in their feeding habits and each species typically takes whatever foods are available to it in the environment by its particular foraging technique. Thus, their diet varies among habitats depending on the local prey supply. At coastal locations or during the winter the diet of Snowy Plovers consists of small crustaceans (isopods, sand crabs and cheliferans), molluscs, annelid worms, and various insects (Johnsgard 1981, Cramp and Simmons 1983, Page and Stenzel unpubl. data). Reeder (1951) found beetle parts, brine fly (*Ephydra* sp.) larvae, and marine invertebrate remains in the stomachs of two Snowy Plovers he collected at Sunset Beach in southern California. Wind-blown insects are also an important food source in some areas (Purdue 1976, Groves and Knopf 1982). In general, at inland (noncoastal) areas during the breeding season a variety of flies and beetles make up the diet of the Snowy Plover.

Based on visual observations of foraging birds and the analysis of feces, the two most important prey items for Snowy Plovers at Mono Lake are the brine fly *Ephydra hians* (adults and larvae) and the carabid beetle *Bembidion ephippigerum*. Ninety-one percent of the fecal samples examined contained the remains of at least one of these two species and many samples contained both. These two insects are also among the most abundant suitably-sized prey items in the microhabitats where plovers forage. Although other arthropods are represented in plover feces, they appear to be only minor elements in the diet. Wind-blown insects, at least those originating in other habitats, are not a major food source. Snowy Plovers therefore feed primarily on the two suitably-sized prey species that are most abundant and available within their foraging habitat. This is a pattern that has been noted by Lack (1970) for many bird predator-prey relationships.

Snowy Plovers feed in particular areas along the northeast shore where the greatest number and variety of arthropods are found: the immediate lakeshore and the Drift Ridge seeps. That birds feed where prey is most abundant is not surprising. Gibb (1960, 1966) found a strong correlation between the density of foraging parids and the density of their insect prey in pine plantations. Goss-Custard (1969) found that Redshank (*Tringa totanus*) density on the coastal mudflats of Scotland was positively correlated with the numerical density of their amphipod prey. Bibby (1979) reports that Dartford Warblers (*Sylvia undata*) confine almost all their foraging to gorse, a relatively scarce plant, because it supports a dense invertebrate fauna compared with more common plants. Gorse occupied only 2.1% of his study plot yet warblers spent 68% of their foraging time in those plants.

Snowy Plovers at Mono Lake also feed in areas that are of little extent when compared with the rest of the habitat that is available. The flats and gravel ridges comprise a very large fraction of the shoreline habitat, but these areas lack prey in any number and relatively few arthropods are captured in pitfall traps placed there. Plovers are rarely seen feeding in either microhabitat. Only one suitably-sized arthropod, the anthicid beetle

Tanarthrus inyo, is common on the flats. For the plovers that do on occasion feed there this beetle is probably a main prey item. The gravel ridges support very little arthropod life and except for a few individuals of Collembola and several other species, they are almost barren.

More plovers were found feeding at the lakeshore between stakes LS 2 and LS 3 in 1981 than in other areas. This region may have more food than other areas along the shore, but this does not seem likely. The pitfall trap data, although variable, do not suggest that prey were more abundant in any specific area along shore. The greater number of plovers occurring in this region may be related to the number of small tufa towers there. The towers may provide some concealment from gulls, especially for families with vulnerable young chicks.

The high numbers of plovers on the eastern half of the DR seeps was clearly related to substrate moisture; the eastern part (DR 1.8-4.0) was much moister than the western part (DR 0-1.8). Arthropod abundance in the eastern part of the seeps was about twice that of the western part.

The use of both the seeps and the lakeshore gives the plovers some choice in foraging habitats and perhaps also in prey selection. At the lakeshore they may feed more on adult brine flies and other arthropods, while at the DR seeps they probably take mostly brine fly larvae. The lakeshore is used more consistently through the season and by more plovers than the DR seeps. This is probably due to the greater food supply and the more extensive area that is available for feeding. The lakeshore also stays moist all season whereas the western half of the seeps becomes increasingly dry and even the eastern half shrinks somewhat in size as the season progresses. As a result, arthropods are available for a shorter period at the seeps. Another reason that plover numbers remain relatively high and fairly stable at the lakeshore is because south-bound migrants from breeding areas to the north stop and feed there in July and August. These migrants augment Mono's breeding population which begins to dwindle at this time as local breeders leave the lake. Migrant flocks were rarely seen at the seeps. They may not respond to the seeps as a suitable feeding location or they may lack the skill to exploit the larval food source.

In early to mid-July plovers decline considerably in number at the seeps. This does not appear to be related to a reduction in the food source since larvae were numerous ($20,000/m^2$) in some areas in early August and brine fly mats were common from mid-August into September. The decline at the seeps probably indicates simply that the nesting season is drawing to a close. After mid-July new nests are not initiated and by mid- to late July most eggs have hatched (Page et al. 1979). Families tend to concentrate more at the lakeshore rather than the DR seeps, which are therefore left fairly deserted after the middle of July.

Mono Lake is presently undergoing ecological changes caused by rising salinity and the rapid decline in its water level. The impact of these changes on the animal life of the lake has just begun to be assessed (Winkler 1977). Certainly as the perimeter of the lake shrinks shoreline feeding areas will be reduced and the prey supply for plovers and other birds will decrease. The salinity may eventually reach such a high level that brine flies and brine shrimp will no longer survive (Herbst and Dana 1977, Herbst 1980). There is some evidence, however, that plovers are able to adapt to strong environmental changes. Owens Lake dried up in 1928, just 15 years after the City of Los Angeles completed its aqueduct, yet Snowy Plovers continue to nest there and the population is currently considered the largest breeding concentration (499 adults) in California (Henderson and Page 1981). At Owens Lake on 19 August 1980 I observed brine flies, *Bembidion* sp., *Tanarthrus inyo* and *Cicindela* sp. as well as a *Dictyna* spider, on the alkali near the mouth of Cottonwood Creek. Shallow creeks, seeps and saline water collecting on the old lakebed apparently support enough arthropod prey for nesting plovers.

Henderson and Page (1981) also found plovers in other inland locations where freshwater is scarce (e.g., Searles Lake and the Alkali Lakes). Nonetheless, access to some water source is probably necessary for an area to support a breeding population of Snowy Plovers (Page and Stenzel 1981). Freshwater may actually be a requirement since plovers were occasionally observed drinking from springs. Purdue (1976), however, found that Snowy Plovers in Oklahoma can obtain all the water they need from their insect diet.

As long as the Drift Ridge seeps or nearby marshes are available Snowy Plovers will probably continue nesting at Mono Lake. If brine flies decline plovers may concentrate more on *Bembidion ephippigerum* and other species. Furthermore, the brine flies at the Drift Ridge seeps will probably continue to reproduce as long as the seeps exist.

The Snowy Plover is adaptable and capable of successful nesting in habitats that fluctuate in quality from year to year. Nonetheless, if water diversions from the Mono Basin are curtailed the continued presence of a viable prey source and of the Snowy Plover will be assured.

TABLES

Table 1. Body lengths of some common arthropods in the study area. Body length measured from front of head to tip of abdomen.

Species	N	Mean Length (mm)	sd	Range
Arachnida				
Aranaea				
Dictynidae: *Dictyna* sp.	20	4.0	0.5	3.2-5.0
Insecta				
Hemiptera				
Saldidae: *Saldula arenicola*[a]	45	2.8	0.7	1.5-4.8
Coleoptera				
Carabidae: *Bembidion ephippigerum*	36	4.1	0.5	3.3-5.1
Staphylinidae: *Bledius* sp.	38	6.2	0.5	5.2-7.2
Anthicidae: *Tanarthrus inyo*	17	3.6	0.4	3.0-4.0
Diptera				
Dolichopodidae:				
Thinophilus spinipes	18	5.8	0.7	5.0-7.0
T. latimanus	19	2.9	0.2	2.5-3.1
Ephydridae:				
Ephydra hians (adult)	69	5.5	0.6	4.2-7.0
E. hians (larvae)[b]	28	7.2	1.3	5.2-10.0
E. hians (pupae)	16	10.0	0.9	8.5-11.5
Mosillus bidentatus	22	3.0	0.3	2.1-3.5
Ptilomyia alkalinella	15	1.3	0.1	1.1-1.5
Anthomyiidae: *Lispe* sp.	9	7.9	0.6	7.0-9.0

[a]Measurements include nymphs and adults.

[b]Measurements are from tip of anterior end to base of cylindrical air-tube; the air-tube is about 2 mm in length.

Table 2. Mean capture rate of arthropods from pitfall traps at lakeshore zone 1 (1-5 m from water). Trapping effort = 157 trap-days; 5 June-14 August 1981.

Species	Number/ Trap-Day Mean	sd	% Total	Number Col-lected
Arachnida				
Araneae				
Dictynidae: Dictyna sp.	1.1	1.0	2.0	192
Salticidae: unid. sp.	< 0.1	-	< 0.1	3
Lycosidae: unid. sp.	< 0.1	-	< 0.1	3
Araneae sp.	< 0.1	-	< 0.1	1
Insecta				
Hemiptera				
Nabiidae: unid. sp.	< 0.1	-	< 0.1	1
Saldidae: Saldula arenicola	6.7	9.7	12.2	1083
Coleoptera				
Cicindelidae: Cicindela sp.	< 0.1	-	0.1	5
Carabidae: Bembidion ephippigerum	7.7	7.0	14.1	1236
B. ephippigerum (larvae)	0.1	0.2	0.2	17
Histeridae: unid. sp.	0.1	0.2	0.2	10
Staphylinidae: Bledius sp.	0.7	0.9	1.3	104
Carpelimus sp.	0.1	0.2	0.2	17
unid. sp.	< 0.1	-	< 0.1	2
Anthicidae: Tanarthrus inyo	2.2	2.4	4.0	366
Lepidoptera				
unid. sp.	< 0.1	-	< 0.1	2
Diptera				
Tipulidae: unid. sp.	< 0.1	-	< 0.1	1
Ceratopogonidae: Leptoconops kerteszi	0.1	0.2	0.2	12
Dolichopodidae: Thinophilus spinipes	10.8	24.5	19.7	1496
T. latimanus	< 0.1	-	< 0.1	1
larva (T. spinipes ?)	< 0.1	-	< 0.1	1
Ephydridae: Ephydra hians	20.6	56.6	37.6	3350
E. hians (larvae)	< 0.1	-	< 0.1	3
E. hians (pupae)	< 0.1	-	< 0.1	2
Mosillus bidentatus	0.6	1.5	1.1	85
Ptilomyia alkalinella	2.9	4.6	5.3	471
Lamproscatella salinaria	0.1	0.4	0.2	15
Anthomyiidae: Lispe sp.	0.6	1.0	1.1	101
Lispe sp. (larvae)	< 0.1	-	< 0.1	2
unid. dipterans	< 0.1	-	0.1	5
Hymenoptera				
Chalcidoidea: unid. spp.	0.4	0.6	0.7	61
Formicidae: unid. sp.	< 0.1	-	< 0.1	1

Table 3. Mean capture rate of arthropods from pitfall traps at lakeshore zone 2 (5-10 m from water). Trapping effort = 247 trap-days; 30 June-14 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	1.1	1.4	3.8	215
Salticid sp.	<0.1	-	<0.1	2
Lycosid sp.	<0.1	-	<0.1	2
Insecta				
Saldula arenicola	4.2	6.8	14.5	824
Cicadellid sp.	<0.1	-	<0.1	2
Chrysopid sp.	<0.1	-	<0.1	1
Cicindela sp.	<0.1	-	0.1	5
Bembidion ephippigerum	7.0	6.0	24.1	1345
B. ephippigerum (larvae)	<0.1	-	0.1	4
Histerid sp.	<0.1	-	<0.1	4
Bledius sp.	0.9	0.9	3.1	194
Carpelimus sp.	0.1	0.2	0.3	26
Staphylinid sp.	<0.1	-	<0.1	2
Coccinellid sp.	<0.1	-	<0.1	1
Tanarthrus inyo	4.7	5.9	16.2	999
Leptoconops kerteszi	<0.1	-	<0.1	2
Thinophilus spinipes	1.1	2.6	3.8	196
Lispe sp.	0.3	0.4	1.0	69
Ephydra hians	6.5	11.8	22.4	1404
Mosillus bidentatus	0.8	2.6	2.8	144
Ptilomyia alkalinella	1.9	3.4	6.6	483
Lamproscatella salinaria	0.1	0.2	0.3	19
Diptera sp.	<0.1	0.2	0.1	18
Chalcidoid sp.	0.3	0.3	1.0	62
Formicid sp.	<0.1	-	<0.1	1
Microbembix sp.	<0.1	-	<0.1	1
Apocrita sp.	<0.1	-	<0.1	1

Table 4. Mean capture rate of arthropods from pitfall traps at lakeshore zone 3 (10-25 m from water). Trapping effort = 472 trap-days; 4 June-14 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	1.1	1.5	6.3	483
Salticid sp.	< 0.1	-	0.1	3
Lycosid sp.	< 0.1	-	0.2	17
Araneae sp.	< 0.1	-	0.1	1
Insecta				
Saldula arenicola	0.7	1.6	4.0	245
Hemiptera sp.	< 0.1	-	< 0.1	1
Bembidion ephippigerum	4.5	7.0	25.9	1601
B. ephippigerum (larvae)	< 0.1	-	0.1	6
Carabid sp.	< 0.1	-	< 0.1	1
Histerid sp.	< 0.1	-	< 0.1	1
Bledius sp.	0.3	0.3	1.7	116
Carpelimus sp.	0.1	0.1	0.5	40
Staphylinid sp.	< 0.1	-	< 0.1	1
Coccinellid sp.	< 0.1	-	< 0.1	2
Tanarthrus inyo	2.4	2.9	13.8	1208
Tipulid sp.	< 0.1	-	< 0.1	1
Leptoconops kerteszi	< 0.1	-	0.2	12
Thinophilus spinipes	1.3	4.5	7.5	338
larva (*T. spinipes* ?)	< 0.1	-	< 0.1	1
Ephydra hians	1.8	2.6	10.4	689
Mosillus bidentatus	3.0	10.2	17.3	851
Ptilomyia alkalinella	1.3	2.7	7.5	482
Lamproscatella salinaria	0.1	0.2	0.3	19
Lispe sp.	0.4	1.0	2.3	122
Diptera sp.	< 0.1	-	0.1	10
Chalcidoid sp.	0.3	0.6	1.7	110
Apoid sp.	< 0.1	-	< 0.1	5

Table 5. Mean capture rate of arthropods from pitfall traps at lakeshore zone 4 (25-50 m from water). Trapping effort = 387 trap-days; 17 June-14 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.8	0.7	6.3	309
Salticid sp.	< 0.1	-	0.2	10
Lycosid sp.	< 0.1	-	0.1	4
Araneae sp.	< 0.1	-	< 0.1	1
Insecta				
Saldula arenicola	0.2	0.4	1.6	32
Cicadellid sp.	< 0.1	-	< 0.1	1
Bembidion ephippigerum	2.1	2.1	16.6	677
B. ephippigerum (larvae)	< 0.1	-	0.1	3
Histerid sp.	< 0.1	-	< 0.1	1
Bledius sp.	0.4	0.5	3.2	120
Carpelimus sp.	< 0.1	-	0.1	3
Tanarthrus inyo	3.4	3.2	26.8	1339
Notoxis sp.	< 0.1	-	< 0.1	1
Leptoconops kerteszi	< 0.1	-	0.1	5
Thinophilus spinipes	< 0.1	-	0.2	5
Ephydra hians	4.4	10.8	34.7	1088
Mosillus bidentatus	0.3	0.6	2.4	120
Ptilomyia alkalinella	0.6	0.8	4.7	225
Lamproscatella salinaria	< 0.1	-	0.3	19
Lispe sp.	0.1	0.1	0.8	24
Diptera sp.	< 0.1	-	< 0.1	1
Moth sp.	< 0.1	-	< 0.1	1
Chalcidoid sp.	< 0.2	0.4	1.6	61

Table 6. Mean capture rate of arthropods from pitfall traps at lakeshore zone 5 (50-150 m from water). Trapping effort = 356 trap-days; 8 July-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.9	0.9	13.3	378
Salticid sp.	< 0.1	-	0.2	5
Lycosid sp.	< 0.1	-	0.1	2
Insecta				
Saldula arenicola	0.3	0.5	4.4	12
Cicindela sp.	< 0.1	-	< 0.1	1
Bembidion ephippigerum	0.9	1.2	13.2	438
B. ephippigerum (larvae)	< 0.1	-	0.2	3
Bledius sp.	0.2	0.2	2.9	65
Carpelimus sp.	< 0.1	-	0.3	8
Tanarthrus inyo	3.0	2.2	44.1	1390
Leptoconops kerteszi	< 0.1	-	< 0.1	1
Ephydra hians	0.5	0.6	7.4	206
Mosillus bidentatus	0.3	0.7	4.4	131
Ptilomyia alkalinella	0.4	0.4	5.9	171
Lamproscatella salinaria	< 0.1	-	0.3	7
Lispe sp.	< 0.1	-	0.2	5
Diptera sp.	< 0.1	-	< 0.1	1
Moth sp.	< 0.1	-	< 0.1	1
Wasp sp.	< 0.1	-	< 0.1	1
Bembix sp.	< 0.1	-	< 0.1	1
Chalcidoid sp.	0.2	0.7	2.9	109

Table 7. Mean capture rate of arthropods from pitfall traps at the dry alkali west site. Trapping effort = 280 trap-days; 4 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.1	0.1	0.6	18
Salticid sp.	$<$ 0.1	-	0.1	3
Lycosid sp.	$<$ 0.1	-	0.1	2
Insecta				
Cicadellid sp.	$<$ 0.1	-	$<$ 0.1	1
Cicindela sp.	0.1	0.1	0.4	10
Bembidion ephippigerum	0.1	0.2	0.6	16
Bledius sp.	0.3	0.7	1.9	48
Staphylinid sp.	$<$ 0.1	-	$<$ 0.1	1
Tanarthrus inyo	12.8	13.4	94.7	3804
Leptoconops kerteszi	$<$ 0.1	0.1	0.2	3
Thinophilus spinipes	$<$ 0.1	-	$<$ 0.1	1
T. latimanus	$<$ 0.1	-	0.2	5
Ephydra hians	0.1	0.1	0.4	9
Mosillus bidentatus	$<$ 0.1	-	0.1	2
Ptilomyia alkalinella	0.1	0.2	0.8	38
Diptera sp.	$<$ 0.1	-	0.1	3
Formicid sp.	$<$ 0.1	-	$<$ 0.1	1

Table 8. Mean capture rate of arthropods from pitfall traps at the dry alkali east site. Trapping effort = 244 trap-days; 5 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.2	0.2	5.5	28
Salticid sp.	< 0.1	-	0.4	2
Insecta				
Collembola	0.4	1.4	14.4	60
Saldula arenicola	< 0.1	-	0.4	2
Cicadellid sp.	< 0.1	-	0.2	1
Hemiptera sp.	< 0.1	-	0.2	1
Bembidion ephippigerum	0.1	0.1	1.8	10
B. ephippigerum (larva)	< 0.1	-	0.3	1
Bledius sp.	0.1	0.1	1.8	7
Carpelimus sp.	< 0.1	-	0.3	1
Tanarthrus inyo	1.9	2.9	68.9	424
Leptoconops kerteszi	< 0.1	-	0.7	8
Ephydra hians	< 0.1	-	0.4	2
Mosillus bidentatus	< 0.1	-	0.4	2
Ptilomyia alkalinella	0.1	0.2	4.1	31
Diptera sp.	< 0.1	-	0.2	1
Chalcidoid sp.	< 0.1	-	0.3	2

Table 9. Mean capture rate of arthropods from pitfall traps at the dry alkali north site. Trapping effort = 254 trap-days; 4 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.2	0.2	0.8	32
Salticid sp.	< 0.1	-	0.1	3
Araneae sp.	< 0.1	-	< 0.1	1
Insecta				
Collembola	16.2	23.0	80.9	3300
Corixa sp.	< 0.1	-	< 0.1	1
Saldula arenicola	< 0.1	-	< 0.1	2
Cicadellid sp.	< 0.1	-	< 0.1	1
Bembidion ephippigerum	0.2	0.3	1.0	54
B. ephippigerum (larvae)	< 0.1	-	0.1	2
Bledius sp.	< 0.1	-	< 0.1	3
Tanarthrus inyo	3.1	2.3	15.5	749
Leptoconops kerteszi	0.1	0.2	0.3	10
Thinophilus spinipes	< 0.1	-	< 0.1	1
T. latimanus	< 0.1	-	< 0.1	1
Ephydra hians	< 0.1	-	< 0.1	1
Ptilomyia alkalinella	0.2	0.2	1.0	41
Diptera sp.	< 0.1	-	0.2	9
Moth sp.	< 0.1	-	< 0.1	1
Formicid sp.	< 0.1	-	< 0.1	2

Table 10. Mean capture rate of arthropods from pitfall traps at the DR seeps west site. Trapping effort = 248 trap-days; 4 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	0.2	0.2	1.3	30
Salticid sp.	< 0.1	-	< 0.1	1
Lycosid sp.	< 0.1	-	< 0.1	1
Insecta				
Collembola	6.1	20.3	52.3	1030
Saldula arenicola	0.2	0.1	1.7	5
Cicindela sp.	0.1	0.1	0.6	14
Bembidion ephippigerum	0.3	0.5	2.9	80
B. ephippigerum (larvae)	< 0.1	-	0.2	5
Histerid sp.	< 0.1	-	< 0.1	1
Bledius sp.	0.2	0.4	1.8	35
Carpelimus sp.	< 0.1	-	< 0.1	1
Staphylinid sp.	< 0.1	-	< 0.1	1
Tanarthrus inyo	3.6	4.2	31.1	1035
Leptoconops kerteszi	< 0.1	-	0.2	5
Thinophilus spinipes	< 0.1	-	< 0.1	1
T. latimanus	< 0.1	-	0.3	7
E. hians	< 0.1	-	0.3	7
Mosillus bidentatus	< 0.1	-	0.1	3
Ptilomyia alkalinella	0.7	2.0	6.4	181
Lamproscatella salinaria	< 0.1	-	< 0.1	1
Diptera sp.	< 0.1	-	0.2	6
Moth sp.	< 0.1	-	< 0.1	1
Bombini sp.	< 0.1	-	< 0.1	1
Chalcidoid sp.	< 0.1	-	0.1	2

Table 11. Mean capture rate of arthropods from pitfall traps at the DR seeps east site. Trapping effort = 276 trap-days; 5 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Araneae				
Dictyna sp.	2.2	1.4	11.2	544
Salticid sp.	< 0.1	-	< 0.1	2
Lycosid sp.	< 0.1	-	< 0.1	9
Insecta				
Saldula arenicola	1.5	2.4	7.7	323
Cicindela sp.	< 0.1	-	0.2	9
Bembidion ephippigerum	4.4	6.2	22.3	1065
B. ephippigerum (larvae)	< 0.1	-	0.2	6
Histerid sp.	< 0.1	-	< 0.1	2
Bledius sp.	0.2	0.3	1.0	36
Carpelimus sp.	0.1	0.2	0.4	14
Staphylinid sp.	< 0.1	-	0.2	8
Tanarthrus inyo	0.7	1.1	3.7	258
Leptoconops kerteszi	2.1	4.2	10.6	386
Thinophilus spinipes	0.4	0.7	2.6	82
T. latimanus	0.3	0.7	1.4	52
Ephydra hians	0.4	0.8	2.2	79
Mosillus bidentatus	0.1	0.4	0.6	25
Ptilomyia alkalinella	6.3	8.3	31.9	1275
Lamproscatella salinaria	< 0.1	-	< 0.1	10
Lispe sp.	0.7	0.2	3.6	14
Diptera sp.	< 0.1	-	< 0.1	4
Chalcidoid sp.	< 0.1	-	0.1	4

Table 12. Mean capture rate of arthropods from pitfall traps at the damp alkali site. Trapping effort = 530 trap-days; 4 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Arachnida				
Hydrachnid sp.	< 0.1	-	< 0.1	1
Dictyna sp.	0.1	0.4	0.2	60
Salticid sp.	< 0.1	-	< 0.1	4
Lycosid sp.	< 0.1	-	< 0.1	1
Araneae sp.	< 0.1	-	< 0.1	1
Eremobates sp.	< 0.1	-	< 0.1	1
Insecta				
Collembola	64.4	130.3	82.9	24,230
Gryllacridid sp.	< 0.1	-	< 0.1	1
Saldula arenicola	< 0.1	-	< 0.1	11
Hemiptera sp.	< 0.1	-	< 0.1	1
Cicindela sp.	< 0.1	-	< 0.1	13
Bembidion ephippigerum	10.7	14.4	13.8	5563
B. ephippigerum (larvae)	0.1	0.2	0.1	47
Histerid sp.	< 0.1	-	< 0.1	2
Bledius sp.	< 0.1	-	0.1	19
Carpelimus sp.	0.1	0.2	0.1	32
Staphylinid sp.	< 0.1	-	< 0.1	8
Tanarthrus inyo	1.0	1.4	1.3	494
Notoxis sp.	< 0.1	-	< 0.1	1
Tipulid sp.	< 0.1	-	< 0.1	1
Leptoconops kerteszi	0.2	0.2	0.2	60
Thinophilus spinipes	< 0.1	-	0.1	14
T. latimanus	0.5	0.8	0.6	161
Ephydra hians	< 0.1	-	< 0.1	15
Mosillus bidentatus	< 0.1	-	< 0.1	6
Ptilomyia alkalinella	0.3	0.9	0.4	231
Lamproscatella salinaria	< 0.1	-	< 0.1	5
Lispe sp.	< 0.1	-	< 0.1	1
Diptera sp.	0.1	0.2	0.1	38
Moth sp.	< 0.1	-	< 0.1	12
Chalcidoid sp.	< 0.1	-	< 0.1	12
Formicid sp.	< 0.1	-	< 0.1	4
Apoid sp.	< 0.1	-	< 0.1	12

Table 13. Mean capture rate of arthropods from pitfall traps at the gravel ridges. Trapping effort = 490 trap-days; 4 June-13 August 1981. See Table 2 for orders and families of common species.

Species	Number/Trap-Day Mean	sd	% Total	Number Collected
Arachnida				
Hydrachnid sp.	0.2	0.3	5.4	48
Dictyna sp.	< 0.1	-	0.4	2
Salticid sp.	< 0.1	-	0.4	4
Lycosid sp.	< 0.1	-	0.2	1
Araneae sp.	< 0.1	-	0.4	2
Eremobates sp.	0.1	0.1	1.8	33
Insecta				
Collembola	1.8	5.8	62.9	475
Lygaeid sp.	< 0.1	-	< 0.1	1
Chrysopid sp.	< 0.1	-	< 0.1	1
Bembidion ephippigerum	< 0.1	-	< 0.1	1
B. ephippigerum (larva)	< 0.1	-	< 0.1	1
Tanarthrus inyo	< 0.1	-	0.7	9
Notoxis sp.	0.1	0.1	1.8	25
Chrysomelid sp.	< 0.1	-	0.2	1
Tipulid sp.	< 0.1	-	0.3	5
Leptoconops kerteszi	0.1	0.3	5.0	43
Thinophilus spinipes	< 0.1	-	0.2	1
T. latimanus	0.1	0.3	3.6	32
Ephydra hians	< 0.1	-	1.1	8
Mosillus bidentatus	0.1	0.2	4.3	33
Ptilomyia alkalinella	0.1	0.1	1.8	14
Lamproscatella salinaria	< 0.1	-	0.2	1
Diptera sp.	0.1	0.1	2.2	18
Moth sp.	< 0.1	-	1.1	15
Wasp sp.	< 0.1	-	< 0.1	1
Chalcidoid sp.	< 0.1	-	1.4	19
Formicid sp.	0.1	0.2	3.9	55
Pompilid sp.	< 0.1	-	0.2	1
Halictid sp.	< 0.1	-	0.1	2
Anthophorine sp.	< 0.1	-	0.3	3
Apoid sp.	< 0.1	-	0.3	7

Table 14. Mean density of ephydrid[a] larvae and pupae in the surface substrate of the DR seeps. Substrate samples from DR 2.0-4.0.

	Larvae/m^2	Pupae/m^2	Number Samples
1980			
23 June	333	433	12
4 July	0	3,100	3
1981			
25 May	26,000	550	20
6 June	4,000	850	20
5 August	20,400	10,500	20

[a]Ephydrids from all samples except those from 5 August 1981 are *Ephydra hians*. Those from 5 August 1981 are probably all *Lamproscatella salinaria*; no *E. hians* were collected on this date.

Table 15. Mean number of *Mosillus bidentatus* attracted to bait in a two-minute period (see Methods). Counts made in 1980 and 1981.

Microhabitat	Mean	sd	Number Counts
Lakeshore[a]	68.5	69.8	23
Lakeshore[b]	58.2	72.9	18
Dry Alkali[c]	11.2	15.1	36
Dry Alkali[d]	5.2	5.3	18
DR seeps	5.5	5.9	21
Gravel Ridges	3.0	4.9	36

[a] 1-10 m from water.

[b] 20-60 m from water.

[c] between DR and UDR.

[d] 500 m south of DR.

Table 16. Mean number of Snowy Plovers feeding along the lakeshore (4.5 km) in 1980 (6 June-2 August) and 1981 (21 May-15 August). N = number of censuses. Means have been recalculated based on repeat sightings of color-marked individuals (see Methods).

	1980 (N = 13)				1981 (N = 21)		
	Mean	sd	% Total		Mean	sd	% Total
Males	14.5	9.9	50.3		40.9	17.6	51.6
	*				*		
Females	7.0	4.1	24.3		15.5	8.9	19.5
Unknown	7.3	7.5	25.3		22.9	27.5	28.9
Total	28.8	17.7		*	79.3	25.0	

<u>Note</u>: An asterisk between adjacent means indicates a significant difference ($p < 0.05$). The t test was used to test for significance.

Table 17. Mean number of Snowy Plovers feeding along the Drift Ridge seeps (4.5 km) in 1980 (6 June-2 August) and 1981 (5 June-4 August). N = number of censuses. Means have been recalculated based on repeat sightings of color-marked individuals (see Methods).

	1980 (N = 13)			1981 (N = 15)		
	Mean	sd	% Total	Mean	sd	% Total
Males	14.6	5.5	61.3	10.4	9.9	52.5
	*					
Females	7.0	3.4	29.4	5.9	4.0	29.8
Unknown	2.2	1.9	9.2	3.5	5.6	17.7
Total	23.8	8.3		19.8	15.8	

Note: An asterisk between adjacent means indicates a significant difference ($p < 0.05$). The t test was used to test for significance.

Table 18. Numbers and percent of color-marked Snowy Plovers observed on censuses.

	Numbers		Percent of Census Total	
	Mean/census	Range	Mean/census	Range
1980				
DR seeps	5	1-9	0.20	0.06-0.39
Lakeshore	4	1-9	0.13	0.05-0.30
1981				
DR seeps	5	0-15	0.18	0-0.46
Lakeshore	12	4-22	0.15	0.08-0.28

Table 19. Prey composition of 68 Snowy Plover fecal samples collected from six areas. N = number of samples examined from each area. See Table 2 for orders and families of insects.

Arthropod Prey Species	Number of samples in which prey fragments occurred							
	LS[a] (N=35)	DR Seeps (N=14)	Damp Alkali[b] (N=8)	Gravel Ridges[c] (N=2)	Spring[d] (N=2)	Warm Springs[e] (N=7)	Total	Percent of Total
Insecta								
Saldula arenicola	1	1				1	3	4
Bembidion ephippigerum	18	4	4	2		3	31	45
Bledius sp.	2	2					2	3
Carpelimus sp.	1	1					1	3
Tanarthrus inyo	7	1	2	1	2		13	19
Coleoptera sp.	5					1	6	9
Thinophilus spinipes			3				3	4
T. latimanus			3				3	4
Ephydra hians (adults)	21	7	1		1	1	31	45
E. hians (larvae)	20	7	1				28	41
E. hians (pupae)	1	3					4	6
Mosillus bidentatus					1		1	1
Lamproscatella salinaria	1						1	1
Lispe sp.	1						1	1
Diptera sp.	2					1	3	4
Crustacea (Branchiopoda)								
Artemia monica	3						3	4

[a]Most samples collected within 25 m of the water.
[b]Most samples from damp alkali just below UDR 0.6-1.0; one sample from UDR 2.5.
[c]Samples from HR 1.5 and HR 2.5.
[d]Samples from spring 400 m south of DR 2.5
[e]Samples from Warm Springs, 2 km east of the study area.

Table 20. Anatomical characteristics used to identify the major prey fragments in Snowy Plover fecal samples.

Species	Anatomical Characteristics
Saldula arenicola	Venation pattern of hindwing
Bembidion ephippigerum	Beaded appearance of elytra Head capsule shape and size Femur size, shape and color
Bledius sp.	Head capsule and bulging compound eyes.
Tanarthrus inyo	Head capsule shape and size Antennal segment size and shape of eleventh antennal segment Leg pieces: shape, size and color
Thinophilus sp.	Metallic, iridescent abdominal tergites Wing venation *T. spinipes* vs. *T. latimanus* distinguished by size of head capsule or wings
Ephydra hians	
adult	Head capsule: bulging appearance of face, mouth shape Shape and size of labrum Tibial claws and lack of empodium Size and shape of leg pieces Wing venation
larvae	White, tissue-like skin with external bristles Larval prolegs Sclerotized air-tube tips
pupae	Chitinous, brown exoskeletal plates

Table 21. Major arthropod prey available to Snowy Plovers along the lakeshore. See Table 2 for orders and families of insects.

Arthropod Prey	Relative Abundance (mean captured per Trap-Day)		Occurrence in Plover Diet	
	1-25 m from water	25-150 m from water	Observed Being Eaten	Recovered from Feces
Insecta				
Dictyna sp.	1.1	0.9		
Saldula arenicola	3.9	0.1		X
Bembidion ephippigerum	6.4	1.5		X
Bledius sp.	0.6	0.3		X
Tanarthrus inyo	3.1	3.2		X
Thinophilus spinipes	4.4	0.1		
Ephydra hians	9.6	2.5	X	X
E. hians (larvae)	0.1	-	X	X
Mosillus bidentatus	1.5	0.3		
Lispe sp.	0.4	0.1		X
Crustacea				
Artemia monica	-	-	X	X

Table 22. Major arthropod prey available to Snowy Plovers along the Drift Ridge seeps. See Table 2 for orders and families of insects.

	Relative Abundance (mean captured per Trap-Day)		Occurrence in Plover Diet	
Arthropod Prey	DR West	DR East	Observed Being Eaten	Recovered from Feces
Insecta				
Dictyna sp.	0.2	2.2		
Saldula arenicola	0.2	1.5		X
Bembidion ephippigerum	0.3	4.4		X
Bledius sp.	0.2	0.2		
Tanarthrus inyo	3.6	0.7		X
Thinophilus spinipes	0.1	0.4	X	
T. latimanus	0.1	0.3	X	
Ephydra hians	0.1	0.4	X	X
E. hians (larvae)	-	-	X	X
E. hians (pupae)	-	-		X
Mosillus bidentatus	0.1	0.1		
Lispe sp.	0	0.7		X

Table 23. Mean foraging rates of Snowy Plovers preying on adult (12 observations) and larval (21 observations) *Ephydra hians*.

	PCA/min[a]		Percent Successful Prey Capture	Prey Capture/min	
	Mean	sd		Mean	sd
Adults	4.8	3.2	48.3	2.4	1.7
Larvae	6.4	3.6	68.3	4.5	2.8

[a]PCA = prey capture attempt.

FIGURES

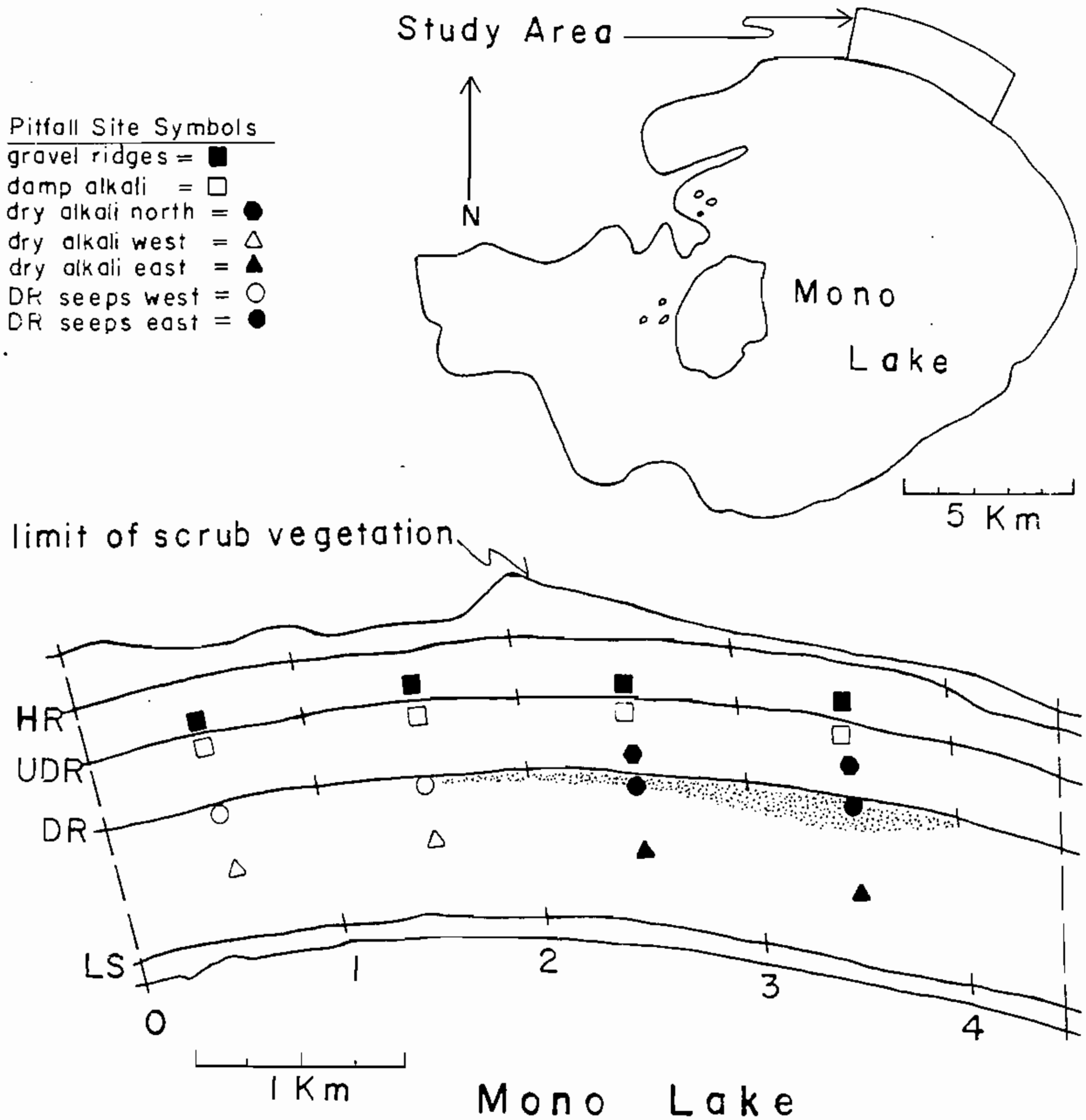

Figure 1. Map of the Mono Lake study area showing pitfall trap locations. Lakeshore pitfall locations are not shown. HR = High Ridge; UDR = Upper Drift Ridge; DR = Drift Ridge; LS = Lakeshore. Numbers along the Lakeshore are kilometer reference stakes. The DR seeps are stippled and the dashed lines indicate the west and east boundaries of study area. (Study area map modified from Page et al. 1983).

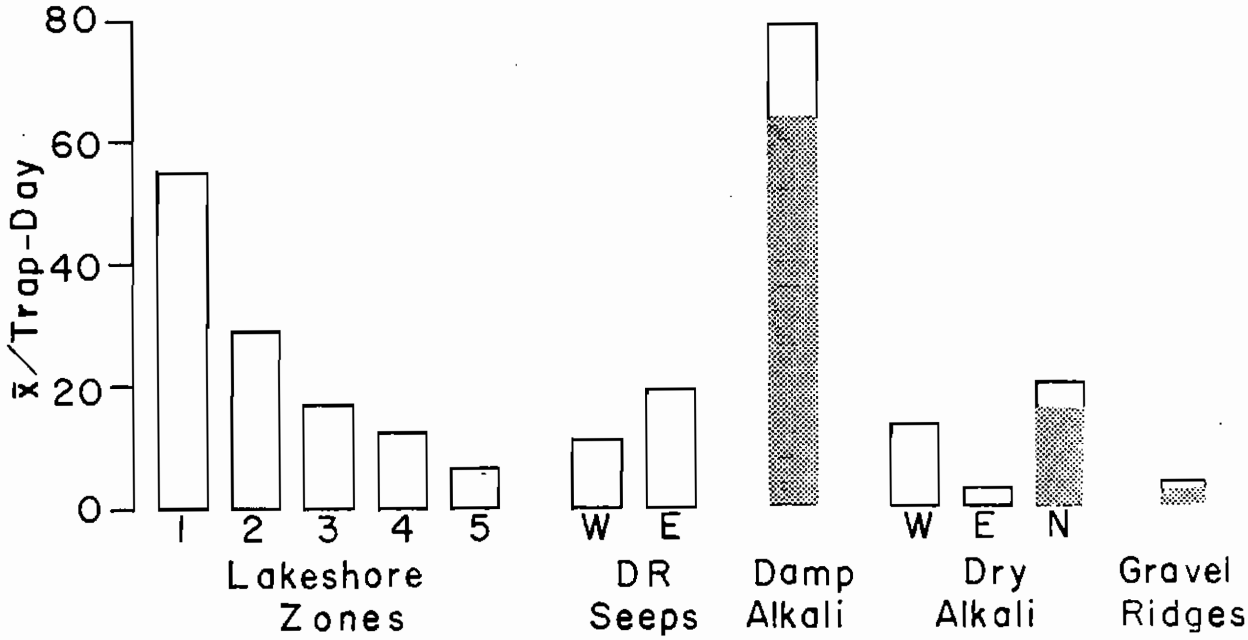

Figure 2. Relative abundance of arthropods among microhabitats as determined by pitfall trapping. Shading indicates the portion of total that is composed of Collembola. Bars represent summed means from Tables 2-13.

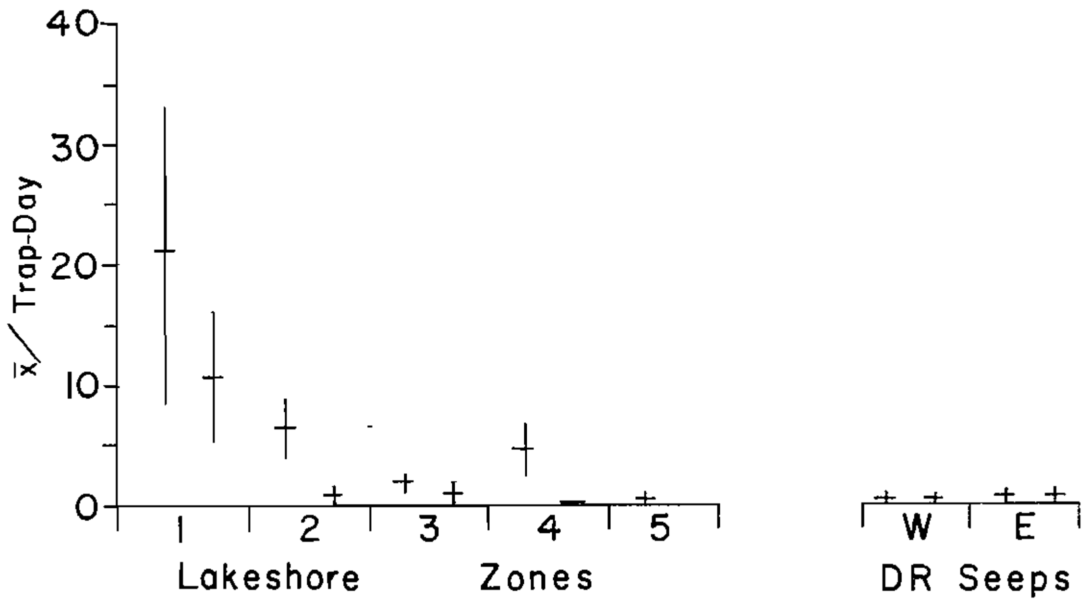

Figure 3. Mean capture rate of Ephydra hians (left bar) and Thinophilus spinipes (right bar) at seven pitfall sampling sites. Horizontal line represents the mean and vertical line represents one standard error to either side of the mean.

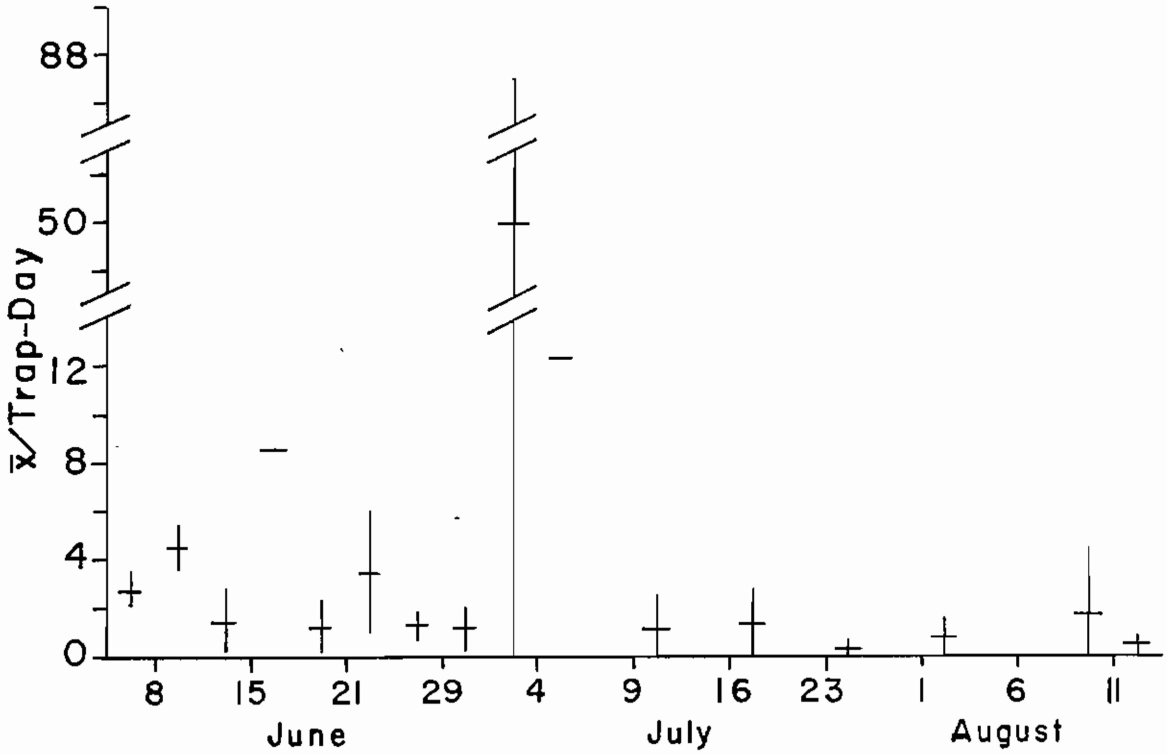

Figure 4. Seasonal changes in the capture rate of Ephydra hians at two pitfall sampling zones. Dates along the horizontal axis indicate the mid-points of trap-exposure periods (see Methods and Appendix 1). Lines immediately to left of dates represent LS zone 1; lines to right represent LS zone 3. Horizontal line is the mean and vertical line is one standard deviation to either side of the mean.

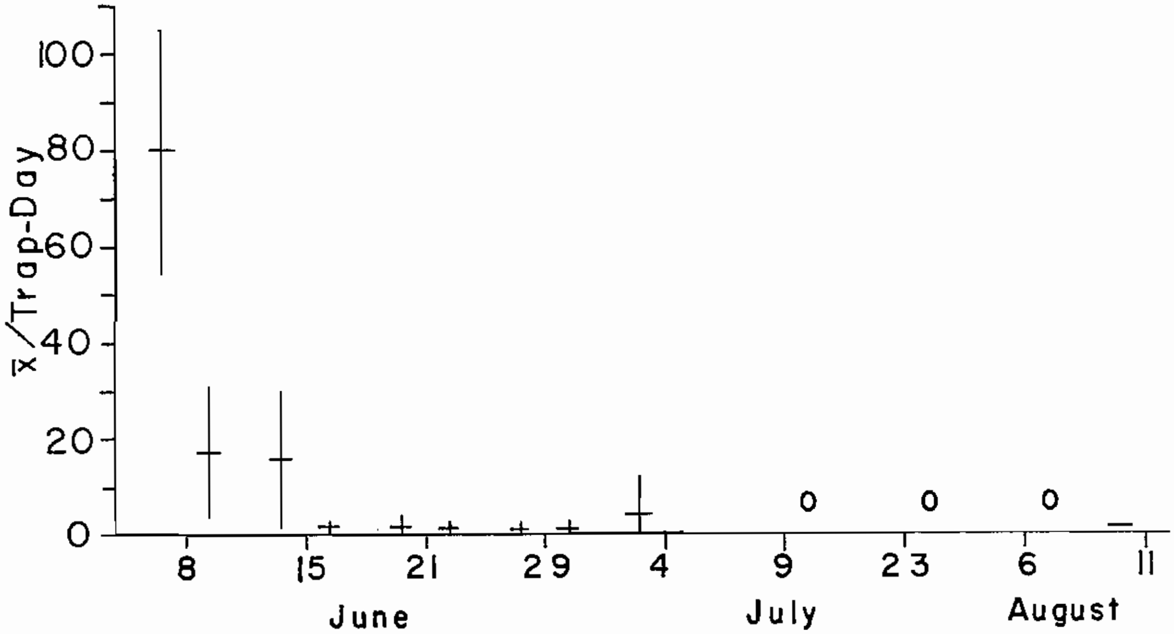

Figure 5. Seasonal changes in the capture rate of Thinophilus spinipes at two pitfall sampling sites. Lines immediately to left of dates represent LS zone 1; lines to right represent DR seeps east site. Zeroes indicate that no individuals were captured. See Fig. 4 for explanation.

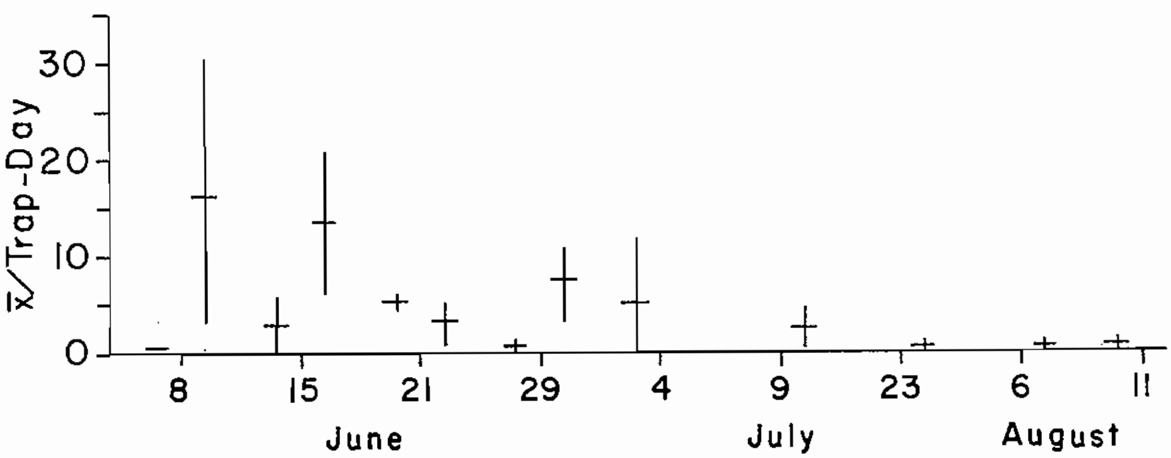

Figure 6. Seasonal changes in the capture rate of Ptilomyia alkalinella at two pitfall sampling sites. Lines immediately to left of dates represent LS zone 1; lines to right represent DR seeps east site. See Fig. 4 for explanation.

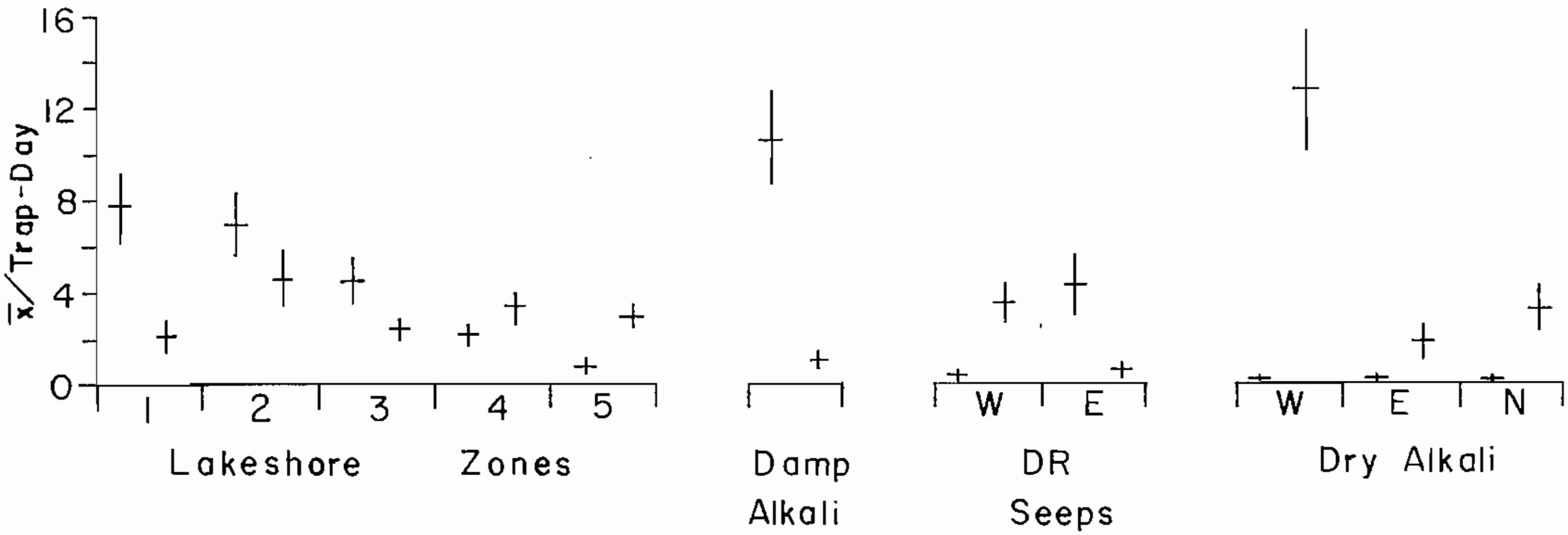

Figure 7. Mean capture rate of <u>Bembidion ephippigerum</u> (left bar) and <u>Tanarthrus inyo</u> (right bar) at 11 pitfall sampling sites. See Fig. 3 for explanation.

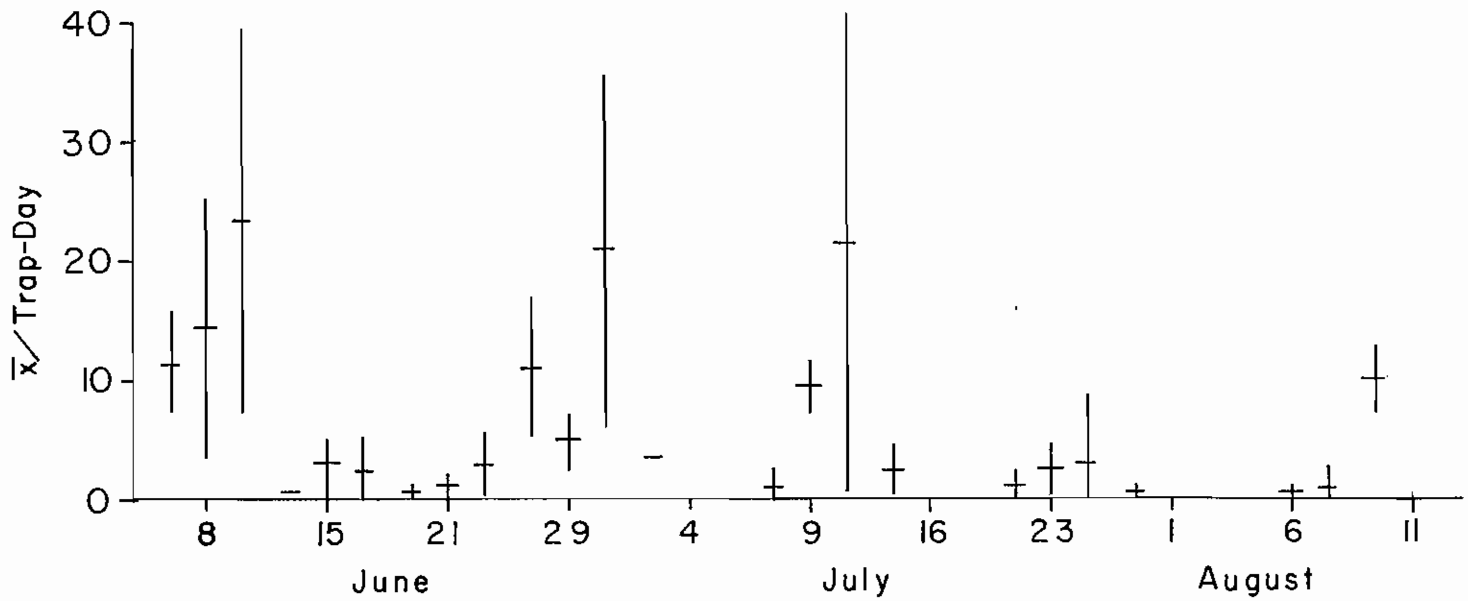

Figure 8. Seasonal changes in the capture rate of <u>Bembidion ephippigerum</u> at three pitfall sampling sites. Lines immediately to left of dates represent LS zone 3; middle lines represent DR seeps east site; lines to right represent damp alkali site. See Fig. 4 for explanation.

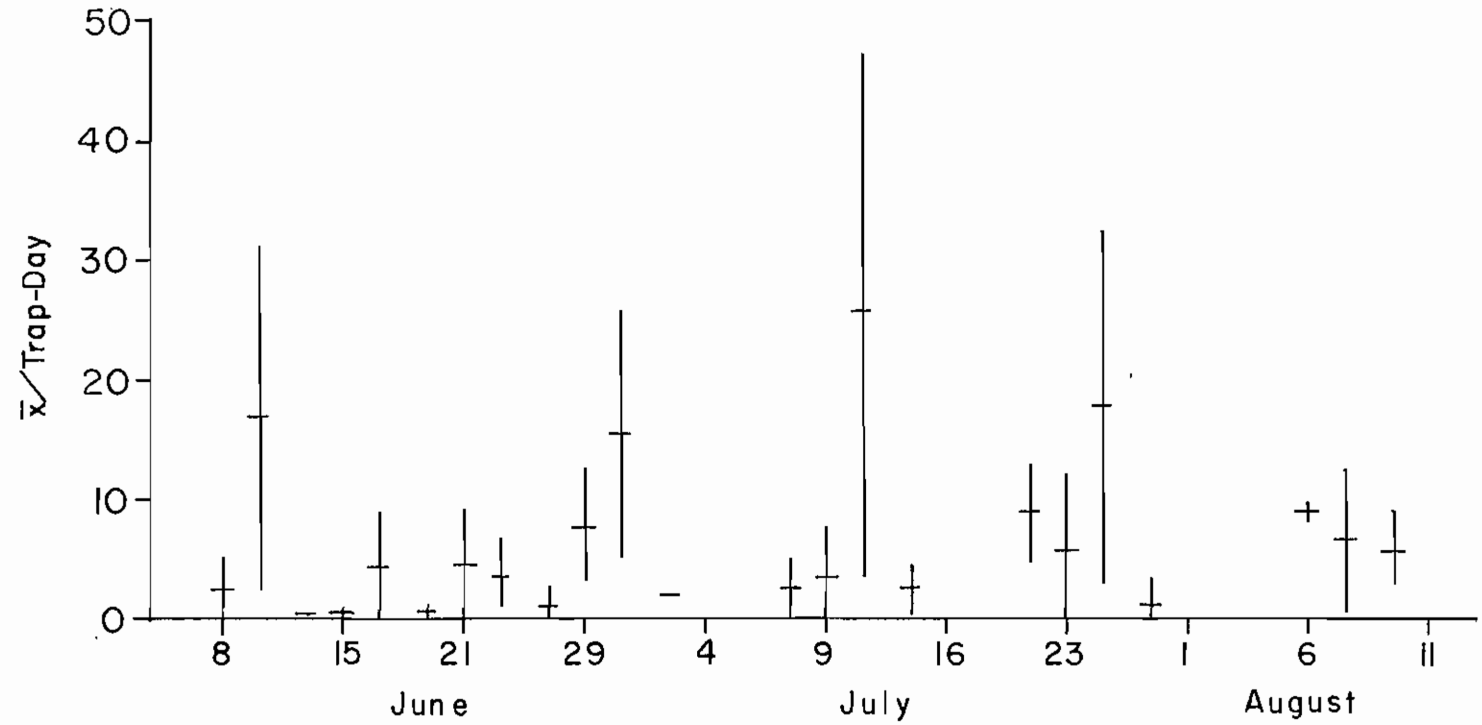

Figure 9. Seasonal changes in the capture rate of _Tanarthrus inyo_ at three pitfall sampling sites. Lines immediately to left of dates represent LS zone 3; middle lines represent DR seeps west; lines to right represent dry alkali west site. See Fig. 4 for explanation.

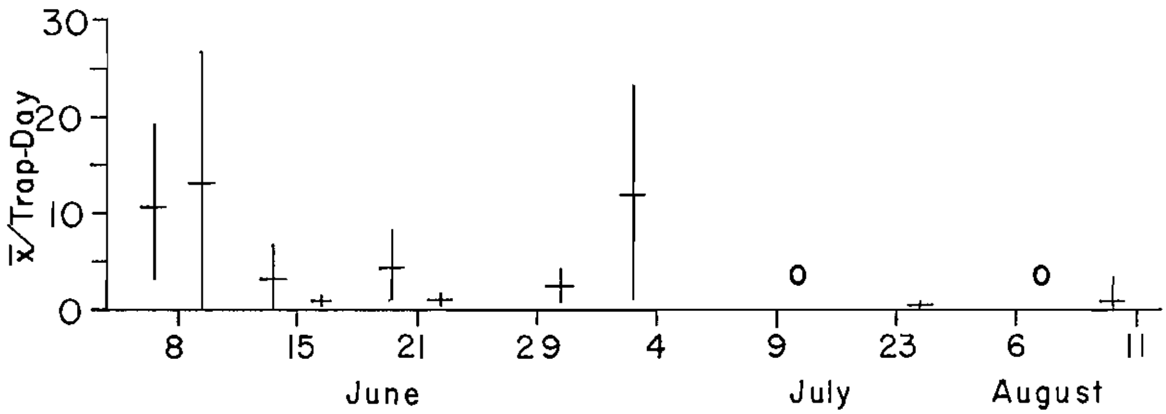

Figure 10. Seasonal changes in the capture rate of <u>Bledius</u> at two pitfall sampling sites. Lines immediately to left of dates represent LS zone 1; lines to right represent dry alkali west site. See Fig. 4 for explanation.

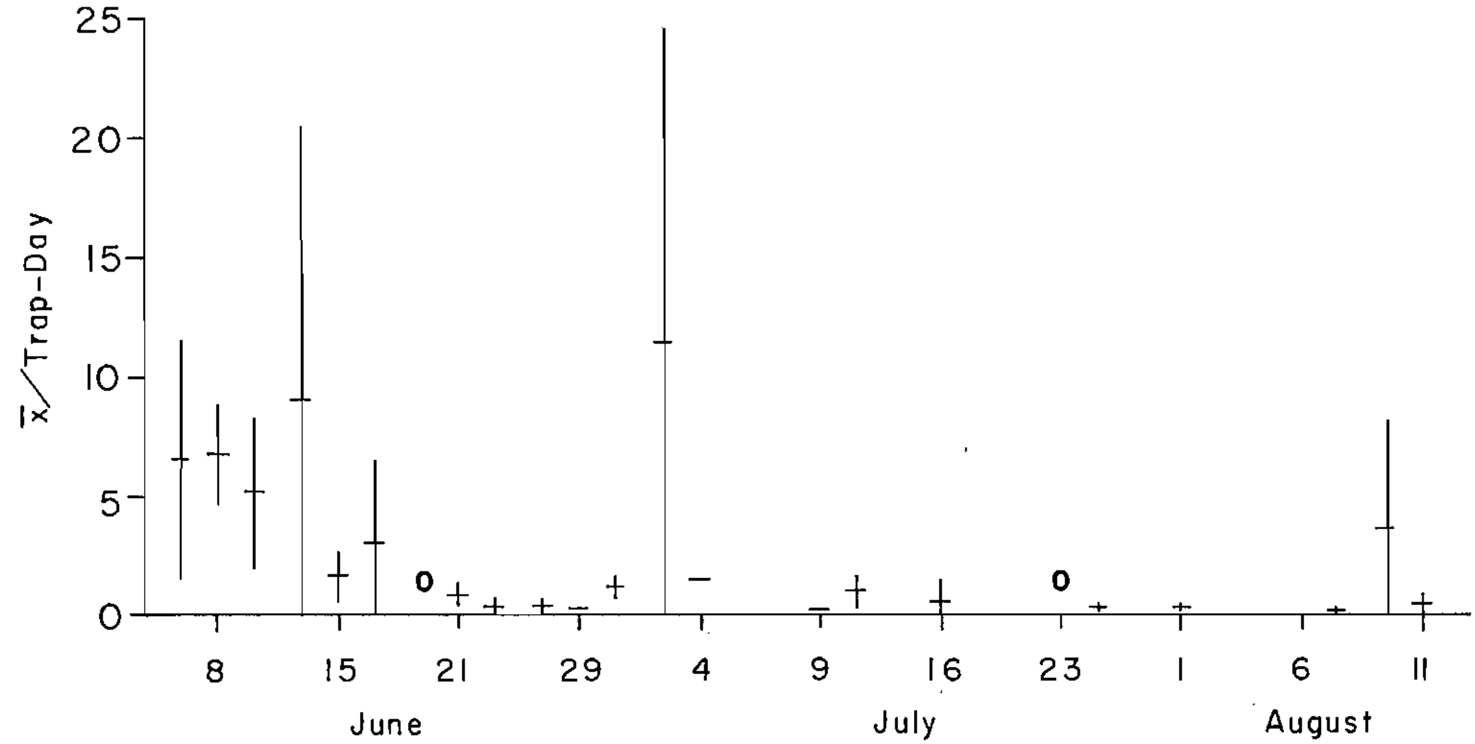

Figure 11. Seasonal changes in the capture rate of <u>Saldula arenicola</u> at three pitfall sampling sites. Lines immediately to left of dates represent LS zone 1; middle lines represent LS zone 3; lines to right represent DR seeps east site. Zeroes indicate that no individuals were captured. See Fig. 4 for explanation.

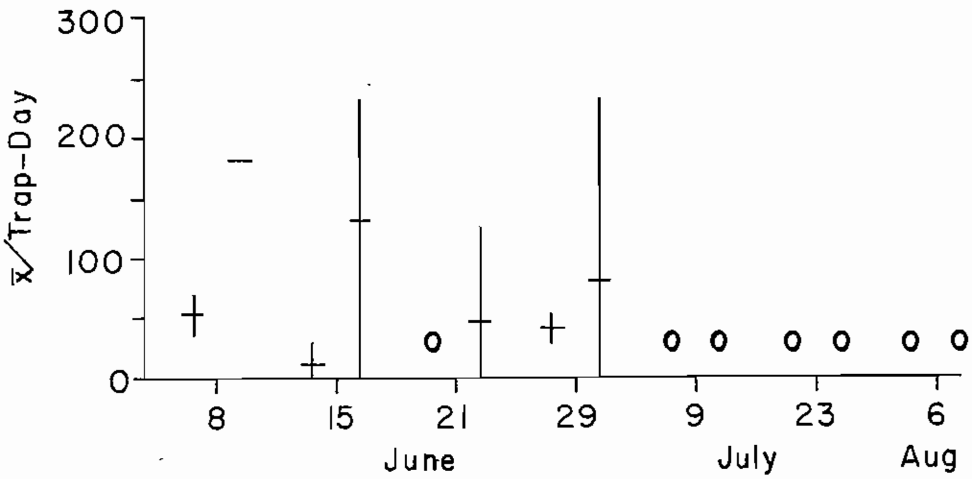

Figure 12. Seasonal changes in the capture rate of collembolans at two pitfall sampling sites. Lines immediately to left of dates represent dry alkali north site; lines to right represent damp alkali site. Zeroes indicate that no individuals were captured. See Fig. 4 for explanation.

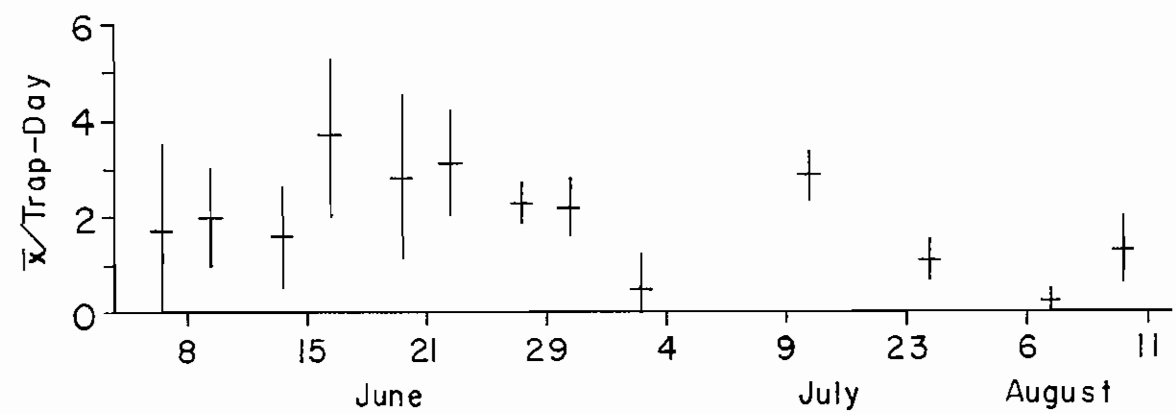

Figure 13. Seasonal changes in the capture rate of Dictyna at two pitfall sampling sites. Lines immediately to left of dates represent LS zone 1; lines to right represent DR seeps east site. See Fig. 4 for explanation.

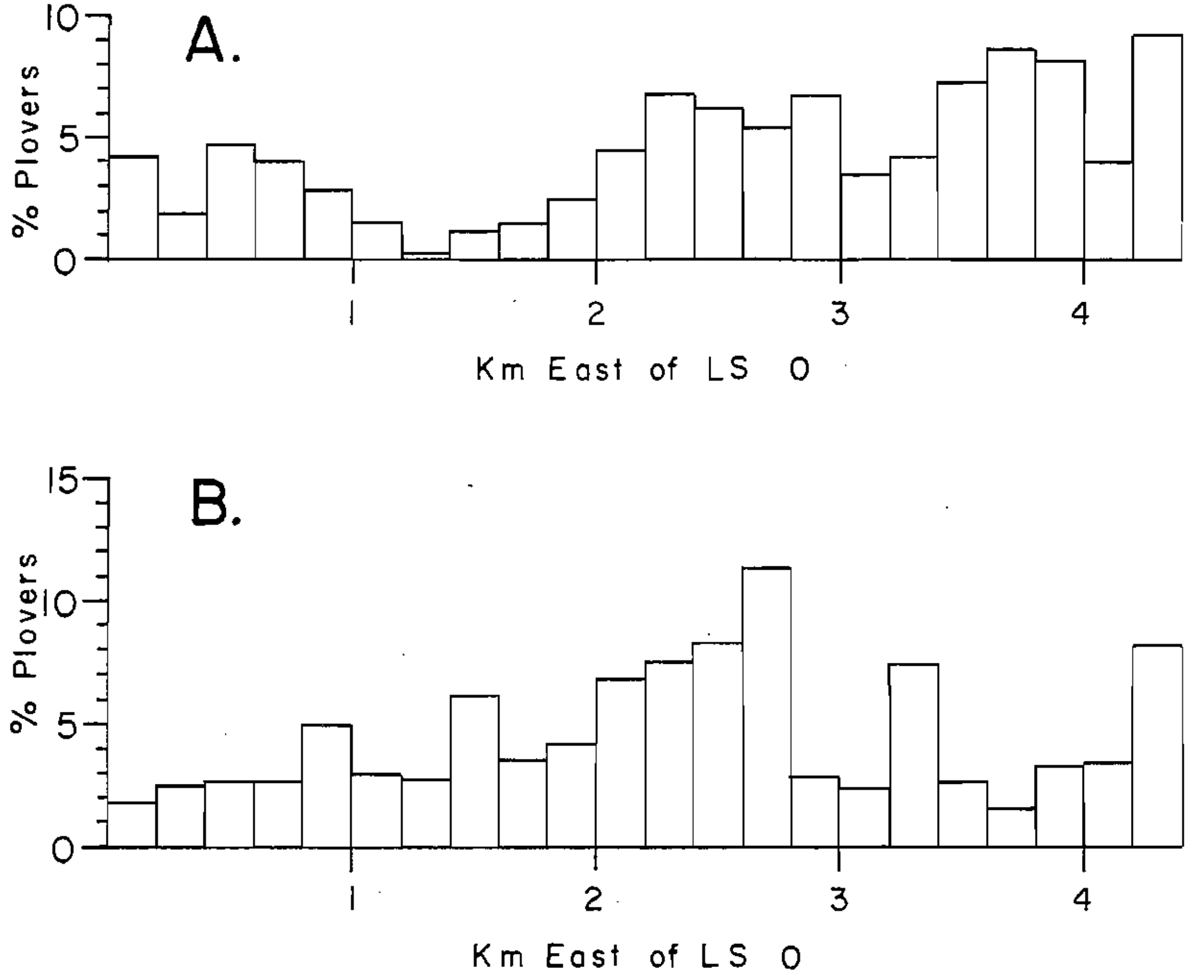

Figure 14. Distribution of Snowy Plovers along the lakeshore in 1980 (A.) and 1981 (B.). Bars represent the mean percent in 200 m sections, all censuses combined.

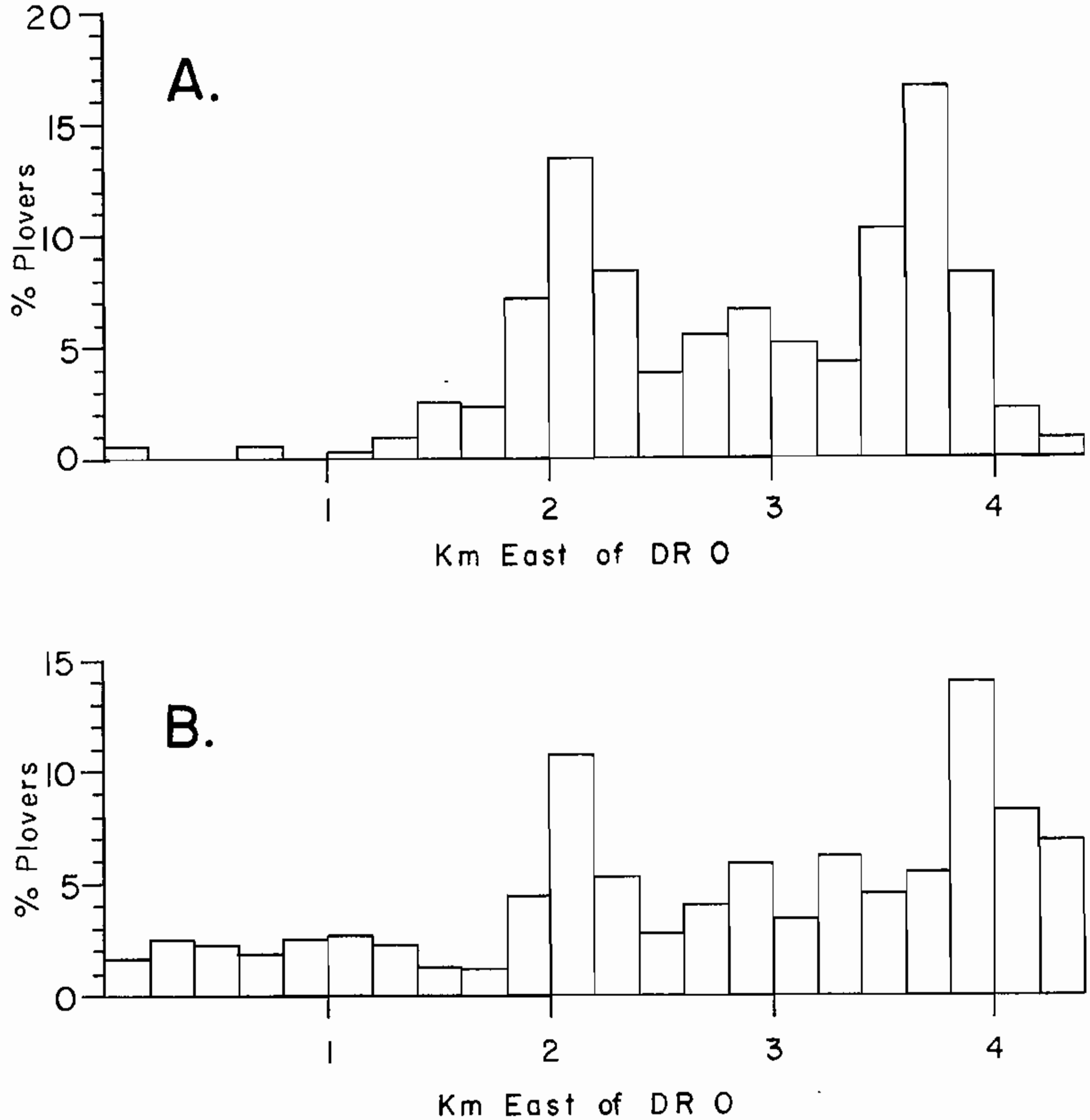

Figure 15. Distribution of Snowy Plovers along the DR seeps in 1980 (A.) and 1981 (B.). Bars represent the mean percent in 200 m sections, all censuses combined.

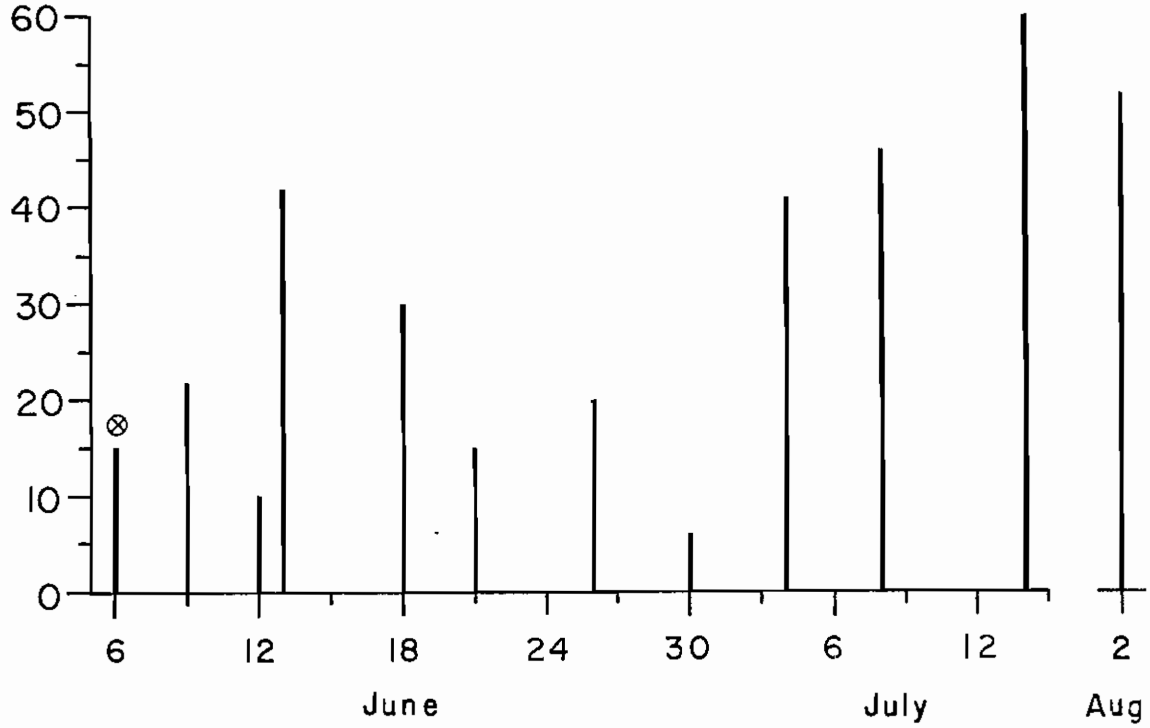

Figure 16. Number of Snowy Plovers counted on censuses along the lakeshore (4.5 km) in 1980. Censuses have been recalculated based on repeat sightings of color-marked individuals (see Methods). Bar marked ⊗ is a mean of two censuses made on this date.

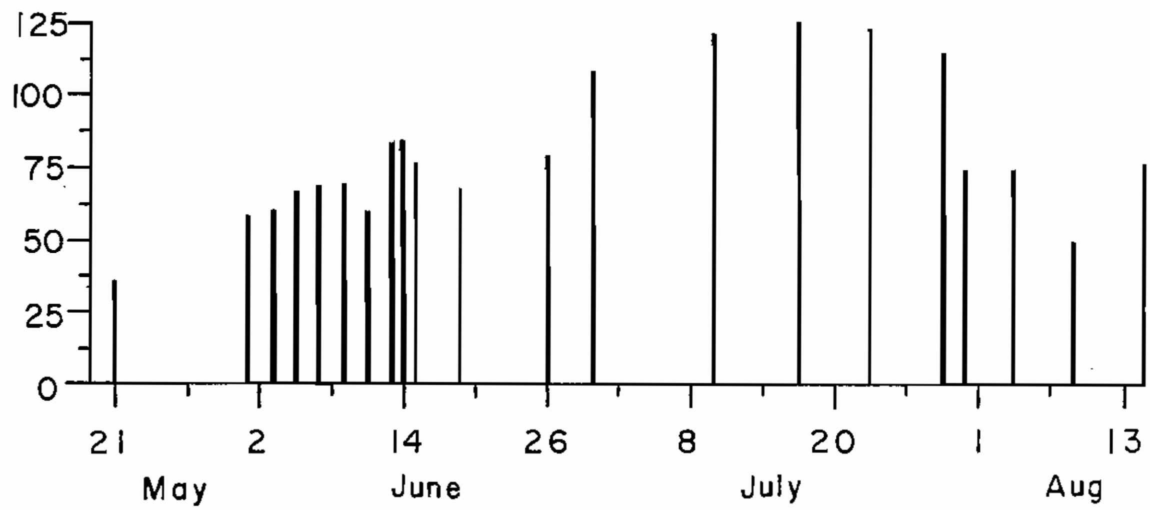

Figure 17. Number of Snowy Plovers counted on censuses along the lakeshore (4.5 km) in 1981. Censuses have been recalculated based on repeat sightings of color-marked individuals (see Methods).

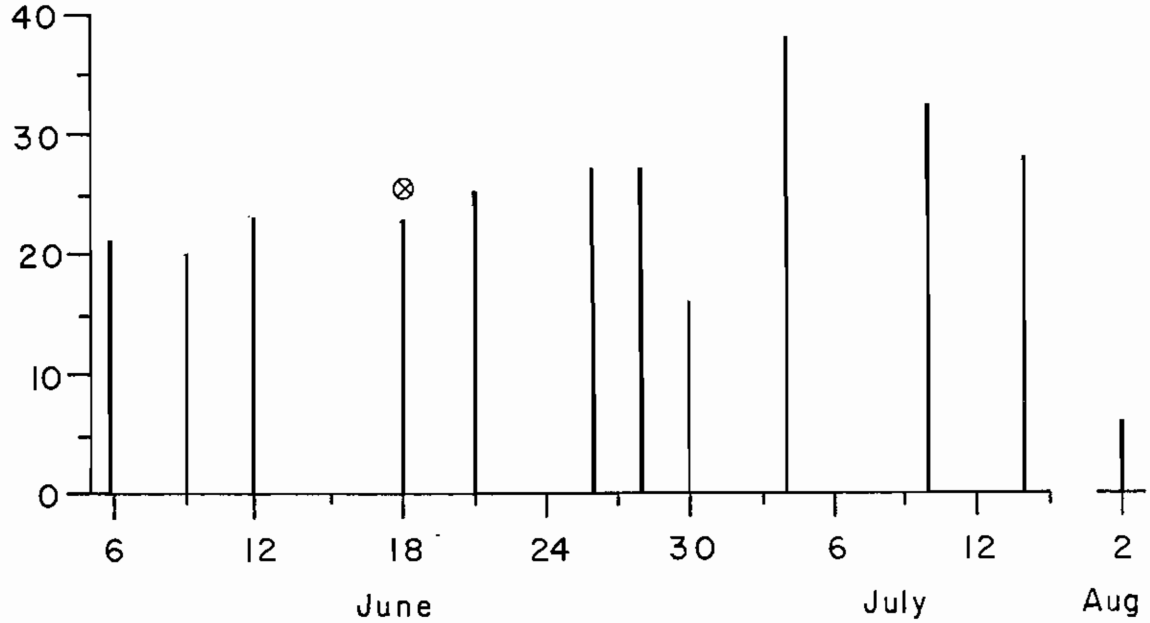

Figure 18. Number of Snowy Plovers counted on censuses along the DR seeps (4.5 km) in 1980. Censuses have been recalculated based on repeat sightings of color-marked individuals (see Methods). Bar marked ⊗ is a mean of two censuses made on this date.

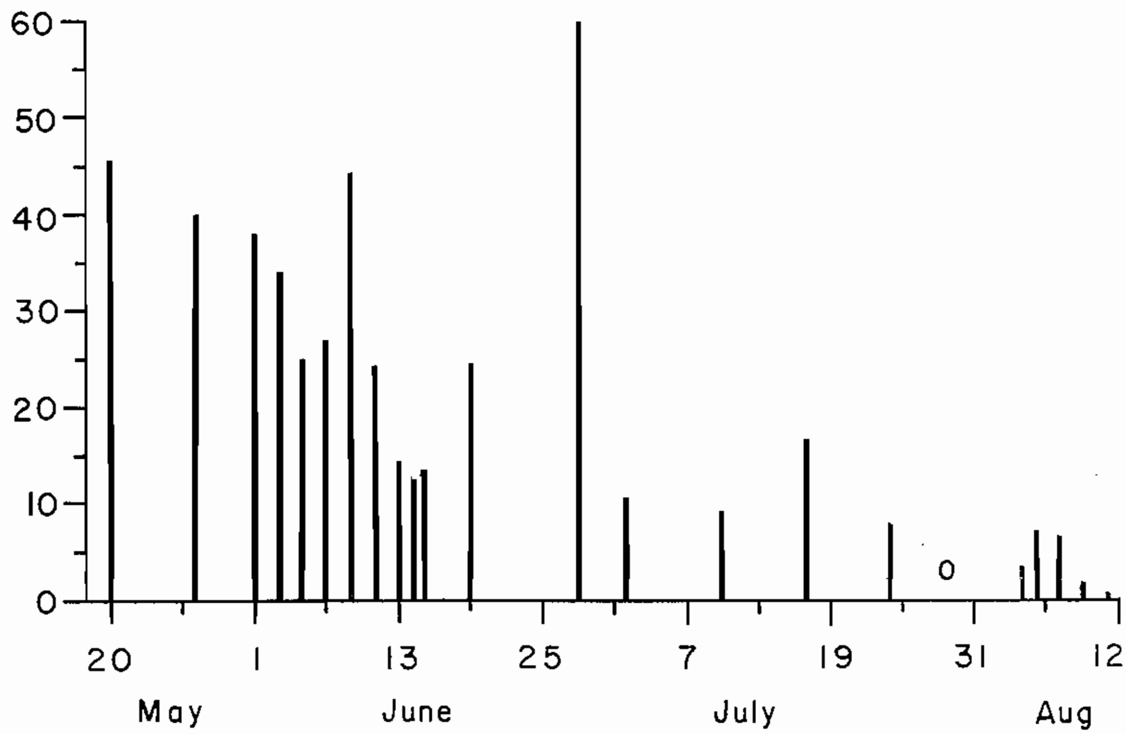

Figure 19. Number of Snowy Plovers counted on censuses along the DR seeps (4.5 km) in 1981. Censuses have been recalculated based on repeat sightings of color-marked individuals (see Methods).

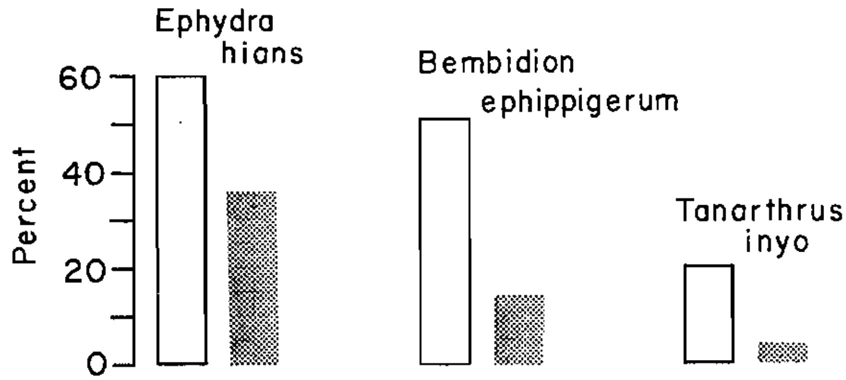

Figure 20. Comparison between the abundance of three lakeshore insects and their occurrence in Snowy Plover feces collected at the lakeshore. Open bars indicate the percentage of fecal samples (N = 35) containing the prey item, and shaded bars indicate the percentage of each species (of total) captured in pitfall traps at Lakeshore zone 1.

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APPENDICES

Appendix 1. Pitfall trapping effort (number of trap-days) among the different microhabitats in the study area.

Microhabitat[a]	Number of Traps (a)	Trap Exposure Period	Number of Exposure Days (b)	Number of Trap-Days (a x b)
Lakeshore				
zone 1	2	5 June - 4 July	29	58
	8	30 June - 8 July	8	64
	5	7 - 14 Aug	7	35
				157
zone 2	14	30 June - 8 July	8	112
	6	8 - 27 July	19	114
	3	7 - 14 Aug	7	21
				247
zone 3	2	4 - 10 June	6	12
	1	10 - 17 June	7	7
	4	17 - 23 June	6	24
	4	23 June - 3 July	10	40
	1	30 June - 8 July	8	8
	4	3 - 13 July	10	40
	9	8 - 27 July	19	171
	2	13 - 31 July	18	36
	9	27 July - 7 Aug	11	99
	5	7 - 14 Aug	7	35
				472
zone 4	2	17 - 23 June	6	12
	1	24 June - 4 July	10	10
	3	30 June - 8 July	8	24
	2	3 - 13 July	10	20
	2	4 - 17 July	13	26
	10	8 - 27 July	19	190
	2	17 - 31 July	14	28
	4	27 July - 7 Aug	11	44
	2	31 July - 13 Aug	13	26
	1	7 - 14 Aug	7	7
				387

[a]Microhabitat locations and lakeshore zone definitions are given in the Methods and Fig. 1.

Appendix 1 (Continued)

Microhabitat	Number of Traps (a)	Trap Exposure Period	Number of Exposure Days (b)	Number of Trap-Days (a x b)
Lakeshore				
zone 5	2	8 - 27 July	19	38
	2	13 - 31 July	18	36
	2	17 - 31 July	14	28
	16	27 July - 7 Aug	11	176
	6	31 July - 13 Aug	13	78
				356
Dry Alkali				
west site	4	4 June - 13 Aug	70	280
east site	4	5 - 18 June	13	52
	2	18 June - 4 July	16	32
	4	4 July - 13 Aug	40	160
				244
north site	4	4 June - 31 July	57	228
	2	31 July - 13 Aug	13	26
				254
Damp Alkali	4	4 June - 31 July	57	228
	4	5 June - 31 July	56	224
	6	31 July - 13 Aug	13	78
				530
DR Seeps				
west site	4	4 - 18 June	12	48
	3	18 - 24 June	6	18
	2	24 June - 3 July	9	18
	4	3 July - 13 Aug	41	164
				248
east site	4	5 June - 13 Aug	69	276
Gravel Ridges	4	4 June - 13 July	39	156
	4	4 June - 17 July	43	172
	6	17 July - 13 Aug	27	162
				490

Total all Microhabitats: 3941 Trap-Days

Appendix 2. Relative abundance and habitat preference of arthropods along the northeast shore of Mono Lake.[a]

Species List	Lakeshore	Alkaline Flats	Wet Seeps	Gravel Ridges
Arachnida				
Araneae				
Dictynidae				
Dictyna sp.	FC	R	FC	R
Lycosidae				
unident. sp.	R	X	R	R
Salticidae				
unident. sp.	R	R	X	R
Solpugida				
Eremobatidae				
Eremobates sp.	X	X	X	R
Acarina				
Hydrachnida				
unident. sp.	X	X	X	R
Insecta				
Collembola				
Poduridae				
unident. sp.	X	A	C	FC
Hemiptera				
Saldidae				
Saldula arenicola	C	R	FC	X
Coleoptera				
Cicindelidae				
Cicindela sp.	R	R	R	X
Carabidae				
Bembidion ephippigerum	C	R	FC	R
Histeridae				
unident. sp.	R	X	R	X
Staphylinidae				
Bledius sp.	R	R	R	X
Carpelimus sp.	R	X	R	X
unident. sp.	R	X	R	X
Anthicidae				
Tanarthrus inyo	FC	C	FC	R
Notoxis sp.	R	X	X	R

[a]A = abundant; C = common; FC = fairly common; R = rare; X = absent.

Appendix 2. (Continued)

Species List	Lakeshore	Alkaline Flats	Wet Seeps	Gravel Ridges
Diptera				
Ceratopogonidae				
Leptoconops kerteszi	R	R	R	R
Dolichopodidae				
Thinophilus spinipes	A	X	FC	X
T. latimanus	X	X	FC	R
Ephydridae				
Ephydra hians	A	R	FC	R
Mosillus bidentatus	C	FC	R	R
Ptilomyia alkalinella	FC	R	C	R
Lamproscatella salinaria	R	X	R	R
Anthomyiidae				
Lispe sp.	R	X	R	X
Hymenoptera				
Chalcidoidea				
unident. spp.	R	X	R	R

Appendix 3. Notes on additional arthropods observed or collected in or near the study area.

Arachnida
   Araneae
      Lycosidae
         A single wolf spider (Alepecosa sp.) was identified to genus from the gravel ridges. Other members of this genus may have been captured in the pitfall traps.

Insecta
   Odonata
      Anisoptera
         Dragonflies were occasionally seen along shore.

   Orthoptera
      Gryllacrididae
         Two Jerusalem crickets were found near Upper Drift Ridge.

   Hemiptera
      Corixidae
         Water Boatmen (Corixa sp.) were abundant in several small springs 0.25 km to 1.5 km east of the study area and also in the shallow creek that flowed out of Warm Springs, 2 km east of the study area.

      Pentatomidae
         About 30 pentatomids, all of the same species, were seen in August 1980 near the base of a Distichlis-covered sand mound 0.1 km east of the study area on Drift Ridge.

   Coleoptera
      Cicindelidae
         Cicindela sp. larvae occurred at the damp alkali below Upper Drift Ridge (UDR 0.3-0.8), at a density of about three burrows per square meter.

   Diptera
      Culicidae
         Mosquitos were occasionally encountered, mostly over the gravel ridges.

      Ceratopogonidae
         Culicoides larvae were identified from the moist substrate next to the pool at Lakeshore 4.3.

Appendix 3. (Continued)

Insecta

Diptera

Tabanidae

Several species of deer flies occurred in the study area, mostly near the gravel ridges. A large tabanid larva was found next to the pool at Lakeshore 4.3.

Therevidae

A single therevid fly was found at DR 2.1 in July 1980.

Asilidae

Asilids were uncommon in the study area; one was seen carrying a moth.

Dolichopodidae

Three specimens of Hydatostega (Hydrophorus) plumbea were collected at the lakeshore on 2 July 1980. These represent the first records for California (Foote et al. 1965, R. Hurley, pers. comm.).

Tephritidae

A single tephritid fly was collected in July 1980 at Drift Ridge 2.1.

Hymenoptera

Formicidae

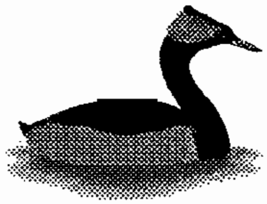
Red ant mounds were common along High Ridge.

Pompilidae

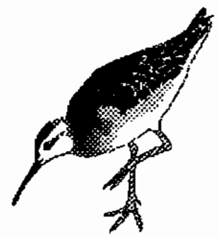
A 2.0 cm long spider wasp captured a 7 mm long salticid spider and dragged it 20 m across the alkali near Lakeshore 0.8 in June 1981.

Vespidae

Several vespid wasps were seen digging in the sand on the gravel ridges in July 1980.



MEMORANDUM



TO: Chris Swarth
ADDRESS:

DATE: 1 March 2004

FROM: J.R.JEHL, JR.
Ph. 410-224-0728
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Chris- There have been a lot of papers generated from Mono Lake. Your thesis is one of the very few that probably will not have to be reconsidered. Nice job. Too bad you didn't publish it, as people are reinventing the wheel.

You may recall my comment that I had not seen many Snowy Plovers recently. In fact, I mostly could not find any, although the PRBO folks say there are still good numbers. Your thesis revived my memory. Nearly all of my work in the past few years has been on the lake (as usual) but starting about 30 July, when the Wilson's Phalaropes peak. The plovers are gone. (Yes, even my thinking needs to be revised once in a while.)

Joe