

AN ABSTRACT OF THE THESIS OF

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the Department of Fisheries and Wildlife presented on October 31, 1986

Title: Foraging Ecology of Migrant Waterbirds, Lake Abert, Oregon

Abstract approved: Signature redacted for privacy.

Robert L. Jarvis

Seven species of water-dependent birds (northern phalarope, Phalaropus lobatus; American avocet, Recurvirostra americana; Wilson's phalarope, P. tricolor; eared grebe, Podiceps nigricollis; ring-billed gull Larus delawarensis; California gull, L. californicus; and northern shoveler, Anas clypeata) were studied during the fall migrations of 1982 and 1983 to determine the diets and foraging strategies of mixed-species feeding assemblages at an alkaline lake in southcentral Oregon. Information on density and distribution of birds and their prey resources was collected at permanent sampling points along the eastern shore of Lake Abert, Lake Co., OR. Determination of diet composition was based on analysis of stomach samples from collected specimens. Between-species comparisons of diet composition were made using classification analyses. Diet samples were compared to prey availability samples to discern whether birds fed preferentially on particular prey types. Timed observations were used to develop time budgets. Multivariate ordination procedures were used to determine the extent of niche overlap and resource partitioning. Structural measurements were taken from collected specimens to aid in assessment of physiological condition of migrants.

Total numbers of migrants using Lake Abert varied from year to year. Numbers of all species except eared grebes and gulls were lower in 1983 than in 1982. Total sample biomass of prey also declined between 1982 and 1983. Fifteen potential prey types were identified within the lake and along the lakeshore. Of these, the alkali fly (Ephydra hians) was the principal prey of all birds except the northern shoveler, whose diet included large percentages of brine shrimp (Artemia salina) and water fleas (Moina sp.). Bivariate correlation analysis revealed no significant relationships between concentrations of birds and aggregations of prey organisms.

Foraging was the predominant activity of all bird species. Northern shovelers foraged for a larger percentage of the day than did other species (71%) while eared grebes foraged least (14% of daylight hours). Morning and afternoon foraging peaks were noted for shovelers and avocets.

Classification and preference analyses indicated substantial overlap in diets of migrant birds, particularly among shorebirds and between gulls. When other dimensions of resource use (i.e. time allocation, foraging substrate, and technique) were examined along with diet, using a reciprocal averaging technique, some partitioning was evident in the foraging time allocation and techniques of shorebirds. Time allocation, diets and foraging techniques of the two gull species were strikingly similar. Mean weights and/or mean fat scores of all species tended to be lower in 1983 than in 1982. Changes in relative abundance of prey types, and availability of foraging macrohabitats, resulting from rising water levels, may have affected foraging patterns and condition of migrants.

FORAGING ECOLOGY OF MIGRANT WATERBIRDS, LAKE ABERT, OREGON

by

Kathryn Marcile Boula

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of


Master of Science

Completed October 31, 1985

Commencement June 1987

APPROVED:


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Date thesis is presented: October 31, 1986

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ACKNOWLEDGEMENTS

Dr. Robert L. Jarvis served as my major professor. I thank him for his guidance, humor and patience. Drs. Robert Anthony, David McIntire and Fred Ramsey, my committee members, contributed greatly to the data analysis and earlier drafts of the thesis.

This study was funded through the Non-Game Check-Off Program of the Oregon Department of Fish and Wildlife. Current and past directors, William Haight and Frank Newton were instrumental in the initial approval and funding and continued to provide cooperation and enthusiasm throughout the study.

Several others gave assistance during the course of this project. Special thanks go to Steve Denny, ODFW biologist at Summer Lake, who gave of his time, skills, and knowledge of the desert lakes. Gene Silovsky and Bill Otani of the Freemont National Forest, and Keith Kreuz of Valley Falls also assisted in the field. The Otani family generously shared their home and property, providing trailer space, utilities and many other comforts of "home" during both field seasons. Dr. David Herbst (Dept. of Entomology) and Dr. Frank Conte (Dept. of Zoology) of Oregon State University contributed data on the invertebrates of Lake Abert. Dr. Joseph Jehl of Hubbs-Sea World Research Institute provided unpublished information on the diets of grebes and phalaropes at Mono Lake.

To my fellow graduate students, I extend affection and gratitude for the enthusiasm, intellectual stimulation and friendship they shared. To my family, much love and thanks for their support and encouragement throughout my studies.

Finally, thanks to LaVon Mauer for her patience with a long-distance typing schedule.

DEDICATION

This work is dedicated to the
memory of my brother, Matt.

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FORAGING ECOLOGY OF MIGRATORY BIRDS, LAKE ABERT, OREGON

I. GENERAL INTRODUCTION

The ways in which animals choose foods and foraging places has long been an important topic in ecology. Recent theoretical and empirical workers have focused on foraging optimization, selectivity, resource partitioning and niche overlap (Pyke et al. 1977, Saether 1983, Schulter 1981, Stein 1977). Collectively, these topics form the framework of "foraging theory", which, simply stated, seeks to predict the ways that animals acquire food necessary to maximize net energy gain.

Early workers in foraging theory focused on autecological problems (see Pyke et al. 1977 for review), closely controlled laboratory situations with limited, pre-determined variables (Krebs et al. 1974, Myers et al. 1980) or field studies of predator species with relatively stable prey resources (Schulter 1982). Studies of resource overlap and partitioning were restricted to relatively simple systems with few, often closely related species (Anthony and Smith 1977, Schoener 1969).

The reductionist approach described above imposes serious limitations on the application of foraging theory to field studies of predator-prey systems. Selection of prey or habitat is rarely without costs in the natural world, and choices are made within the context of complex, dynamic arrays of physiological, behavioral and environmental circumstances (Pulliam 1975, Reichman 1977, Schulter 1981). Evaluating theories of foraging ecology in a variety of field situations, as well as in the laboratory, is important for accurately assessing their predictive strength in the natural world.

Birds have been extensively studied in both field and laboratory investigations of foraging theory. Most studies dealt with foraging relationships between breeding birds of closely related taxa (Bartonek and Hickey 1969, Holmes and Pitelka 1968, Noyes 1982). The importance of adequate food resources to the success of nesting birds is well documented, particularly for northern temperate breeding species (Holmes 1966, Pienkowski et al. 1979, Wiens and Scott 1975).

The importance of migration and overwintering in the year-round foraging ecology of migrant birds has been suggested (Evans 1976), but seldom investigated (but see Baker and Baker 1973, Holmes and Pitelka 1968, Recher 1966). Some authors argue that, while foods may be readily available or even super-abundant in northern breeding areas (Cooper 1984, Pienkowski and Evans 1984, Rosenberg et al. 1982), resource limitation is more likely to occur on the wintering grounds (Baker and Baker 1973, Evans 1976).

Few researchers have investigated resource use by birds during the migration season specifically. Many species (i.e. waterfowl and shorebirds) use traditional migratory routes along which are located key "staging" areas. These staging areas provide critical feeding and resting stops between long-distance flights to the wintering area (Cherry 1982, Page and Middleton 1972). Myers (1983) termed migratory staging areas "geographic bottlenecks", and stressed that environmental conditions at staging grounds could affect the entire population within a migration corridor. Staging areas are often used by large, multi-species aggregations of birds (Burger et al. 1977, Recher and Recher 1969). Where large aggregations occur, food and or

space may become limited. This is particularly true of coastal staging areas, where the availability of food and of foraging and roosting space is governed by the tides (Recher 1966, Schneider and Harrington 1981).

Mixed-species assemblages using inland migration routes face different environmental constraints at staging areas. Although their prey and roosting space may not change dramatically from hour to hour, as in coastal areas, year-to-year climatic changes may have extreme and unpredictable affects on resources. One year's shallow lake, which provided abundant food and roosting habitat, both necessary for replenishing fat stores, may be either flooded, or completely dry another year, diminishing or totally eliminating a critical staging area.

Lake Abert, a large saline-alkaline lake in southcentral Oregon, is an inland staging and stopover point for fall migrants in the Pacific Flyway. Large numbers of water-dependent birds rest and feed at the lake before continuing in their southward migration. Birds were presumably attracted to the lake by abundant populations of the brine shrimp Artemia. This small planktonic crustacean was thought to be the primary food source for fall-migrating birds; however, no direct observation or quantification of bird diets were attempted prior to this study. The brine shrimp is commercially harvested as a pet food and is an important high quality food resource for the aquaculture industry (Conte 1981, Herbst et al. 1984). In the mid-1970's the Oregon Department of Fish and Wildlife (ODFW) granted one limited permit for the harvesting of brine shrimp from Lake Abert.

This is the only active shrimp harvest operation at the lake at present, however, other companies have expressed interest in expanded harvest operations (W. Haight, pers. comm.).

The study reported here was initiated in 1981 at the request of ODFW in order to assess possible impacts of existing and/or future shrimp harvesting on the migratory bird "community". The goals of this study were to describe the foraging ecology and interspecific relationships of fall-migrating birds at Lake Abert, and to assess the importance of the lake as a feeding and resting area for migratory birds. Primary objectives were to determine what prey organisms were available to migrating birds and to document patterns of prey utilization by each species.

II. STUDY AREA

The study was conducted at Lake Abert, a large saline/alkaline lake located at the northern edge of the great Basin in southcentral Oregon (Figure 1). The area is characterized by shrub-steppe vegetation and massive fault-scarp landscapes, dotted with saline and brackish lakes. Precipitation averages 12 inches annually, mostly as winter snow. Phillips and Van Denburgh (1971) described Lake Abert as a classic closed-basin, carbonate-alkaline lake lying in an impermeable basin. At high water levels, Lake Abert is approximately 8 km wide and 26 km long, with depths of over 7 m. Maximum water volume has approached 1 million acre-feet at highest recorded levels (1958, 1984). The lake was completely dry as recently as 1937. The Chewaucan River, which discharges into the south end of the lake is the major freshwater source for the lake. Annual inflow is approximately 48,000 acre-feet. Several freshwater springs are present along the periphery of the lake, but contribute little to the freshwater inflow in most years. River flows decrease dramatically by mid-summer, due in part to upstream irrigation diversions. Evaporation loss often exceeds 30 inches between May and October. Shoreline structure varies from alkali playa and mudflats to rocky beach, with relative proportions dependent on changing water levels (Table 1).

Figure 1. Map of Lake Abert, Lake County, Oregon with sampling stations (1-5).

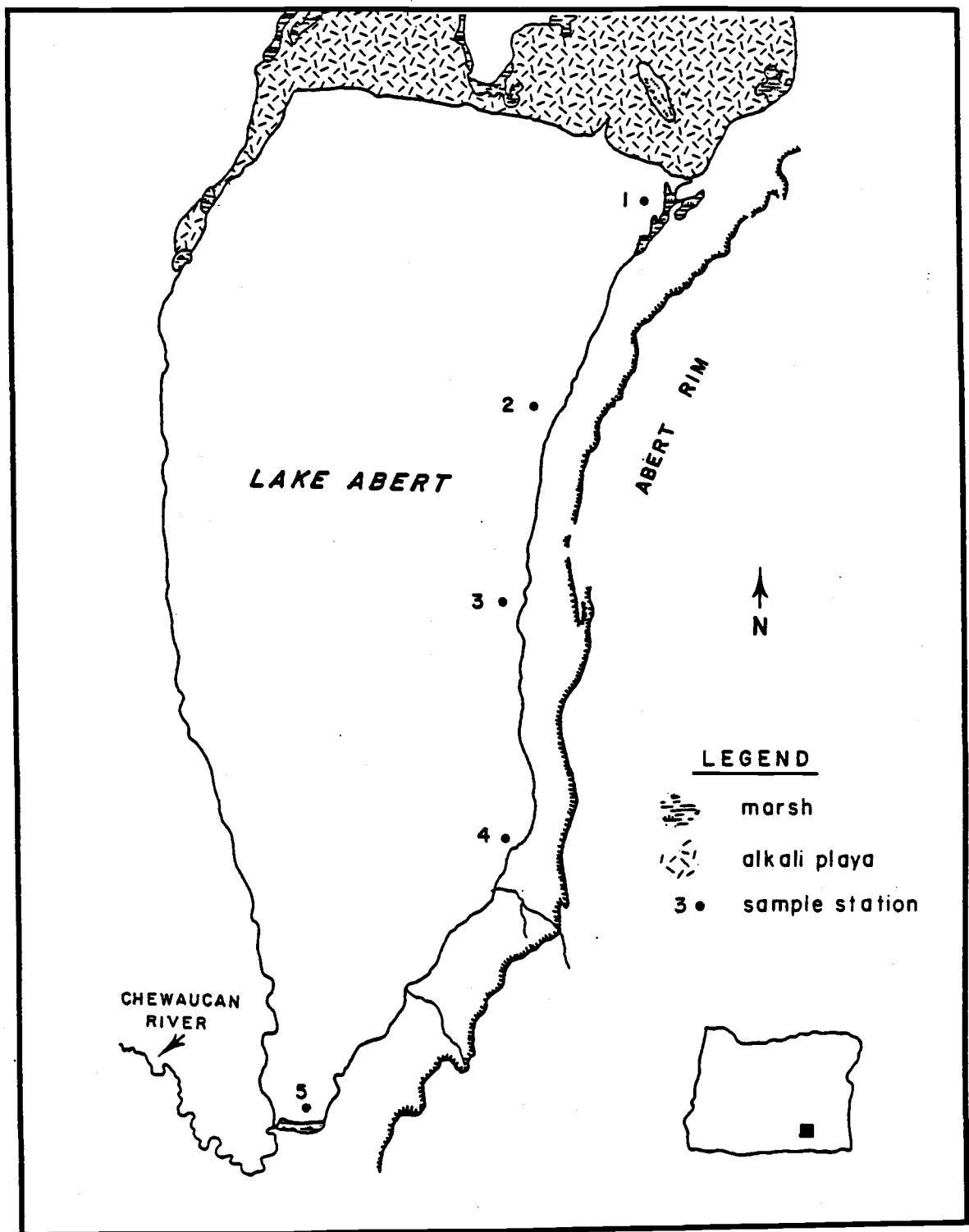


Figure 1.

Table 1. Types and approximate proportions of shoreline macro-habitats¹, 1982-83, Lake Abert, Oregon.

Habitat type	Proportion of shoreline (%)
Alkali mudflat	44
Rocky/cobble	42
Gravel beach	4
Sandy beach	4
Marshy, vegetated	6

¹ North, east and south shoreline only.

III. METHODS

Birds species included in these investigations were the northern phalarope (Phalaropus lobatus), Wilson's phalarope (P. tricolor), American avocet (Recurvirostra americana), eared grebe (Podiceps nigricollis), ring-billed gull (Larus delawarensis), California gull (L. californicus) and northern shoveler (Anas clypeata). These species comprised the majority of all birds observed at the lake during both years of the study. Data were collected during the fall migration periods of 1982 and 1983 (on the migratory calendar, "fall" begins in early July for shorebirds and ends in late October for ducks).

Densities and distribution of birds and their prey were determined by censusing at regular intervals at permanent sampling stations. All major habitat types were represented by at least one sampling station. Diet composition of each predator species was determined through analysis of stomach contents of collected birds. Data from stomach samples were compared to prey density and distribution information to determine whether birds fed preferentially on particular types of prey.

Observations of individual birds were used to develop time budgets for each species. Several behavioral, biotic, and abiotic factors were considered in determining the degree, if any, of resource overlap and/or partitioning. Finally, structural measurements made at the time of collection were used to assess the physiological condition of fall migrants.

IV. FORAGING ECOLOGY OF MIGRANT WATERBIRDS

INTRODUCTION

Birds that migrate between disjunct breeding and wintering grounds incur energetic costs beyond those of maintenance and reproduction (Berthold 1975, Metcalfe and Furness 1984, Tucker 1971). The additional energy demands of migration may impose important constraints on foraging behavior, prey selection, and resource partitioning within and among species along the migration route. The availability of adequate, nutritious prey resources at traditional migratory stopovers is critical to the immediate and, ultimately, overwinter survival of fall migrants (Myers 1983).

All of the birds species included in this study are known to prey on invertebrates (Dodson and Egger 1980, Hohn and Barron 1963, Ryser 1985); the northern shoveler also feeds on vegetative structures (Bellrose, 1978). Given the severe environmental conditions in and around Lake Abert (i.e. high pH and total dissolved solids, limited freshwater inputs, sparse shoreline vegetation) one might expect limited taxonomic diversity within the invertebrate community, and thus a limited range of foods available to the bird community. In another harsh environment, the Alaskan tundra, Holmes and Pitelka (1968) found a dense and taxonomically diverse bird population to be supported by a dense but taxonomically limited prey community. They also found a high degree of overlap in diets of shorebird species, which they attributed to the limited diversity of prey species.

In this study, I describe the diets of birds and relate interspecific differences or similarities in diet to the density and distribution of potential prey species. My specific objectives were to:

1. determine bird and prey densities and distributions
2. document composition of the diets of all bird species
3. compare diets among species and assess the degree (if any) of overlap in food utilization and
4. determine whether birds fed preferentially on specific types of prey

STUDY AREA AND METHODS

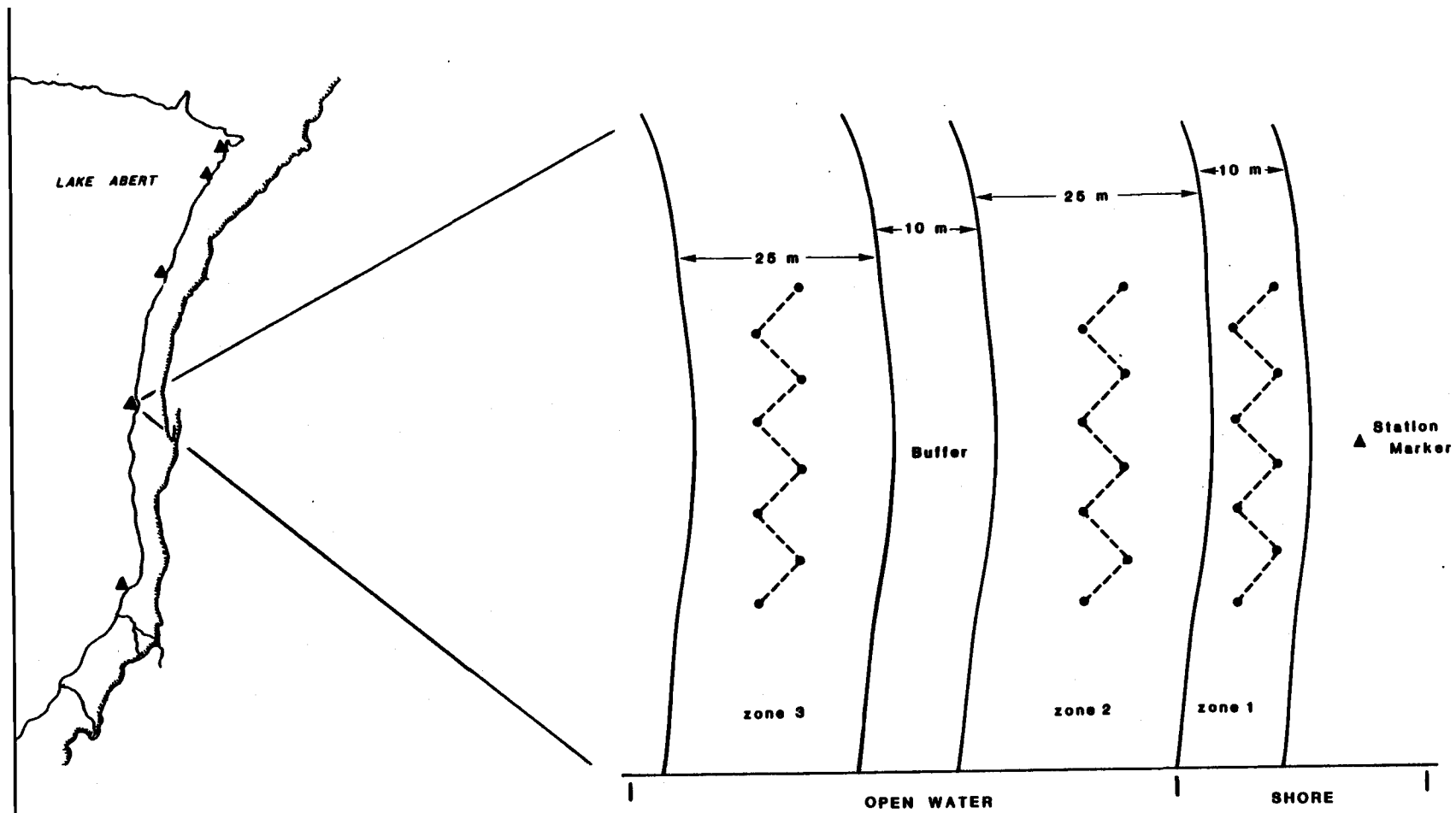
All observations and sampling for this study took place along the eastern, northeastern and southeastern shores of the lake; the western shore was inaccessible due to road and shoreline conditions. Five stations were established at elevated points (rock outcrops, etc.), several hundred meters from the lakeshore to facilitate surveys and to avoid disturbance to birds.

Information on foraging ecology of migrating birds was collected at two levels: initially, I made a general assessment of densities and distribution for all potential prey species, with concurrent collection of information on distribution and densities of birds. Second, stomach samples of birds were analyzed to directly determine composition of diets.

Methods for collection of baseline information consisted of weekly bird counts at each observation station, biweekly sampling of prey populations at each station, and estimates of relative availability of foraging habitat types. For both bird and prey counts the lake was delineated into 4 zones paralleling the shoreline: 1) a shore zone extending landward 10 m from the water's edge; 2) a near-shore zone extending from the shoreline 25 m (horizontally) into the open water; 3) a 10 m "buffer" zone in which birds were not counted, to avoid duplicate counts; and 4) a far-shore zone extending 25 m beyond the buffer zone (Figure 2). Open water zones (2 and 4) were measured from a boat and marked with permanent buoys to aid in delineation of census areas. During each count, all birds within 100 m north and south of a

Figure 2. Sample point layout for bird counts and prey collections of each sampling station.

Figure 2.



shoreline station marker were counted for each zone. Bird species, number of individuals, date, time, weather and water conditions were noted for each count. Weekly counts were made at all 5 stations in a single day to prevent possible distortion of counts by daily movements of birds. Counts were conducted during the early morning to avoid visibility problems with heat waves.

For prey counts, eight sampling points were established along the water's edge in a zig-zag pattern at each station, resulting in 4 water and 4 shoreline points (Figure 2). For each biweekly sampling period, 3 randomly chosen points (of the eight possible) were sampled in the shoreline and nearshore zones, with a similar pattern of "imaginary" points sampled in the far-shore zone. Water depth, temperature and hydrometer readings were recorded for each sample. Prey sampling methods varied with the substrate type. Samples of aquatic organisms were obtained from the water column with a long-handled plankton net with mesh openings of 0.5 mm. Three, 1.5 m sweeps were made for each sample; one near the bottom substrate, one midway in the water column, and one just below the water surface. Water and shoreline surfaces were sampled for flying insects by placing 2, 15 cm² sampling boards coated with "sticky trap" adhesive on the ground (or floating on the water surface) at the sampling point. Boards were collected after 10 minutes; flies trapped on the boards were tallied by species. Shoreline infauna were sampled by removing 2, 15 x 15 x 5 cm cores of substrate for each shoreline sample. On cobble beaches this entailed removing stones from within the sample frame and examining each for clinging larvae or pupae.

Water and substrate samples were returned to the laboratory where prey items were separated from the substrate using a series of screens, and hand sorted under a dissecting scope. Potential prey were identified to species and life stage and counted. Prey sample volumes were mathematically weighted according to sample type (net, core, etc.) to arrive at a standard sample volume.

Diet Description - Field Methods

Actively feeding individuals of all study species were collected at two week intervals over both field seasons, from all habitat types at various times of day. Upon collection, specimens were immediately weighed, measured, and dissected. The esophagus, proventriculus and gizzard were removed and placed in a solution of 70% ethanol for later examination. Food items were rarely digested beyond recognition. Thus, I concur with Marsh (1983), that injection of digestive tracts with alcohol is unnecessary for preserving stomach contents. In the laboratory, contents of esophagi and gizzards were identified and counted separately with the aid of a dissecting scope. Empty digestive tracts were excluded from statistical analyses.

Diet Description - Statistical Methods

Average dry weights were calculated for most prey species after drying samples to a constant weight at 65° C. Weights for adult Artemia were supplied by D. Herbst (pers. comm.). Weights of brine shrimp cysts followed estimates by Clegg (1974). Stomach contents for each bird specimen were converted to biomass estimates by multiplying

the number of each prey type in the sample by it's average dry weight. Average weights of indigestible portions of food items (such as pupal cases of alkali flies) were subtracted from the average dry weight as necessary. Only prey items found in at least one stomach were considered as potential foods in statistical analyses. Finally, foods consumed were expressed as percent occurrence and aggregate percentage (Swanson et al. 1974) by weight for the entire sample of each bird species. Diet composition was compared among bird species over the entire study period and within each species between the two field seasons. Preliminary analysis indicated diets of all species were sufficiently consistent over the two years to allow pooling diet data for statistical tests (Appendix 1).

An initial analysis of diet data compared diet similarity among all bird species simultaneously. The multidimensional scaling technique described by Mardia et al. (1979) was used to "map" distances in overall diet composition, giving a graphic display of how "close" or how "far" diets of bird species were from one another. This analysis was based on aggregate percent weight. Next, a non-parametric multinomial model (Ramsey and Marsh 1984) was used with paired species samples to test whether diets were sufficiently different to identify pair members on the basis of diet alone. This method is based on a classification procedure, in which individual prey types are allocated scores calculated as the logits of Bayes posterior probabilities. From these scores, two scales are derived, one based on a diet model, the other based on the observed diet proportions for each predator species. A "coefficient of diet

dissimilarity", calculated as the average logit score for correctly classifying all individuals, is then used to describe the total diet dissimilarity (DIS) between pairs of bird species. The "overall average certainty of correct classification" (Marsh 1983) of an individual to a given species was interpreted as a measure of the total diet dissimilarity between two species. The accuracy of the classification model depended not only on the overall differences between diets of two species, but also on variety and consistency within the diet of a species (Marsh 1983).

To determine whether meaningful differences existed between diets, we compared dissimilarity indices with diet percentages for pairs of shorebirds and pairs of gulls. The relative contribution of each prey type to the total dissimilarity index was calculated for pairs of shorebirds and pairs of gulls. Ramsey and Marsh (1984) noted that a single prey taxon might contribute a large proportion of the overall dissimilarity index, meaning that its occurrence in the diet was strongly suggestive of one predator. If, however, that same prey rarely occurred in both diets, it was probably unimportant in the determination of total diet dissimilarity. Conversely, prey taxa which were taken with high but differing frequencies by both species, thus having only moderate dissimilarity factors, might actually reflect important separations between diets.

Prey Use vs Prey Availability - Field Methods

In order to assess availability of prey to foraging birds, samples of appropriate substrate (shoreline, near- or far-shore water) were

taken at the time and site of bird collections. Methods for collection and processing of prey samples were identical to those described for baseline samples (see above). Numbers of individuals of each prey type were converted to biomass estimates and expressed as mean aggregate percentages of the total prey density.

Prey Use vs. Availability - Statistical Methods

I used Johnson's (1980) non-parametric ranking procedure to determine diet preference among birds. For each predator species, prey were ranked by use (percent of predator's diet) and availability (relative percentage of total prey in the immediate foraging environment). Preference was measured as the mean difference in rank (over all samples for a given predator) between use and availability. Large differences indicated highly preferred prey. Differences between use and availability rankings were then compared to a test statistic to determine significance (see Johnson 1980: 68).

RESULTS

Density and Distribution of Birds

In 1982, peak numbers of both Wilson's and northern phalaropes were observed during the first week of August (Figure 3). In 1983, highest numbers of Wilson's phalaropes were again observed during the first week in August, while northern phalaropes reached season high numbers two weeks later (Figure 3). Initial peaks for both species were followed by sharp mid-season declines and minor late-season peaks. Northern phalaropes were observed at Lake Abert as late as mid-October; no Wilson's phalaropes were observed at the lake after mid-September.

In 1982 the avocet population reached a peak in mid August, approximately two weeks later than the phalaropes, and remained fairly stable for three to four weeks before declining sharply. A second, minor influx was noted in mid-September (Figure 3). In 1983, the population was smaller, peaked earlier (mid-July), and again declined sharply; however, the population in August/September remained at higher levels than that of the same period in 1982 (Figure 3).

Numbers of eared grebes were highest on 8 August in both years (Figure 4). Subsequent fluctuations in estimated densities may have been a function of movements of grebes between the near shore and mid-lake zones. Grebes were often observed moving shoreward in the early morning from the center of the lake where they apparently roosted overnight. Numbers of grebes began to decrease by early September in 1982, but stayed relatively high throughout September and

Figure 3. Numbers of shorebirds censused on Lake Abert, 1982-1983.

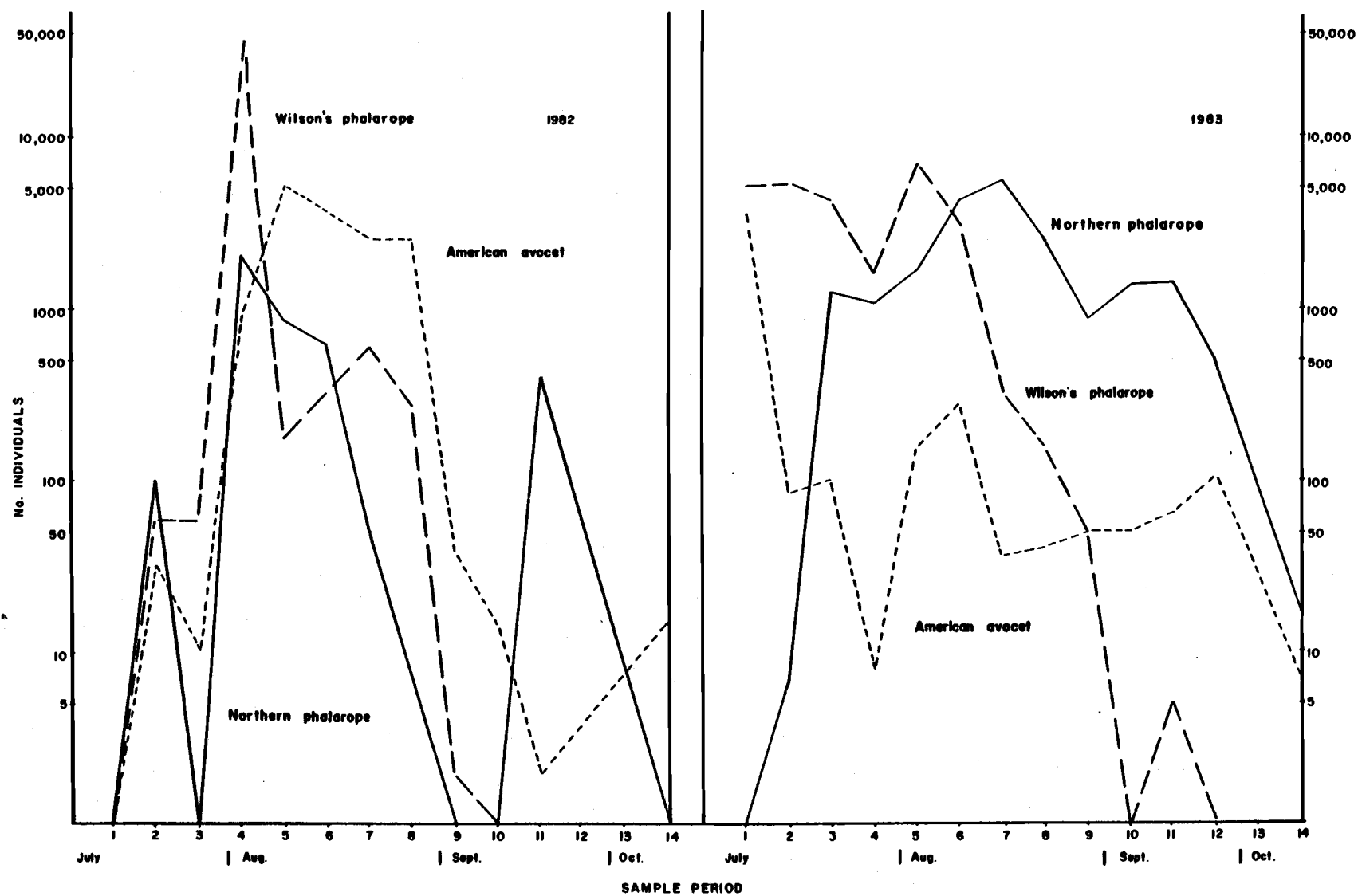


Figure 3.

Figure 4. Numbers of grebes, gulls and ducks censused on Lake Abert, 1982-1983.

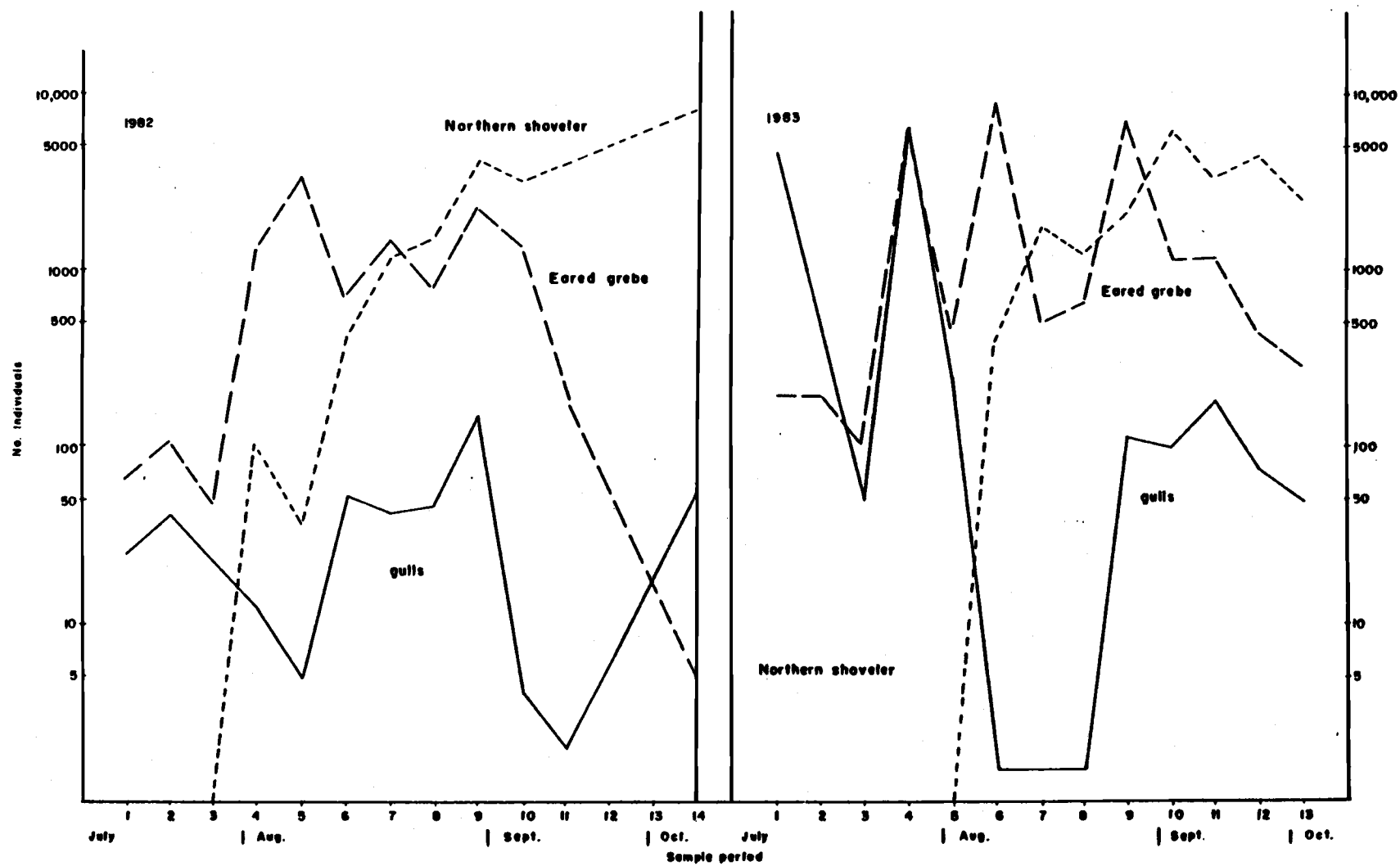


Figure 4.

into October in 1983. Some adult grebes observed early in June may have nested at the lake.

Northern shovelers were the latest arrivals at the lake. Observed peaks in numbers of shovelers varied by four weeks between 1982 (11 Oct.) and 1983 (6 Sept.). No marked secondary influx was noted for either shovelers or grebes.

Numbers of gulls were variable over both seasons. The presence of a large roost at the extreme northeast end of the lake in 1983 elevated the count considerably. Many of the gulls counted in 1983 may have been breeding birds which lost territories at Summer Lake, 50 miles to the northwest, when an important nesting island flooded (S. Denny, pers. comm.).

Total numbers of birds varied from 1982 to 1983. Eared grebes and gulls were most numerous on the study area in 1983 (Figure 4), while shovelers, northern and Wilson's phalaropes and avocets were more numerous in 1982. A decline was especially noticeable in numbers of Wilson's phalaropes which decreased from 30,000 in August 1982 to 7,000 in 1983. The secondary peaks noted for phalaropes and avocets (and to a lesser degree, gulls) may have represented an influx of young-of-the-year: 70 percent of all phalaropes and avocets observed after September 1 were identified as juveniles. The staggering of migration schedules between adults and juveniles is well documented for a number of migratory species (Pitelka 1950, Recher 1966).

Birds used all available macro-habitat types to some extent. Avocets were the only species which appeared to be restricted to the shore and shallows; no avocets were observed in water deeper than 1 m.

Gulls also tended to stay near or on shore, although they were occasionally observed up to 1 km offshore. Phalaropes, grebes and shovelers used both shallow and deep water zones. Phalaropes used the shoreline for feeding as well as resting. Phalaropes, avocets, gulls and shovelers congregated in very large roosts on the extensive mudflats at the north end of the lake. Most grebes and some shovelers appeared to move to mid-lake each evening, and returned to their near shore feeding area at daybreak.

Density and Distribution of Prey

Total sample biomass (\bar{x} mg/m³) of prey decreased from 1982 to 1983 (Table 2). Densities of adult brine shrimp, adult and pupal alkali flies (Ephydra hians), long-legged flies (Hydrophorus plumbeus) and "other" Dolichopodid flies, and beetles, were highest in 1982, while sample biomass of juvenile shrimp, alkali fly larvae, amphipods (Hyallela azteca) and waterfleas (Moina sp.) were highest in 1983 (Table 2).

Peaks in total sample biomass occurred between 28 August and 10 September for both sampling seasons. These peaks were generally reflected in peaks among individual prey species with the exception of amphipods and waterfleas. Peaks in sample biomass for these two species occurred 3 to 6 weeks later in 1983 than in 1982.

Bird/Prey Distribution

Bivariate correlation analysis of the distribution of birds and their prey did not reveal any significant ($P > 0.05$) correlations

Table 2. Peak sample biomass and year to year changes for prey species, Lake Abert, Oregon, 1982-83.

Species	1982 (mg/m ³)	1983 (mg/m ³)
Diptera		
<u>Ephydra hians</u>		
adult	12,357.61	9,055.64
larvae	1,405.11	2,149.77
pupae	45,392.99	39,214.42
<u>Hydrophorus plumbeus</u>		
adult	466.21	281.16
larvae	21,719.84	3,375.79
other Dipteran fly		
adult	130.68	59.27
larvae/pupae	255.16	1,190.21
Amphipoda		
<u>Hyallolella azteca</u>	4.66	34.82
Coleoptera		
<u>Hygrotus masculinus</u>	1,609.05	889.05
Anostraca		
<u>Artemia</u> sp.		
adult	518.54	513.24
juvenile	22.17	1,066.82
cyst	1.06	0.12
Cladocera		
<u>Moina</u> sp.	1.22	39.23
Cyperaceae		
<u>Scirpus</u> sp. seed	1,508.53	1,516.73

between distribution of birds and prey species for any station or habitat. Further, there were no significant ($P > 0.05$) relationships between peak numbers of birds and peak densities of their primary prey species.

Diet Composition

Although relative proportions varied, the alkali fly was the primary prey of birds at Lake Abert during autumn (Table 3). When all three life stages (larvae, pupae, and adult) were combined, alkali flies accounted for at least 65 percent of the biomass consumed by each species except the northern shoveler (Table 3). Seeds of bulrush (Scirpus sp.), waterfleas (10.7%), cysts of brine shrimp (22.3%), and larvae of alkali fly (17.6%) were common components of shoveler diets. Gulls had the least diverse diets: 75 and 68 percent of the diet biomass for ring-billed gulls and California gulls, respectively, consisted of alkali fly pupae. Larvae of alkali fly were the principal prey of northern phalaropes (55.3%), American avocets (34.3%) and eared grebes (48.3%). Brine shrimp occurred frequently only in the diets of eared grebes (35.5%) and shovelers (41.6%).

When the 1982 and 1983 diets were mapped in 2 dimensions (accounting for over 80 percent of the total diet variation over all 7 species), several patterns emerged (Figure 5). Diets of shovelers were markedly different from those of all other species, with most of the difference accounted for by the inclusion of seeds, waterfleas, and cysts of brine shrimp in the diet. Diets of eared grebes were also widely separated from other species, reflecting the large

Table 3. Mean dry weight, percent occurrence, and mean aggregate percent, by weight, of prey items consumed by fall-migrating birds, Lake Abert, OR.

Prey Item	\bar{x} dry weight (mg)	Northern phalarope		American Avocet		Wilson's phalarope		Eared grebe		Ring-billed gull		Northern shoveler		California gull	
		N=91		N=41		N=78		N=63		N=17		N=28		N=28	
		% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.	% occur.	\bar{x} agg. % wt.
Diptera															
<u>Ephydra hians</u>															
adult	2.70	59.3	10.1	48.8	10.2	81.8	34.9	75.8	10.3	4.7	8.0	0	0	3.8	4.4
larvae	3.04	89.0	55.3	62.3	34.3	51.9	27.4	85.5	48.3	58.8	14.9	31.6	17.6	3.5	10.2
pupae (without case)	2.12	84.6	23.8	87.8	27.7	81.8	24.8	61.3	6.7	100.0	75.0	22.8	7.2	92.3	68.0
<u>Hydrophorus plumbeus</u>															
adult	2.07	1.1	0.1	2.4	0.2	5.2	0.3	1.6	0.1	0	0	0	0	0	0
larvae	2.33	32.9	8.8	58.5	22.2	36.4	9.0	64.5	15.1	17.6	0.2	1.8	0.7	50.0	6.6
other Dipteran fly															
adult	2.00	54.9	0.9	0	0	0	0	8.1	0.7	0	0	0	0	7.7	0.3
larvae/pupae	3.78	1.1	0.1	19.5	3.3	1.3	0.1	2.1	2.3	1.8	0.2	0	0	3.8	4.1
Amphipoda															
<u>Hyalalella azteca</u>	0.56	0	0	2.4	0.1	0	0	0	0	0.6	0.1	0	0	0	0
Coleoptera															
<u>Hygrotus masculinus</u>	30.00	2.2	0.3	2.4	0.6	1.3	1.0	7.7	2.8	11.7	1.0	0	0	3.8	4.1
Anostraca															
<u>Artemia</u> sp.															
adult	1.96	0	0.4	0.1	1.3	10.4	1.6	32.3	12.9	5.9	0.7	1.2	8.0	7.7	1.7
juvenile	0.98	1.1	0.1	0	0	1.3	0.4	1.6	0.1	0	0	1.8	0.9	0	0
cyst	0.0063	0	0	4.8	0.2	1.3	0	1.6	0.7	0	0	38.6	22.3	0	0
Cladocera															
<u>Moina</u> sp.	0.0094	0	0	0	0	0	0	0	0	0	0	42.1	10.7	0	0
Cyperaceae															
<u>Scirpus</u> sp. seed	1.97	7.6	0.4	2.4	0.1	9.1	0.5	1.6	0.1	0	0	35.1	24.7	0	0

Figure 5. "Map distances" between diets of birds. Long distances between diet ordinations of species indicate very different diets, while short distances indicate similar diets (after Mardia et al. 1979). Triangles and circles with connecting lines show changes in the diets of each species from 1982 to 1983.

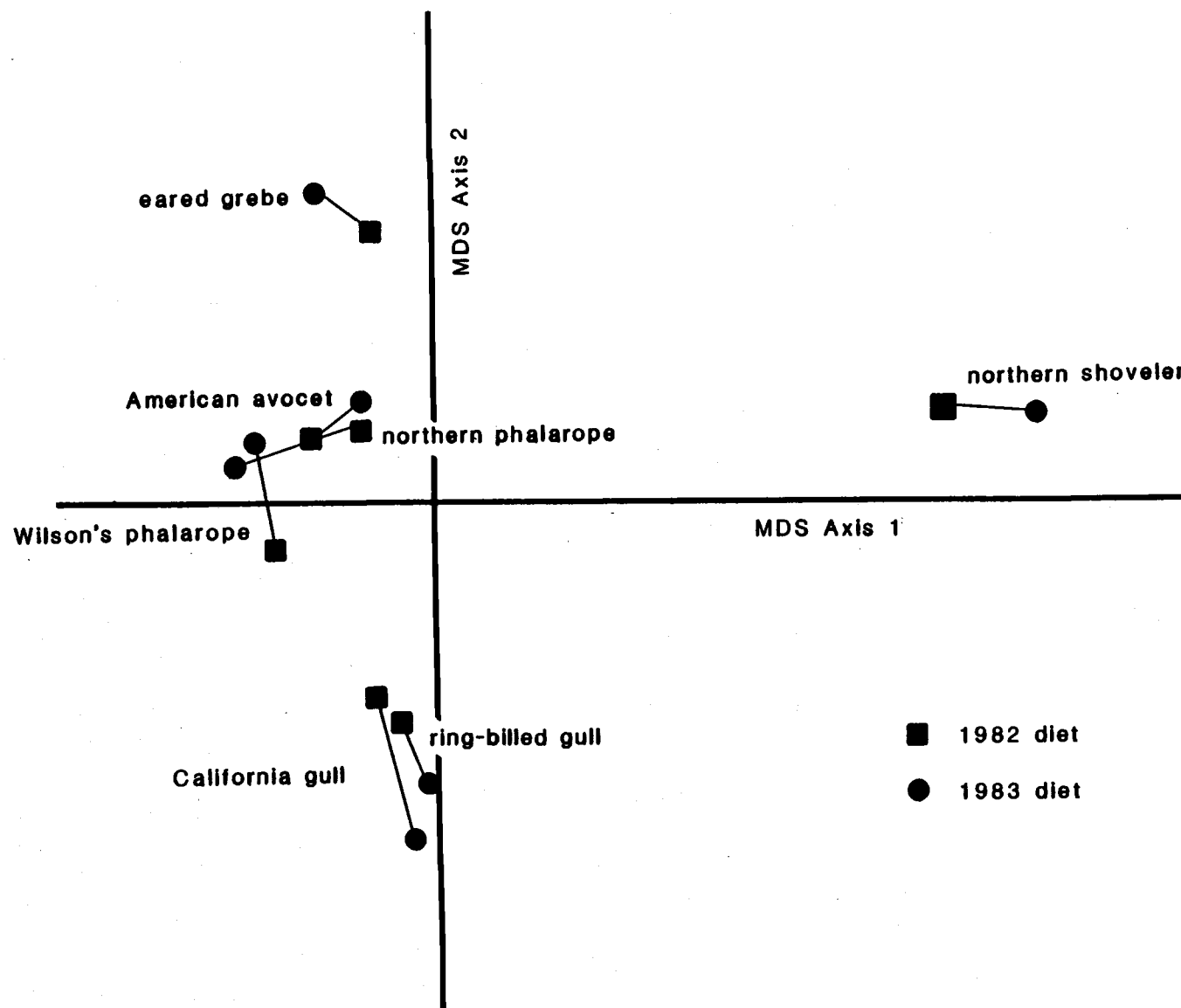


Figure 5.

contribution of adult brine shrimp to their diet. Diets of phalaropes and avocets, on the other hand, were tightly clustered, as were diets of gulls.

Based on the above observations, I made further comparisons for all possible species pairs, with emphasis on shorebirds and gulls. In pairs which included shovelers or grebes, the percentage of correct classifications was generally high, supporting the wide separations in diets indicated by long map distances (Table 4). For both shorebirds and gulls, the model was less successful in predicting a bird's species from its diet. Two interpretations were possible: 1) diets of one or both species within a group were variable, 2) the overall diets of the two species were too similar for classification to be accurate, or 3) both. Diets of shorebirds tended to vary considerably in the proportions of the major prey taxa taken by individuals, while diets of gulls were extremely similar in composition and relative proportions.

The combination of dissimilarity indices with diet percentages tended to clarify diet differences and further emphasize the importance of various prey types to individual bird species. For example, larvae of the alkali fly were the primary prey of both northern phalaropes (55%) and avocets (34%), while also accounting for 26 percent of the dissimilarity in the diets of avocets and northern phalaropes (Table 5). Long-legged flies were indicative of avocet diets, accounting for 22 percent of the diet of avocets compared to 9 percent of diets of Wilson's and northern phalaropes. Long-legged flies contributed 27 percent of the total dissimilarity between

Table 4. Overall average certainty of correct classification of birds to species based on interspecific diet comparisons.

Species pair	Percent correct classification
northern shoveler - Wilson's phalarope	94.9
northern shoveler - northern phalarope	94.0
northern shoveler - American avocet	94.0
northern shoveler - ring-billed gull	93.4
northern shoveler - California gull	93.0
eared grebe - ring-billed gull	92.5
eared grebe - northern shoveler	89.3
eared grebe - California gull	87.9
Wilson's phalarope - ring-billed gull	85.3
northern phalarope - California gull	82.4
Wilson's phalarope - California gull	80.2
northern phalarope - ring-billed gull	79.6
American avocet - California gull	76.8
northern phalarope - eared grebe	76.6
American avocet - ring-billed gull	75.9
Wilson's phalarope - eared grebe	75.2
American avocet - eared grebe	73.1
northern phalarope - American avocet	72.7
northern phalarope - Wilson's phalarope	70.4
American avocet - Wilson's phalarope	65.6
California gull - ring-billed gull	48.9

Table 5. Contribution of prey types to the diet dissimilarity index and to the diet biomass for paired species of birds, Lake Abert, 1982 and 1983.

Bird Species	Prey category	Percent dissimilarity	Percent biomass (sp. 1)	Percent biomass (sp. 2)
Northern phalarope (sp. 1)	AFL	21.2	55.3	34.3
vs	AFP	1.3	23.8	27.7
American avocet (sp. 2)	AFA	0.0	10.1	10.2
	LLL	26.7	8.8	22.2
	OFLP	32.7	0.0	3.3
	OFA	8.4	0.9	0.0
Northern phalarope (sp. 1)	AFL	34.4	55.3	27.4
vs	AFP	0.1	23.8	24.8
Wilson's phalarope (sp. 2)	AFA	54.2	10.1	34.9
	LLL	0.0	8.8	9.0
	OFA	4.5	0.9	0.1
	BSA	3.4	0.4	1.6
Northern phalarope (sp. 1)	AFL	1.0	55.3	48.3
vs	AFP	24.1	23.8	6.7
Eared grebe (sp. 2)	AFA	0.0	10.1	10.3
	LLL	3.9	8.8	15.1
	BSA	48.3	0.4	12.9
	OFLP	10.8	0.0	2.3
Northern phalarope (sp. 1)	AFL	35.8	55.3	14.8
vs	AFP	42.5	23.8	75.0
Ring-billed gull (sp. 2)	AFA	0.4	10.1	8.0
	LLL	16.8	8.8	0.2
	OFA	2.1	0.9	0.3
Northern phalarope (sp. 1)	AFL	9.8	55.3	17.6
vs	AFP	4.6	23.8	7.2
Northern shoveler (sp. 2)	AFA	6.3	10.1	0.5
	LLL	4.5	8.8	0.7
	BSC	28.6	0.0	22.3
	VEG	22.2	0.4	24.7
	WF	13.7	0.0	10.7
Northern phalarope (sp. 1)	AFL	46.0	55.3	10.2
vs	AFP	29.5	23.8	68.0
California gull (sp. 2)	AFA	3.0	10.1	4.4
	LLL	0.4	8.8	6.6
	BTL	6.2	0.3	4.1

Table 5. Continued

Bird Species	Prey category	Percent dissimilarity	Percent biomass (sp. 1)	Percent biomass (sp. 2)
American avocet (sp. 1) vs Wilson's phalarope (sp. 2)	AFL	2.7	34.3	27.4
	AFP	0.5	27.7	24.8
	LLL	20.3	22.2	9.0
	AFA	50.8	10.2	35.0
	OFLP	17.4	3.3	0.1
	VEG	3.0	0.0	0.5
American avocet (sp. 1) vs Eared grebe (sp. 2)	AFL	6.7	34.3	48.3
	AFP	42.0	27.7	6.7
	LLL	3.8	22.2	15.1
	AFA	0.0	10.2	10.3
	BSA	36.6	1.3	12.9
American avocet (sp. 1) vs Ring-billed gull (sp. 2)	AFL	11.2	34.3	14.9
	AFP	33.4	27.7	75.0
	LLL	48.5	22.2	0.2
	AFA	0.4	10.2	8.0
	OFLP	5.2	3.3	0.2
American avocet (sp. 1) vs Northern shoveler (sp. 2)	AFL	2.7	34.3	17.6
	AFP	6.8	27.7	7.2
	LLL	17.2	22.2	0.7
	AFA	7.0	10.2	0.5
	VEG	26.2	0.0	24.7
	BSC	20.8	0.2	22.4
	WF	11.4	0.0	10.7
American avocet (sp. 1) vs Eared grebe (sp. 2)	AFL	29.0	34.3	10.2
	AFP	36.5	27.7	68.0
	LLL	18.8	22.2	6.6
	AFA	5.0	10.2	4.4
Wilson's phalarope (sp. 1) vs Eared grebe (sp. 2)	AFA	28.0	34.9	10.3
	AFL	11.1	27.4	48.3
	AFP	22.4	24.8	6.7
	LLL	3.0	9.0	15.1
	BSA	21.4	1.6	12.9
Wilson's phalarope (sp. 1) vs Ring-billed gull (sp. 2)	AFA	28.8	34.9	4.4
	AFL	5.8	27.4	10.2
	AFP	43.2	24.8	68.0
	LLL	18.8	9.0	6.6

Table 5. Continued

Bird Species	Prey category	Percent dissimilarity	Percent biomass (sp. 1)	Percent biomass (sp. 2)
Wilson's phalarope (sp. 1)	AFA	28.1	34.9	0.5
vs	AFL	0.9	27.4	17.6
	AFP	4.7	24.8	7.2
Northern shoveler (sp. 2)	LLL	4.3	9.0	0.7
	VEG	19.7	0.0	24.7
	BSC	25.5	0.2	22.4
	WF	12.2	0.0	10.7
Wilson's phalarope (sp. 1)	AFA	42.7	34.9	4.4
vs	AFL	11.9	27.4	10.8
	AFP	31.3	24.8	68.0
California gull (sp. 2)	LLL	0.6	9.0	6.6
Eared grebe (sp. 1)	AFL	13.0	48.3	14.9
vs	LLL	15.2	15.1	0.2
	BSA	10.1	12.9	0.7
Ring-billed gull (sp. 2)	AFA	0.2	10.3	8.0
	AFP	58.5	6.7	75.0
Eared grebe (sp. 1)	AFL	8.8	48.3	17.6
vs	LLL	12.0	15.1	0.7
	BSA	0.7	12.9	8.0
northern shoveler (sp. 2)	AFA	8.1	10.3	0.5
	VEG	32.9	0.1	24.7
	BSC	20.2	0.7	22.4
	WF	15.2	0.0	10.7
Eared grebe (sp. 1)	AFL	24.0	48.3	10.8
vs	LLL	3.0	15.1	6.6
	BSA	9.1	12.9	1.7
California gull (sp. 2)	AFA	2.1	10.3	4.4
	AFP	59.6	6.7	68.0
Ring-billed gull (sp. 1)	AFP	40.1	75.0	7.2
vs	AFL	0.1	14.9	17.6
	AFA	5.1	8.0	0.5
Northern shoveler (sp. 2)	LLL	0.2	0.2	0.7
	BSA	3.8	0.7	8.0
	VEG	20.2	0.0	24.7
	WF	8.8	0.0	10.7
	BSC	18.3	0.0	22.5

Table 5. Continued

Bird Species	Prey category	Percent dissimilarity	Percent biomass (sp. 1)	Percent biomass (sp. 2)
Ring-billed gull	AFP	1.7	75.0	68.0
(sp. 1)	AFL	4.3	14.9	10.2
vs	AFA	5.3	8.0	4.4
California gull	LLL	43.7	0.2	6.3
(sp. 2)	OFLP	24.3	0.2	4.1
	BTL	10.5	1.0	4.1
Northern shoveler	VEG	21.8	24.7	0.3
(sp. 1)	BSC	22.0	22.4	0.0
vs	AFL	2.1	17.6	10.2
California gull	WF	10.5	10.7	0.0
	AFP	34.9	7.2	68.0

¹ AFA = alkali fly, adult; AFL = alkali fly, larvae; AFP = alkali fly, pupae; AMPH = amphipod; BSA = brine shrimp, adult; BSC = brine shrimp, cyst; BSJ = brine shrimp, juvenile; BTL = beetle; LLA = long-legged fly, adult; LLL = long-legged fly, larvae; OFA = other fly, adult; OFLP = other fly, larvae/pupae; VEG = seeds; WF = water flea.

avocets and northern phalaropes and 20 percent of the difference between avocets and Wilson's phalaropes. "Other" fly larvae, which accounted for 33 percent of the total dissimilarity index for avocets and northern phalaropes, made up less than 5 percent of either bird's diet, and thus were of little importance in differentiating between the two species.

Adult alkali flies were most indicative of Wilson's phalaropes, accounting for 35 percent of their diet and over 50 percent of the total dissimilarity between Wilson's phalaropes and the other shorebirds.

Diets of the two species of gull were very similar, as indicated by the low percentage of correct classifications of gulls to the proper species. Alkali fly pupae were the predominant food of both species. Long-legged fly larvae, which accounted for 44 percent of the pair's total dissimilarity, contributed less than 10 percent of the total biomass to the diets of either gull.

Relative Prey Preference

Preference measurements were based on the mean difference in rank between use and availability, with large differences indicating highly preferred foods (Table 6). Initially, simple preference rankings were compared to ranked biomass percentages of quantity consumed (percent biomass) of each species of bird. Rare, seldom taken prey, which often contributed little to the total diet biomass, were highly preferred. I then tested both prey ranks and biomass percentages for significant differences between all possible prey pairs. When foods

Table 6. Mean difference in rank of use versus rank of availability of major prey of migrant birds at Lake Abert, 1982-83.

Bird Species	Prey category	\bar{x} difference ¹ in ranks	Preference rank and significant differences ²
Northern phalarope	AFP ³	-2.65	1
	LLL	-1.43	2
	AFL	-1.30	3
	VEG	-0.74	4
	BTL	-0.73	5
	LLA	-0.61	6
American avocet	AFL	-1.66	1
	BTL	-1.35	2
	VEG	-1.32	3
	BSC	-0.99	4
	OFLP	-0.80	5
	AMPH	-0.71	6
	LLA	-0.55	7
Wilson's phalarope	VEG	-1.55	1
	BTL	-1.09	2
	AFP	-0.38	3
	LLL	-0.07	4
	BSA	0.11	5
	AFA	0.19	6
Eared grebe	AFL	-4.05	1
	LLA	-3.60	2
	AFP	-2.89	3
	OFLP	-1.42	4
	BSC	-0.84	5
	BTL	-0.65	6
	OFA	-0.46	7
Ring-billed gull	BTL	-1.44	1
	AFL	-0.82	2
	BSA	-0.79	3
	AFP	-0.38	4
	AMPH	-0.32	5

Table 6. Continued

Bird Species	Prey category	\bar{x} difference in ranks	Preference rank and significant differences
Northern shoveler	BSC	-3.30	1
	VEG	-2.12	2
	LLL	-0.31	3
	BSJ	-0.03	4
	AFL	0.35	5
	AFP	0.78	6
	BSA	1.40	7
California gull	OFA	-1.07	1
	BTL	-0.78	2
	BSA	-0.38	3
	AFP	-0.15	4
	AFL	0.75	5
	OFLP	0.76	6
	LLL	1.13	7

¹ Mean difference in rankings of use vs availability.

² Items not connected by a common line had significantly different ($P < 0.05$) preference rankings.

³ AFA = alkali fly, adult; AFL = alkali fly, larvae; AFP = alkali fly, pupae; AMPH = amphipod; BSA = brine shrimp, adult; BSC = brine shrimp, cyst; BSJ = brine shrimp, juvenile; BTL = beetle; LLA = long-legged fly, adult; LLL = long-legged fly, larvae; OFA = other fly, adult; OFLP = other fly, larvae/pupae; VEG = seeds; WF = water flea.

were re-ranked in groups according to significance levels, agreement between preference ranking and dietary importance improved. In fact, for all birds except phalaropes, the most highly preferred food group included the most dominant food in the bird's diet in terms of total biomass (Table 7). At least one lifestage of the alkali fly was among the most preferred foods for all birds except northern shovelers and Wilson's phalaropes, and one or more lifestages of the alkali fly occurred in the highest-ranked biomass group for all birds.

Table 7. Comparison of rankings of preference and biomass of prey categories in diets of fall migrants, Lake Abert, 1982-83.

Bird Species	Preference rank	Prey species	Biomass rank	Prey Species
Northern phalarope	1	AFP ¹	1	AFL
	2	AFL,LLL	2	AFP
	3	VEG,BTL	3	AFA,LLL,OFA
	4	LLA	4	BTL
American avocet	1	BSC,AFL,AFP,LLL,VEG,OFLP,AMPH,BTL	1	AFL,AFP,LLL
	2	BSJ	2	AFA,OFLP
	3	BSA	3	BSA
	4	LLA	4	BSC,BTL
Wilson's phalarope	1	VEG	1	AFA,AFL,AFP
	2	AFP,BTL	2	LLL
	3	BSA,AFA,LLA,LLL	3	BSA,BSJ,BTL
	4	AFL		
	5	BSJ		
Eared grebe	1	AFL,AFP,LLA	1	AFL
	2	BSC,OFA,OFLP,BTL	2	BSA,AFA,AFP,LLL
	3	VEG	3	BTL
	4	LLL	4	OFLP,BSC
	5	AFA		
	6	BSJ		
	7	BSA		
Ring-billed gull	1	BSA,AFL,AFP,BTL,OFLP,AMPH	1	AFP
	2	LLA	2	BSA,AFA,AFL,LLL
	3	AFA		
	4	LLL		
Northern shoveler	1	BSC,VEG	1	BSC,AFL
	2	BSJ,AFL,LLL	2	BSA,AFP,WF
	3	AFP	3	BSJ,LLL
	4	BSA		
	5	WF		
California gull	1	BSA,AFP,OFA,BTL	1	AFP
	2	AFL	2	BSA,AFA,AFL,LLL,OFLP
	3	LLA,LLL,OFLP	3	OFA,AMPH
	4	AFA		

¹ AFA = alkali fly, adult; AFL = alkali fly, larvae; AFP = alkali fly, pupae; AMPH = amphipod; BSA = brine shrimp, adult; BSC = brine shrimp, cyst; BSJ = brine shrimp, juvenile; BTL = beetle; LLA = long-legged fly, adult; LLL = long-legged fly, larvae; OFA = other fly, adult; OFLP = other fly, larvae/pupae; VEG = seeds; WF = water flea.

DISCUSSION

Despite the fact that only actively feeding birds were collected, esophagus samples rarely (< 15%) contained prey items. Therefore, stomach analyses were based on gizzard contents only. Several authors criticized the use of gizzard contents in studies of bird diets as being subject to substantial bias. Major sources of bias associated with analysis of gizzard contents included 1) over-estimation of hard foods (such as seeds) which may be retained in the gizzard for long periods, 2) rapid breakdown of soft foods, resulting in under-estimation, and 3) post-mortem digestion if samples were not preserved immediately after collection (Dillery 1965). When comparing contents of shorebird esopaghi and gizzards, Rundle (1982) found gizzard contents to be biased towards hard items such as seeds, while a large proportion of the soft bodied prey items were digested beyond recognition. Other authors suggested that seeds and other resistant plant structures were incidental to shorebird diets and should not be included as food items in analyses of diet composition (Fritzell et. al. 1979, White and Harris 1966). Swanson and Bartonek (1970) documented retention of seeds in gizzards of blue-winged teal (Anas discors) for over 24 hours. Seeds were minor components of the diets of shorebirds at Lake Abert and probably of little concern in terms of bias. However, bulrush seeds occurred in 35 percent of shoveler stomachs and accounted for 24.7 percent of the total biomass calculated for shovelers (Table 4). The high percentage of seed biomass likely was an over estimate of the actual importance of seeds

in the diets of shovelers. Shovelers were also the only species for which the contents of some gizzards were digested beyond recognition. Restricting diet analysis to esophageal contents would probably have avoided these problems. However, because few shoveler esophagi contained food, use of esophageal contents alone might have introduced other sources of bias as a result of small sample size.

Most authors have described shorebirds as opportunistic foragers (Burger et al. 1977, Couch 1966, Goss-Custard 1970a, Rundle 1980). In this study, avocets had relatively diverse diets, with 11 of 15 possible prey types identified in stomach samples. However, 93 percent of the diet of avocets was accounted for by only 4 prey types. Eighty-eight and 87 percent of the diet of northern and Wilson's phalaropes, respectively, consisted of adults, larvae, and pupae of the alkali fly. At Mono Lake, a large alkaline salt lake 400 miles south of Lake Abert, northern phalaropes fed almost exclusively on alkali flies (Jehl 1983). Thus, these inland-migrants may not fit the "generalist" role generally assumed for shorebirds (Ryser 1985).

At Lake Abert, densities of adult alkali flies, although patchily distributed, frequently exceeded 30,000 per m² of shoreline by mid-August. Larvae and pupae of the alkali fly were also abundant both in the water column and the top 0.5 cm of the shoreline substrate. Therefore, the substantial amount of overlap in the diets of avocets and phalaropes is not surprising. The combined preference/dissimilarity indices, however, suggested differences in patterns of prey utilization. Optimal foraging theory states that as overall prey availability increases, predators should become more selective, and

foraging niche breadth should decrease (Pianka 1981, Schoener 1971). "Increased prey availability" is usually assumed to refer to increased diversity of prey as well as increased density. Fifteen potential prey were identified at Lake Abert: of those, only 4 or 5 types were present in great numbers. Given the limited diversity of abundant prey, efficient foragers should concentrate on those few dense types, resulting in high diet overlap among predator species.

Larvae of the alkali fly dominated the diet of eared grebes accounting for nearly half of the biomass consumed during both seasons. At Mono Lake, Jehl (1982) found a high incidence of brine shrimp in the diets of eared grebes throughout the migration period, with an increase in the proportion of shrimp in the diet in late autumn. Shrimp appeared to be less important to eared grebes at Lake Abert, occurring in 32 percent of grebe stomach samples, and accounting for only 13 percent of the biomass of the diet. A slight increase in consumption of shrimp by eared grebes was noted in late September at Lake Abert.

At Lake Abert, brine shrimp occurred in 7.7 percent of the stomach samples of California gulls, accounting for 1.7 percent of the biomass of the diet (Table 4). In contrast, diets of California gulls at Mono Lake consisted almost entirely of brine shrimp (91%), with alkali flies being a minor component of the diet (8%) (Winkler et al. 1977, J. Jehl, pers. comm. 1983). Pronounced differences in diets of gulls and grebes at Mono and Abert Lakes, under similar environmental conditions, with many common prey seems unlikely; two explanations are plausible. First, Lake Abert was often extremely turbid compared to

Mono Lake. A lower incidence of shrimp in diets of birds at Abert may simply have been a function of poor visibility. For visual predators, food that is not visible is not available. Secondly, densities of brine shrimp at Lake Abert declined in 1982 and again in 1983, after reaching high numbers in 1981 (K. Kreuz, pers. comm. 1983).

Availability of shrimp to predators presumably also declined during that period. Low proportions of shrimp in diets of birds at Lake Abert may have reflected reduced levels of absolute availability.

Northern shovelers had fairly restricted fall diets. In light of the shoveler's indiscriminant feeding methods of simply sieving the water surface as it swims, a generalist diet might be expected, but in fact, the range of foods available to shovelers was limited by the structural constraints of the jaws and bill. Limited collections in 1981 suggested that brine shrimp were frequently consumed by shovelers. In 1982 and 1983, populations of water fleas increased markedly, while numbers of adult shrimp declined. Water fleas were not present in shoveler stomach samples in 1981, but were present in 42 percent of the pooled 1982 and 1983 samples. Such changes suggested that shovelers were opportunistic feeders within morphologically imposed constraints.

Although adult shrimp accounted for only 8 percent of the biomass of the diet of shovelers, brine shrimp cysts made up an additional 22 percent of the diet. Presence of a large number of cysts in shoveler stomachs indicated either direct ingestion or disintegration of adult shrimp and release of cysts within the digestive tract. On several occasions I observed shovelers "sieving" the water surface in areas

where floating shrimp cysts had accumulated in bands. Although the possibility existed for bias in these results, I believe that the majority of shrimp cysts ingested by shovelers were taken directly from the water column.

The importance of the alkali fly as a food source for migrant waterbirds was reaffirmed by preference rankings. At least one life stage of the alkali fly was represented in the most preferred group of foods for all birds except Wilson's phalaropes and shovelers (Table 6). Adult brine shrimp were among the most preferred foods only of ring-billed and California gulls. Populations of alkali flies were much more available to foraging birds than shrimp, both numerically and in duration of availability, and thus would be expected to dominate the diets of opportunistic feeders. Herbst et al. (1984) found all stages of the alkali fly to be nutritionally superior to brine shrimp in both total caloric value and lipid content. Selective feeders, then, might also be expected to prey more heavily on flies, if energetic costs of capture were comparable between the two prey.

Changes in the physical environment, specifically water levels and, consequently, salinity levels, may have direct effects on the prey base and on the availability of roosting habitat. Unusually high inflows of fresh water over the course of this study (1981-84) have resulted in physical and chemical changes in the lake that affect both predator and prey communities. Ctenocladus circinnatus, a filamentous green alga, is, in most years, a common benthic species in the lake. Ctenocladus is important to both shrimp and flies as a food resource, and to the alkali fly as a substrate for the development of aquatic

larvae (Herbst 1980). Growth and development of Ctenocladus are slowed both above and below a range of optimum salinity. At low salinity, the slow-growing Ctenocladus may not compete well with faster-growing, resident blue-green algae (Microcystis and Phanocapsa) which increase with lowered salinity (R.W. Castenholz, Univ. of Oregon, pers. comm., 1985). Similarly, the brine shrimp is well-adapted to saline waters where potential competitors and predators cannot survive. As Lake Abert has become less saline, populations of waterfleas and amphipods have increased dramatically, with a concurrent decline in populations of adult shrimp; suggesting competitive interactions between the two species (D. Herbst, pers. comm.). The apparent increase in numbers of juvenile shrimp from 1982 to 1983 may reflect slowed growth rates of shrimp as a result of increased competition for algal food resources (D. Herbst, pers. commun., 1986). Similar situations in which Cladocerans replaced other invertebrates after decreases in salinity were reported by Hairston (1981) and Edmunson (1959).

Low water levels, resulting from low precipitation and irrigation diversion from the Chewaucan River, might also affect fall migrating birds. As water volume decreases, the proportion of total dissolved solids (TDS) increases. During "average" years, the salinity of Lake Abert varies between 30 and 40 grams/liter TDS. In 1979, a very dry year, salinity readings of 54.5 g/l were recorded (Herbst 1980). Herbst et al. (1984) found reproduction and growth of laboratory-cultured Ctenocladus to be reduced at salinity levels exceeding 50 g/l, and severely restricted above 75 g/l. Increased salinity may

affect shrimp and flies directly as well as their foods and habitats. Studies at Mono Lake have indicated that both brine shrimp and alkali flies, despite well developed osmoregulatory abilities, would not be able to cope with predicted increases in salinity as the level of the lake was lowered by diversion (Winkler et al. 1977). Extreme drought could result in the desiccation of large expanses of mudflats at the north and south ends of Lake Abert, where the majority of migrants gather to feed and loaf.

During the high water years of 1983 and 1984, migrating birds were not dependent on brine shrimp as a major food source. Under the current conditions of high water levels and limited removal, the commercial harvest of brine shrimp is probably not a major threat to birds foraging at Lake Abert, with the possible exception of the northern shoveler.

Expanded harvest operations at Lake Abert may not be feasible, due to the erratic nature of the shrimp population (Conte 1981), and to difficulties of access along the shoreline. Depending on the extent of expansion, increased levels of shrimp removal may or may not affect the food resources of birds. However, the increased human activity and disturbance associated with expansion of harvest operations might well be detrimental to birds. Impacts might be especially severe at the north and south ends of the lake where birds roost in large numbers. Activities which disturb birds may result in a loss in fat reserves needed for the southward migration.

V. FORAGING BEHAVIOR OF MIGRATORY BIRDS, LAKE ABERT

INTRODUCTION

Studies of the ecology of mixed-species assemblages in most cases have indicated some degree of overlap, either in food or spatial resources, among member species (Baltz and Morejohn 1977, Wiens and Rotenberry 1979, Hoffman et al. 1981). Often a high degree of overlap along one resource axis, for example, diet, was countered by divergence along another, such as foraging microhabitat (Cody 1968, Hutto 1981) or feeding behavior (Baker and Baker 1973, Schoener 1974). Overlap in foods eaten or in the ways those foods are obtained may affect the ability of migrant birds to accumulate fat reserves for their southward migration. At Lake Abert, an inland staging area for an assemblage of fall migrating birds, overlap in diets was particularly high among three species of shorebirds, and between two species of gulls. To more accurately assess the foraging strategies, inter-specific relationships and physiological condition of migrants at Lake Abert, I addressed the following questions:

1. How do birds allocate their time at a migratory stopover?
2. Do foraging patterns and behaviors exhibited by a multi-species migrant community tend to increase or decrease overall resource overlap? In other words, are there differences among species in foraging time, techniques, substrates (habitats), or rates (intensity) that would tend to counter the observed overlap in diet?

3. If differences in patterns of resource use exist, are there relationships between those observed differences and the physiological condition (i.e. fat stores) of migrating birds?

STUDY AREA AND METHODS

The study was conducted at Lake Abert, a large saline-alkaline Lake in southcentral Oregon. A remnant of pleistocene Lake Chewaucan, the present day Lake Abert was described as a classic closed-basin carbonate-alkaline lake (Phillips and Vandenburg 1971). Compared to other saline lakes in the Great Basin, Lake Abert is relatively fresh and quite variable in terms of both water and salinity levels. The northern Great Basin experienced severe drought between 1918 and 1934 (Antevs 1938) and the lake was completely dry as recently at 1937 (Phillips and Vandenburg 1971). In 1983, the second field season of this study, the lake reached a 100 year high water mark.

Shoreline habitats available to migrating birds at Lake Abert included alkali playa, mudflats, marshy areas, and gravel and cobble beaches. Relative proportions of shoreline habitat types varied within and between field seasons according to changing water levels.

Activities of fall migrants were documented during the fall migration seasons (June through October) of 1982 and 1983. Observations were made in all macro-habitat types along the eastern shore. Habitat types were classified as follows:

shoreline: alkali flat

mudflat

marshy, vegetated shoreline

gravel beach

cobble beach

open water: zone 1 (shoreline to 25 m lakeward)

zone 2 (35 m to 60 m from shore)

Observations were made during all daylight hours; however, the majority of observations took place during the morning. Daylight hours were divided into 4 equal "timeblocks"; 0600-1000, 1000-1400, 1400-1800, and 1800-2200 h. Observational data were pooled within timeblocks.

Two methods were used to describe activity patterns of birds. Daily activity budgets were estimated by the "instantaneous scan" method (Altman 1974). For each flock selected, the activity of 10 or more individuals was recorded, along with information on habitat type, time of day, weather, flock size and species composition. Birds were observed from a vehicle, portable blind, or natural hiding place (boulders, large shrubs, etc.) through binoculars or a 20-40x scope. Observations were recorded on a portable tape recorder. The activity of each individual was classified as 1) foraging, 2) movement (walk, swim or fly), 3) comfort (preen, bathe), 4) alert, 5) inactive (roosting or sleeping), 6) inter- or intra-specific interaction. Results of these observations were expressed, by species, as the percentage of total individuals engaged in each activity.

I used "focal animal" sampling (Altman 1974) to more closely examine feeding behaviors and intensity (rates) during foraging bouts. These observations were made during all daylight timeblocks. Feeding behavior was further classified into distinct foraging techniques. Actively foraging individuals were arbitrarily selected and observed

for 5 minutes or until lost from view. Initial behavior and each subsequent change in behavior was recorded, as it occurred, on a tape recorder. The procedure was repeated for a minimum of 3 focal birds within a flock. Duration of each activity within 5 minute observation periods was later timed to the nearest 0.10 second with a digital stopwatch and total times for all behaviors tallied. Raw data were pooled for each species to derive season-long foraging activity budgets. Results were expressed as the percentage of the total observation time spent by individuals in each activity. Foraging budgets were then examined by timeblock to determine if time of day influenced foraging patterns.

Whenever possible I determined foraging rates by recording the number of feeding attempts made by a focal bird over a 2 to 3-minute period. Foraging attempt rate for each species was calculated as the number of feeding attempts per minute. Foraging attempt rates were not calculated for shovelers using "sieve" techniques or for diving grebes. Birds were often too far away and prey too small to determine if foraging attempts were successful, therefore no estimates of foraging efficiency were attempted.

The influence of foraging patterns and behaviors on total overlap in resource use among birds was assessed by reciprocal averaging, a multivariate ordination procedure (Gauch 1982). Program ORDIFLX was used to ordinate bird species in two dimensions for several factors: time allocation, foraging substrate, foraging technique, and diet. Plots of the resulting ordinations were compared for changes in the relative positions of bird species.

Individuals of each study species were collected at 2-week intervals throughout both field seasons. Immediately after collections, each specimen was weighed and measured. Birds were then dissected and digestive organs removed. Sex was determined by internal examination. Age (adult or juvenile) was determined by the presence or absence of the Bursa of Fabricius (McNeil and Burton 1972). Average body weights were calculated, by species, for the entire season, and for each sampling period.

A variety of condition "indices" have been developed in attempts to quantify the physiological condition of nesting and migrating birds (Ringleman and Szmczak 1985, Davidson 1983, McNeil and Cadieux 1972). Most of these indices are based on fat-free weights derived from ether extraction of soluble fats from whole carcasses. A lack of time and facilities precluded use of fat extraction in this study. Visual estimates of subcutaneous fat (at the pectoral muscle) and organ fat (heart and intestines) were made at the time of collection. Fat was scored on an increasing scale for each measurement (Appendix 2). To obtain an index of condition based on overall fat resources, subcutaneous and organ fat measurements were summed and a mean calculated for each specimen collected. Total fat scores were correlated with weight for each species. Weight and mean fat scores were compared within species for differences attributable to age, sex, sample period and year.

RESULTS

Allocation of Time

Season-long, diurnal time budget, indicated foraging as the primary daytime activity of all birds except eared grebes and ring-billed gulls (χ^2 test $P < 0.05$, Table 8). Movement (swimming) and preening were the predominant activities among grebes. Inactive and interactive behaviors generally involved very small percentages of flocks at any one time, except in the case of ring-billed gulls (inactive: 39.4%) and avocets (inactive: 28.9%). Alert behavior, where birds lifted their heads from foraging to look around them, was most frequent among gulls.

Results of "focal animal" observations paralleled those of scan counts, with the percentages of time spent in actual feeding (within foraging bouts) being greater than the percentage of time spent in any other behavior, again with the exception of eared grebes (Table 8). The proportion of time spent in various activities was relatively constant from year to year for all birds except ring-billed gulls, which spent much more time preening in 1982 than in 1983 with an opposite trend in time spent foraging (Figure 6).

When focal animal observations were sorted by timeblock, temporal differences in foraging patterns were apparent. Avocets and shovelers appeared to have bimodal feeding peaks, one in the early morning and one in the late afternoon/early evening (Table 9). A low in feeding activities occurred at mid-day. Grebes and phalaropes tended to concentrate feeding during late morning and mid-day. Among

Table 8. Instantaneous scan and focal animal time budgets for migrant waterbirds, Lake Abert, Oregon, 1982 and 1983.

Species	Instantaneous Scan Sampling (% of observations)					Focal Animal Sampling (% of time)				
	N	Forage	Move	Preen	Other ¹	N ²	Forage	Move	Preen	Other
Northern phalarope	263	48.2	30.8	12.4	8.5	39	73.0	15.0	11.0	1.0
American avocet	279	60.0	6.6	4.4	28.9	43	75.0	11.0	5.0	8.5
Wilson's phalarope	274	56.1	13.3	25.9	4.4	41	65.0	13.0	19.0	3.0
Eared grebe	441	13.7	48.8	30.9	6.6	63	31.0	39.0	27.0	2.1
Ring-billed gull	102	35.8	13.3	10.8	43.0	31	59.0	13.0	9.0	19.0
Northern shoveler	509	70.9	10.7	5.2	13.1	58	80.0	11.0	4.0	5.0

¹ "Other" category = alert, interaction and inactive behaviors combined.

² N = number of 5 min. observation periods.

Figure 6. Year to year comparisons of time budgets of migrant water birds, Lake Abert, 1982 and 1983.

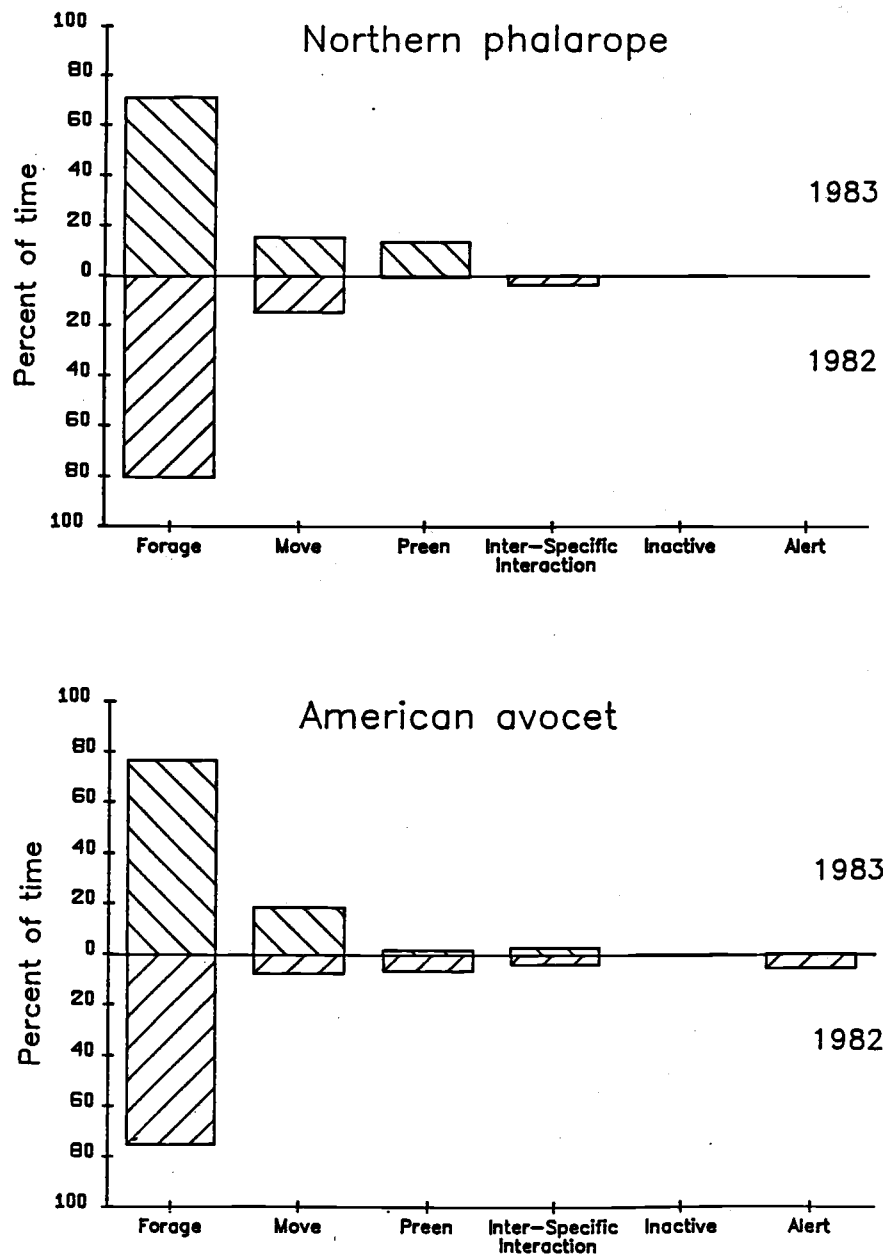


Figure 6.

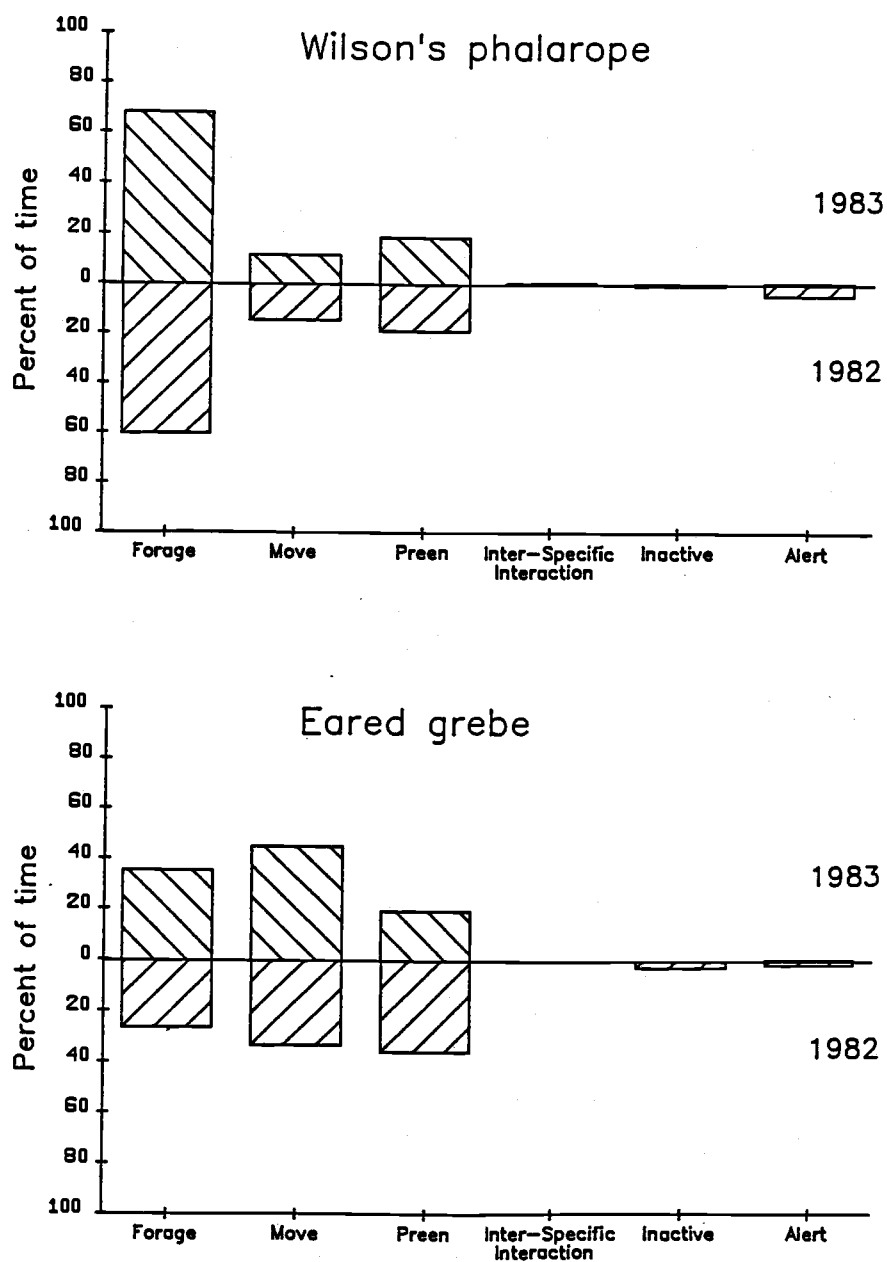


Figure 6. (continued)

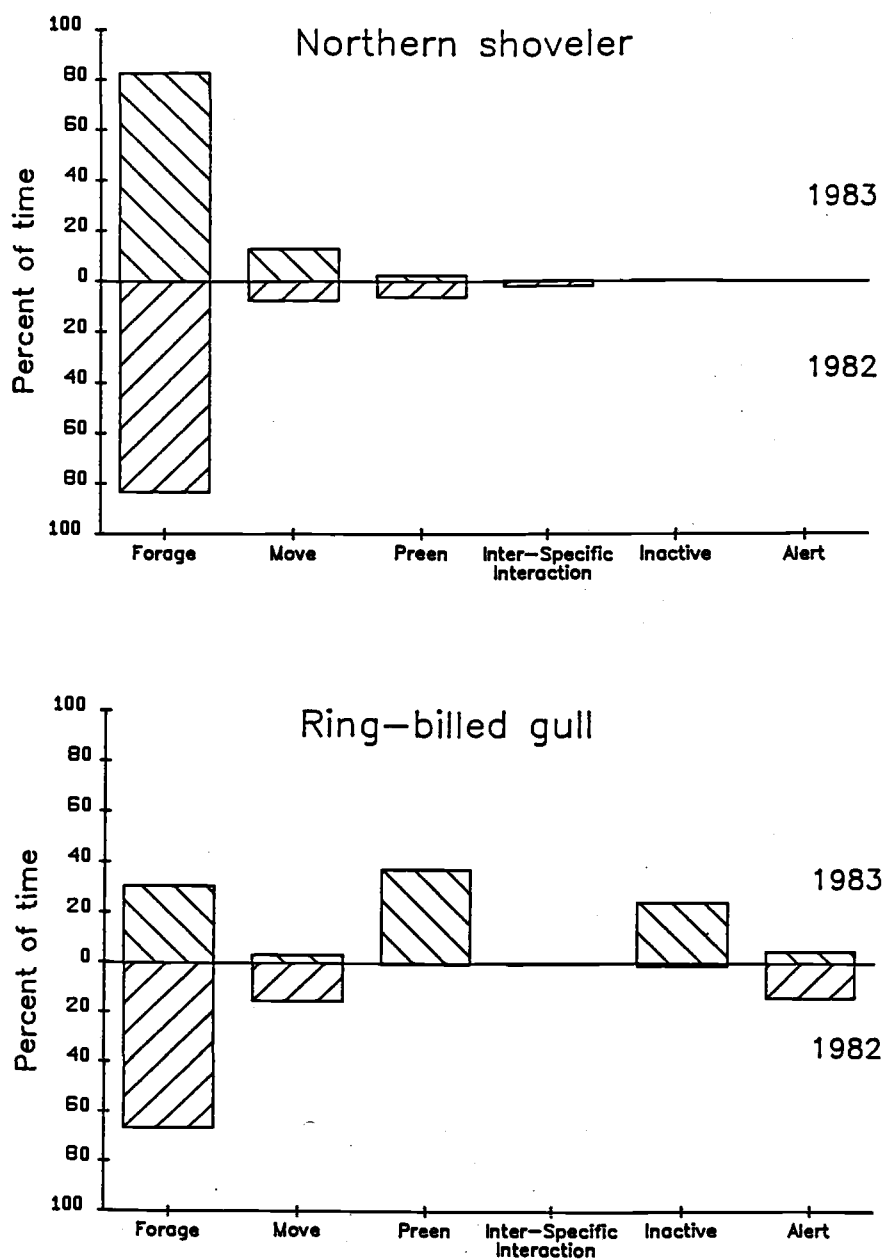


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Table 9. Foraging activity budgets, by timeblock (focal bird observations, 1982 and 1983 pooled).

Species/ Behavior	Time block (% of time)							
	1		2		3		4	
	N	%	N	%	N	%	N	%
Northern phalarope								
Forage	11	65.6	8	78.1	19	73.4	-	-
Move		20.5		16.2		13.1		-
Preen		13.8		0.8		13.4		-
Other		0.1		4.8		0.1		-
American avocet								
Forage	23	73.4	14	11.6	5	93.8	-	-
Move		11.1		48.6		3.6		-
Preen		5.5		28.6		0.0		-
Other		9.9		11.1		2.6		-
Wilson's phalarope								
Forage	24	55.0	12	85.8	-	-	5	80.0
Move		15.1		9.3		-		12.9
Preen		28.1		4.1		-		0.0
Other		1.0		0.8		-		7.0
Eared grebe								
Forage	23	21.1	24	46.6	10	21.4	6	24.4
Move		36.9		42.8		39.2		49.8
Preen		38.7		10.1		38.9		5.3
Other		3.3		0.5		0.5		20.5
Ring-billed gull								
Forage	5	65.0	19	56.6	-	-	2	16.9
Move		14.0		12.0		-		6.5
Preen		0.4		11.8		-		60.0
Other		20.2		19.5		-		16.5
Northern shoveler								
Forage	24	91.8	14	49.6	9	69.3	13	96.8
Move		4.8		26.7		23.5		1.2
Preen		1.0		10.5		2.1		1.8
Other		2.4		13.2		5.1		16.5

phalaropes, active foraging occupied at least 50 percent of the available time during all timeblocks.

Foraging Habitats and Behaviors

Birds used all available macro-habitats to some extent, either for feeding or roosting. Avocets were generally restricted to the shoreline and shallows, feeding on shore or in water less than 1 m deep, and roosting on mudflats, alkali playa or gravel beaches. Wilson's phalaropes also tended to stay near shore, usually feeding in shallow water within 50 m of the shoreline. Small groups of phalaropes roosted along gravel beaches, but the majority of shorebirds roosted in very large aggregations on the extensive mudflats at the north end of the lake. Northern phalaropes, like their coastal conspecifics, were primarily pelagic, feeding and roosting in open water, often more than 1 km from shore. Grebes were strictly aquatic. Although they often foraged in shallow water near the shoreline, grebes were never observed on land. Shovelers and gulls used almost all available habitats, for either foraging or roosting. Shovelers, however, were rarely observed on cobble beaches, while gulls often searched for alkali fly (Ephydra hians) larvae and pupae among shoreline rocks.

Birds used a variety of techniques to obtain food from the lakeshore and water column. Avocets (89.9% of observations) and gulls (ring-billed: 100.0%, California: 98.7%) pecked at fly larvae and pupae while walking along the shoreline or in shallow water. Pecking was also the predominant foraging technique of Wilson's (64.5%) and

Figure 7. Reciprocal averaging plots for diet, foraging techniques, foraging time and foraging substrates of migrant water birds at Lake Abert, 1982 and 1983. AMAV = American avocet, CAGU = California gull, EAGR = Eared grebe, NOPH = Northern phalarope, NOSH = Northern shoveler, RBGU = Ring-billed gull, WIPH = Wilson's phalarope

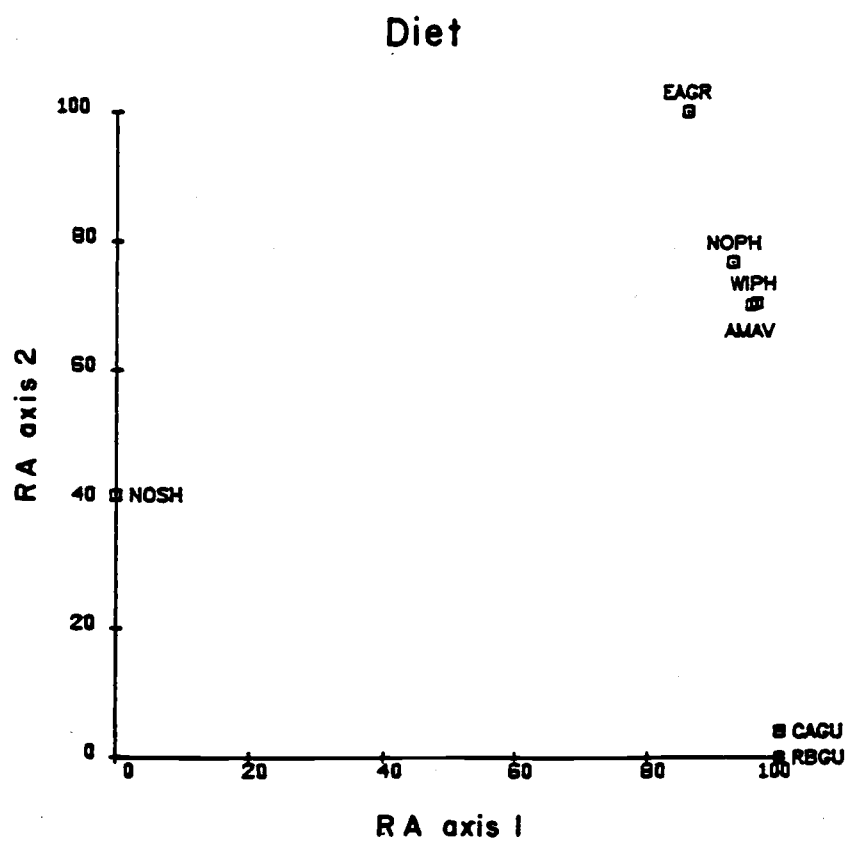


Figure 7.

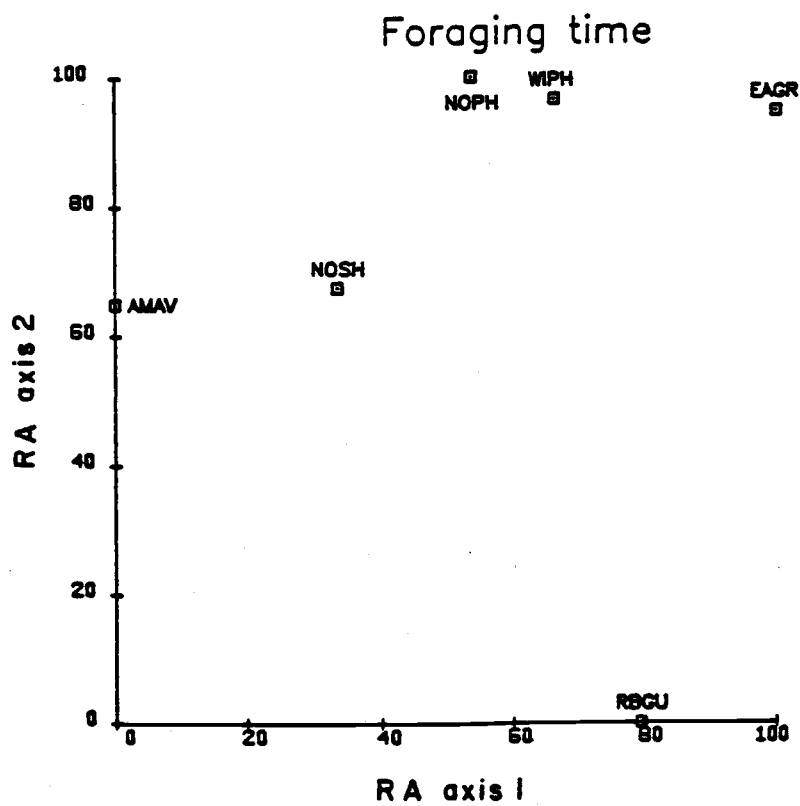


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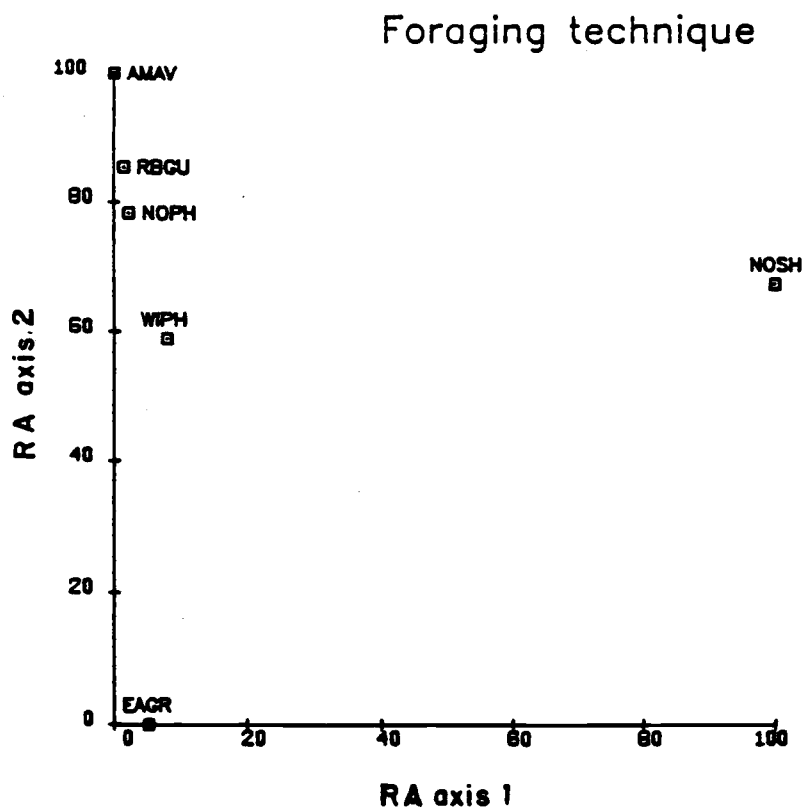


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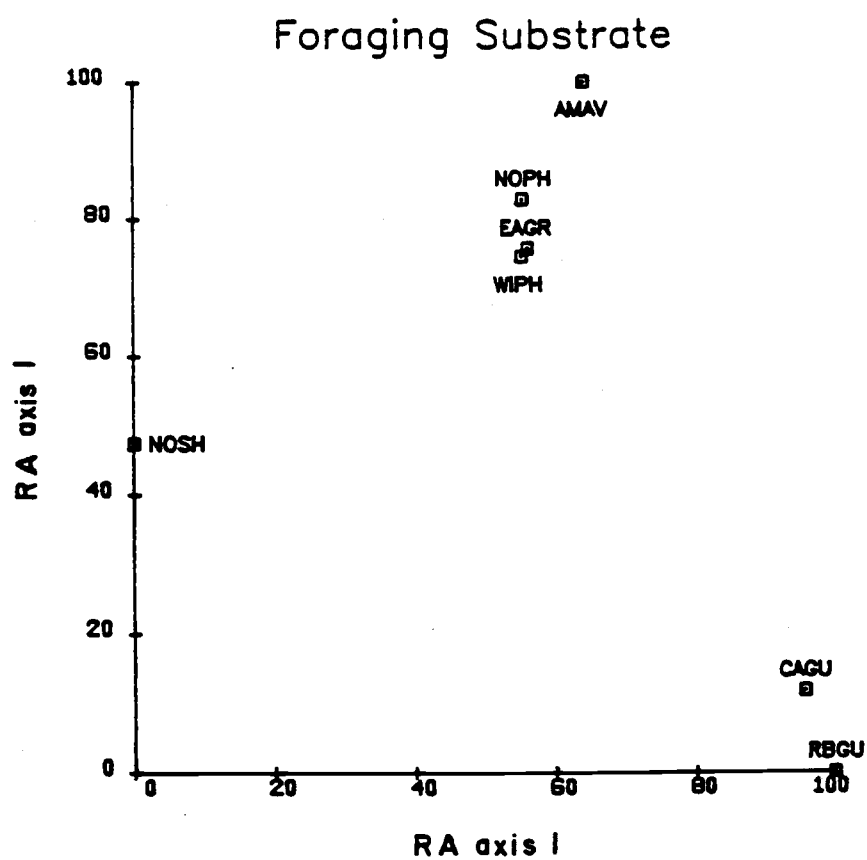


Figure 7. (continued)

northern phalaropes (79.8%). Wilson's phalaropes occasionally foraged along the shoreline (6.1%), while northern phalaropes were pelagic foragers. Both northern and Wilson's phalaropes (20.0%, 19.7%, respectively) used the "spin and peck" strategy so often reported among shorebirds (Bent 1932, Ryser 1985). Avocets, on the other hand, seldom (4.8%) used the side-to-side "scything" behavior commonly associated with this species in mudflat and shallow water habitats. Wilson's phalaropes often "hawked" at flying insects, jumping off the ground or running along the shoreline in attempts to catch flies. Diving (72.7%) was the primary foraging technique of grebes. Northern shovelers filtered water through the fine lamellae of their bills to obtain prey near the water surface (77.8%). Shovelers also used the "tipping" foraging behavior common among dabbling ducks (10.9%).

Ring-billed gulls had the highest overall foraging attempt rate (41.9 attempts/min.), closely followed by Wilson's phalaropes (40.3) and avocets (38.0). Grebes foraging on the water surface had the lowest foraging rates (19.8 attempts/min).

Foraging Patterns and Niche Overlap

When ordinated in two dimensions the relative positions of reciprocal averaging plots of bird species changed with each factor considered. The ordination plot of diets illustrated the substantial similarity in foods chosen by shorebirds, as a group, and by the two gulls (Figure 7). The diet of the northern shoveler was widely separated from those of all other species. The gulls, as a group,

also had a unique diet. Shorebirds had very similar diets, but used different foraging techniques (Figure 7) and fed at different rates. Avocets were further separated from phalaropes by their allocation of foraging time.

Physiological Condition of Migrants

Mean weights were lower in 1983 than in 1982 for eared grebes and northern shovelers (un-paired t-test, $P < 0.05$). Adult birds tended to be heavier than juveniles, although differences were not significant. Female Wilson's phalaropes weighed more than males, while male avocets, shovelers, grebes, and California gulls were heavier than females (Table 10, un-paired t-test, $P < 0.05$).

Mean fat scores were significantly higher in 1982 than in 1983 for eared grebes and northern shovelers (Table 11). Fat scores increased from early season (first collection period for each species) to late season (last collection period) for Wilson's phalaropes and northern shovelers, but declined for ring-billed gulls.

Table 10. Mean weights (g) of birds by species and sex, Lake Abert, Oregon, 1982 and 1983.

Species	Species mean wt.	Sex			
		Female		Male	
		n	\bar{x}	n	\bar{x}
Northern phalarope	37.1	41	37.9	52	36.4
American avocet	324.8	24	306.4*	15	343.1
Wilson's phalarope	58.1	33	63.0*	17	53.2
Eared grebe	349.4	32	334.4*	30	364.3
Northern shoveler	628.5	36	606.5*	41	650.4
California gull	594.7	18	542.3	10	647.0

* denotes significant difference ($P < 0.05$)

Table 11. Mean fat scores, by species, for fall migrants at Lake Abert, Oregon, 1982 and 1983.

Species	1982		1983	
	N	\bar{x} score ¹	N	\bar{x} score
Northern phalarope	33	1.93	61	1.36
American avocet	31	2.00	8	1.25
Wilson's phalarope	20	1.57	57	1.24
Eared grebe	36	2.36	26	1.97*
Ring-billed gull	12	1.67	5	0.93
Northern shoveler	66	2.17	12	1.44*
California gull	25	1.73	3	1.00

¹ \bar{x} fat score = mean of 3 scores; subcutaneous, intestinal and cardiac.

* Indicates a significant change from 1982 to 1983.

DISCUSSION

Allocation of Time

Foraging was the predominant activity of migrant birds at Lake Abert. Changes in diel activity patterns, accompanied by deposition of large fat reserves, is well documented for many migratory species (see Berthold 1975 for review). Increases in both the rate of foraging and the percentage of daylight hours allocated to feeding have been recorded for many species just prior to migration. In South Africa, curlew sandpipers (Caladris ferruginea) increased the proportion of time devoted to feeding and increased their body weight by 40% just before migrating northward (Puttick 1979). Morton (1967) suggested that changes in the metabolism of energy reserves in white-crowned sparrows (Zonotrichia leucophrys) just before migration resulted in greatly increased appetites and increased foraging.

A high proportion of time spent in foraging might be predicted for birds during migration as well as prior to migration, because a portion of those reserves gained before migration had been depleted. Increased appetite and higher feeding rates would help ensure that energy reserves were adequate for the remainder of migration. Little comparative data on seasonal change in time allocation is available for species studied here: information was available only for American avocets and northern shovelers.

At Summer Lake, Lake Co., OR, avocets increased the time spent foraging, from 31 to 48 percent, after the nesting season ended (Gibson 1979), but the change was attributed to decreased prey

densities. At Lake Abert, staging avocets spent 60 percent of the day feeding.

Afton (1979) reported that foraging by shovelers varied from 35% for males during the laying period to 69% for females just arriving on the breeding grounds. At Lake Abert, northern shovelers spent approximately 71 percent of their day foraging (instantaneous scan counts). McKinney (1970) speculated that the plankton-straining foraging techniques of northern shovelers would require them to spend a large proportion of their time foraging. In this study, shovelers spent more time feeding than any other species.

Morning and afternoon foraging peaks had been noted for such diverse groups as magpies (Pica nuttalli) (Verbeek 1972), mourning doves (Zenaidura macroura) (Schmid 1965), and sparrows (Zonotrichia leucophrys) (Beer 1961, Morton 1967). Bimodal activity patterns were also reported for breeding shovelers (Afton 1979) and avocets (Gibson 1979). Time budgets of avocets and shovelers at Lake Abert indicated that bimodal foraging also occurred during migration.

Other species at Lake Abert did not have pronounced peaks in foraging activity. Phalaropes increased their foraging time from early to mid-morning, then continued to spend a large percentage of their time foraging for the remainder of the day. Foraging also reached a peak at midmorning among eared grebes. Differences in peak feeding periods among species may be attributable to behavioral patterns of their prey. Midmorning highs in foraging among phalaropes and grebes were likely the result of increased activity levels of the adult alkali fly. Abert Rim, rising abruptly from the eastern

lakeshore, casts a shadow over much of the study area in the early morning, keeping temperatures low until the sun finally rises above the escarpment between 0800-0900 h. Ambient temperatures then begin to rise rapidly resulting in increased activity levels of alkali flies and other insects (Herbst 1986).

Brine shrimp, an important food source for shovelers, were found to be negatively photokinetic in strong light (Mason 1966), while under low light conditions they may exhibit a weakly positive photokinetic response (D. Herbst, pers. comm.). Availability of shrimp should therefore be increased when light levels are low, i.e., early morning and late evening. This pattern corresponds well with peaks in foraging activities of shovelers, the only species that fed extensively on brine shrimp.

Larvae and pupae of the alkali fly accounted for much of the avocet's diet. Pupae were attached to rocks along the shoreline or in shallow water, where their availability as prey remained constant throughout the day. Larvae, on the other hand, were passive drifters in the water column, and their distribution was affected by wind. Wind had two important effects on the availability of larvae to predators: 1) reduced visibility of prey as a result of wave induced turbidity; and 2) changes in distribution of prey patches. Winds on the lake were generally calm through the morning, but often increased substantially by early afternoon. Early morning foraging peaks among avocets may have been related to the overall higher visibility of their prey at that time, particularly since avocets at Lake Abert used visual foraging techniques. Reasons for the evening foraging peak

among avocets were less apparent. Perhaps avocets needed to acquire additional energy reserves for the coming night as has been suggested for other species (Hintz and Dyer 1970, Verner 1965) and/or as a response to increased appetite after the mid-day low in foraging activity.

Gibb (1960) noted that small birds spent more of their time foraging than did large species. Daily time budget data from this study did not support Gibb's findings: phalaropes spent less time foraging, over an entire day, than the larger avocet or shoveler. However, within foraging bouts, phalaropes foraged most intensively of all species.

Both the daily and foraging time budgets differed markedly between eared grebes and other species. Grebes devoted substantially less time to foraging while spending more time moving and preening. Increased levels of movement seemed intuitively counter-productive to maintaining (or increasing) energy reserves, but locomotion among grebes was mostly by swimming, a relatively "low cost" activity. Movement among other migrants was primarily by flight, the most energetically expensive of all locomotion behaviors (Utter and Le Febvre 1970).

Verbeek (1972) associated increased time spent preening in late summer with the onset on the molt. Most shorebirds arrived at Lake Abert already in winter plumage, but the collection of several flightless grebes indicated that at least some portion of the grebe population underwent their prebasic molt at the lake. The high percentage of time devoted to preening among grebes was consistent with Verbeek's observations. Time allocation was relatively

consistent from year to year within each species, except for gulls, which spent considerably less time foraging in 1983 than in 1982.

Foraging Behaviors and Niche Overlap

Holmes and Pitelka (1968) found extremely high overlap in summer diets of six species of tundra-nesting shorebirds. At Lake Abert, two groups of closely related and morphologically similar species (i.e., shorebirds, gulls) had very similar diets. Both the diet and foraging substrate variables for gulls were closely spaced (Fig. 2) indicating a high degree of similarity in foods and foraging places. Qualitative observations indicated that gulls used similar foraging techniques as well, mostly pecking at prey organisms along the shoreline. Unless a substantial degree of separation existed in the temporal patterns of foraging or along other resource axes which I did not measure, the total feeding niches of these two larids may be very similar. Niche overlap theory holds that there is some upper threshold in the degree of overlap between two species, beyond which they cannot continue to coexist (Pianka 1981, Wiens and Rotenberry 1979). Possibly other factors in the year-round ecology of gulls, such as allopatry or diet separation during other times of the year, reduces the degree of year round overlap.

Similarities and differences in foraging strategies among shorebirds became evident when the original ordination plots were combined (Fig. 8). The high degree of diet overlap was evident from the tightly grouped diet coordinates. Similarity in feeding substrates was also apparent but some divergence was indicated by the

Figure 8. Combined ordination plots of diets and foraging behaviors for northern and Wilson's phalaropes and American avocets. Solid symbol = northern phalarope, dotted symbol = American avocet, open symbol = Wilson's phalarope.

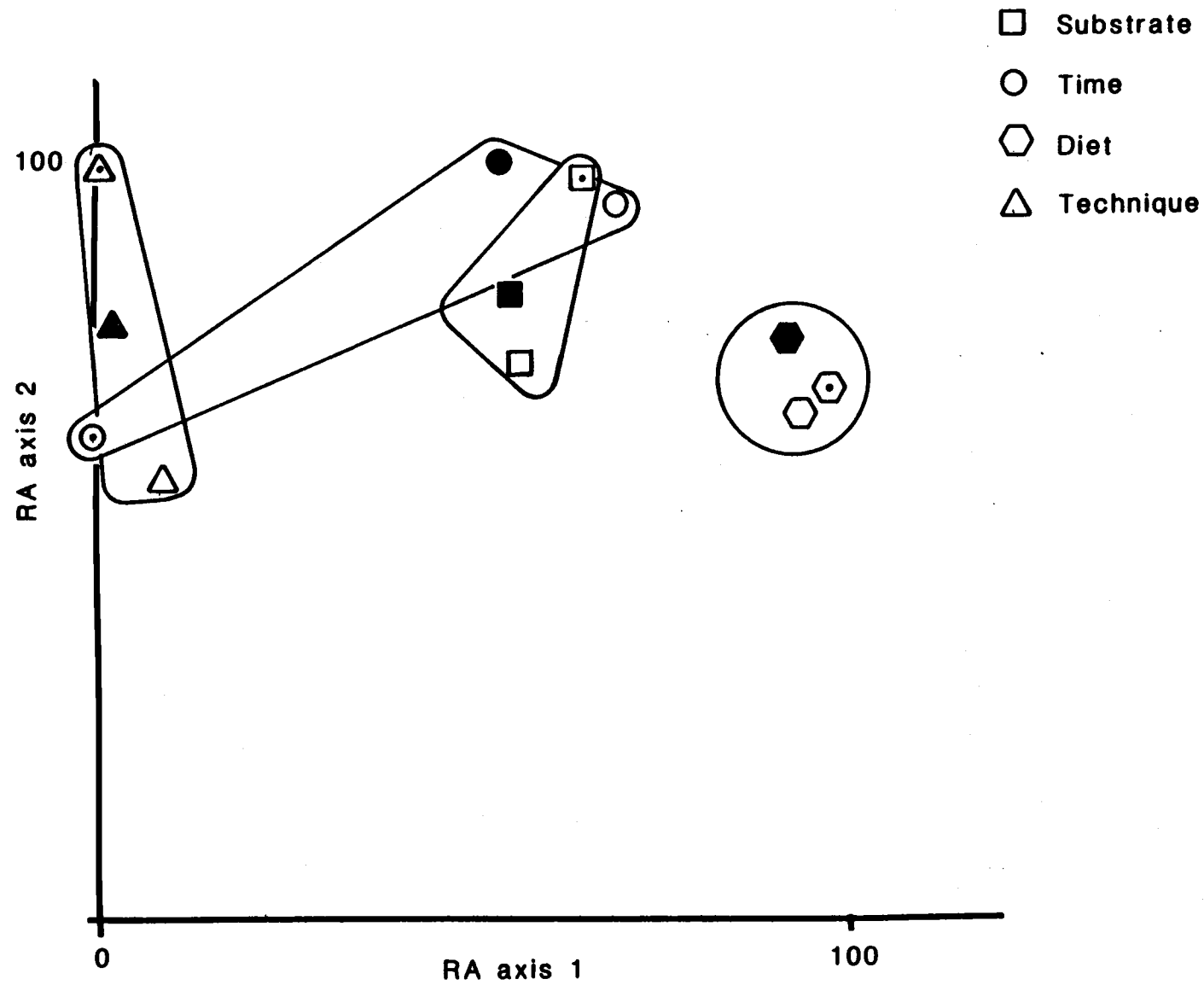


Figure 8.

wide spacing among ordination points for foraging technique. Temporal separation, resulting from bimodal foraging patterns of avocets, was the most obvious factor in decreasing overall similarity in resource use among shorebirds.

Little similarity in resource use patterns was evident among grebes, gulls and shovelers as would be expected considering their divergent feeding morphologies and diets (Fig. 9). The ordination plot of foraging techniques indicated a high degree of overlap between northern phalaropes and ring-billed gulls (Fig. 7). However, substantial differences in diet and foraging times minimized any overall similarity. Grebes and phalaropes tended to use similar foraging habitats (i.e. open water) as illustrated by the tight cluster of ordination points for the substrate variable (Fig. 7), but a wide separation was evident in foraging technique. Grebes diverged widely from all other species in this respect; only grebes foraged by diving.

Timing of migration may also reduce overlap among and within species. Phalarope populations reached a peak in mid to late July and declined to very low numbers by late August, when populations of shovelers were building towards October peaks. Functional overlap was therefore minimal between ducks and phalaropes. Intra-specific niche competition may be reduced by differential migration phenology. Staggered migration schedules have been noted between sexes and between adults and young of the year in several investigations (Holmes and Pitelka 1968, Pitelka 1950, Recher 1966). Observations at Lake Abert indicated that juvenile shorebirds migrated later than did adults (see Chapter IV).

Figure 9. Combined ordination plots of diets and foraging behaviors for California and ring-billed gulls, northern shovelers, and eared grebes. Solid symbol = ring-billed gull, dotted symbol = eared grebe, open symbol = California gull.

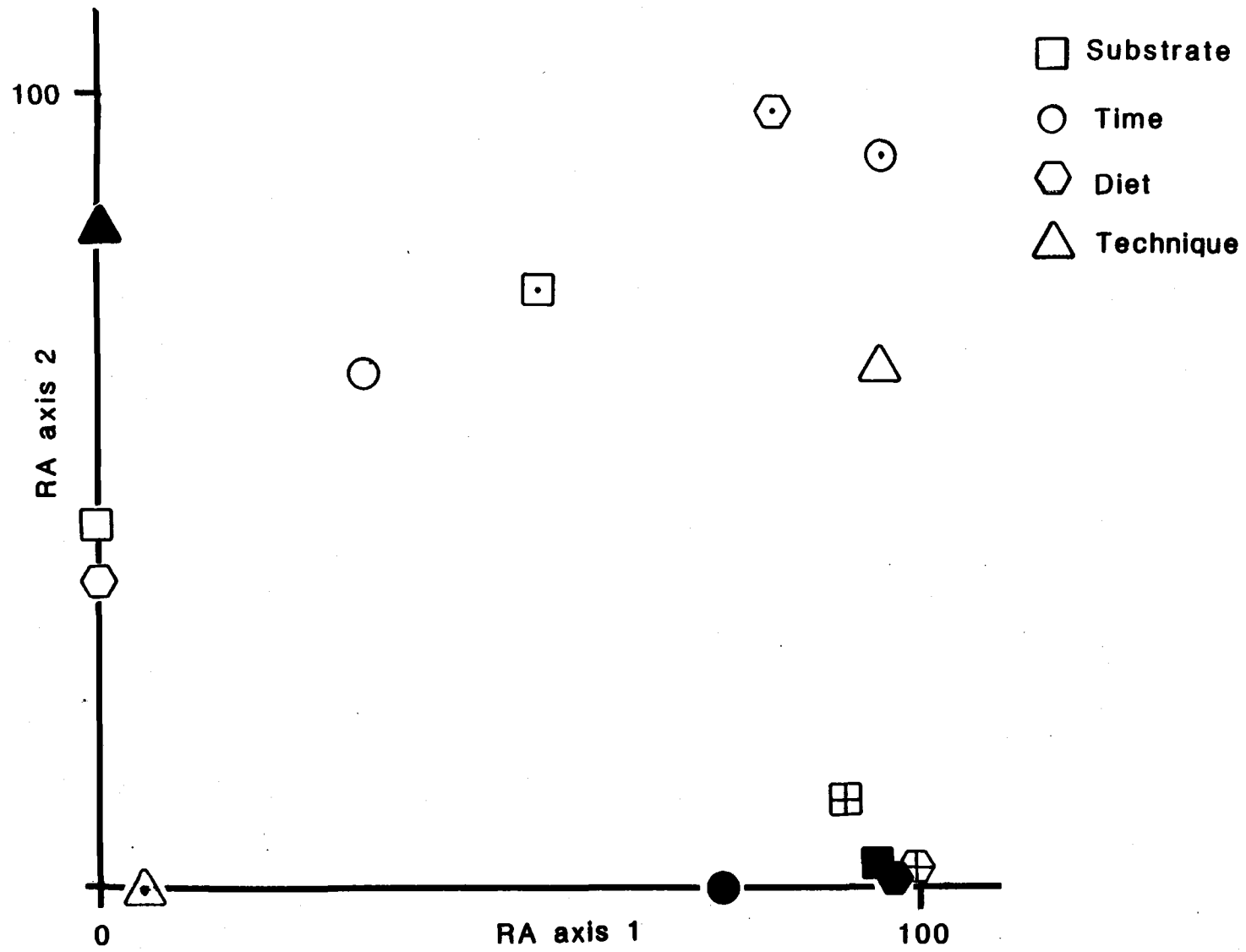


Figure 9.

Time and technical limitations hindered the collection and interpretation of weight and fat data. Fat indices were only approximations of condition, and the duration of residency at the lake of collected individuals was unknown. The latter problem hindered assessment of changes in energy reserves during the migratory stopover. However, weights and fat indices of most species were higher during later collecting periods, suggesting that birds were accumulating energy reserves before continuing their migration. Northern phalaropes and ring-billed gulls did not follow the general trend. Both mean weight and mean fat indices were higher in the early collection period for ring-billed gulls. The influx of apparently unstressed birds from Summer Lake might account for altered behavioral and physiological patterns among gulls at least in 1983.

Differences in diet or foraging behaviors may have contributed to observed differences in the relative condition of the study species. Eared grebes had unique foraging techniques (i.e. diving), expended relatively less energy in obtaining food, and were separated from other species in terms of diet composition. Grebes also had substantially higher fat scores than other species (Table 11). Unique diet and foraging technique characterized the northern shoveler as well, and fat indices for this species also were relatively high, second only to grebes in 1982. Shorebirds as a group had extremely similar fat indices, as did California and ring-billed gulls. Similar patterns of fat deposition would seem logical among species having similar diets, morphologies and behavioral patterns.

VI. SUMMARY DISCUSSION

Results of this study indicated that migrating birds make extensive use of Lake Abert as a stop-over for feeding and resting during fall migration. Birds spent most of the available daylight hours foraging, concentrating on a few, numerically abundant prey. An initial assumption, that migrating birds fed primarily on brine shrimp, proved incorrect, at least during the migrations of 1982 and 1983.

A high degree of overlap in diets was noted among bird species, particularly within two separate groups of morphologically and behaviorally similar species. Diets of three shorebird species differed primarily in the relative proportions of the diet; the species composition of the diet being quite consistent. California and ring-billed gulls differed very little in either their diets or foraging behaviors. Limited taxonomic diversity within the prey base restricted the degree to which birds could be selective in their diets, and thus contributed to high levels of overlap.

In addition to being taxonomically limited, prey stocks at Lake Abert were patchy (see Chapter IV) and subject to distributional changes resulting from environmental conditions and the life cycles of individual prey species. The changing distribution of prey, both on a daily and seasonal basis, could explain the lack of any clear relationship in distributional patterns (either in time or space) between birds and prey. Alternate explanations for the lack of synchrony are that 1) prey populations at Lake Abert reach their peak

too early (or too late) for predators to fully exploit, given the constraints of breeding schedules and winter weather, or 2) prey population peaks, which vary with environmental conditions, are too unpredictable from year to year for birds to key their migration schedule to.

An abundance of high quality food ostensibly draws large numbers of birds to Lake Abert in autumn. The combination of taxonomically limited and patchy prey resources, large populations of hungry migrants and a narrow time frame would seemingly increase the potential for interspecific competition. On the other hand, high densities of nutritional prey within those patches would tend to offset that potential.

The study of avian community ecology has developed over the past two decades on the assumption that interspecific competition was the driving force in the structuring of communities (Cody and Diamond 1975, Lack 1971, MacArthur 1958). Recently, the importance of competition as a structuring agent in avian communities has been increasingly challenged, particularly by Wiens (1977b, 1983) and Rotenberry (1980, Wiens and Rotenberry 1981). While they do not discount the role of competition entirely, these authors stress that other factors, particularly environmental variability, may play important roles in determining interspecific relationships within the community. Such variability (ie. changes in water levels and prey distribution) might have important effects on community dynamics of bird assemblages at Lake Abert.

Partitioning of spatial, temporal, and to some degree, food resources appeared to be taking place among birds at Lake Abert. I

interpreted such partitioning as indicative of some sort of resource limitation, i.e. birds partitioned their available resources in such ways as to avoid energetically expensive interspecific competition. Alternately, "partitioning" of resources might occur in the absence of scarcity, as the result of different morphologies or nutritional requirements, independent of current resource levels at a site used only for a few days by a given individual.

From 1982 to 1983, a general downward trend was noted in weight, fat score, or both, for all study species. Changes in the density, distribution, and species composition of the prey community, as well as the relative availability of each foraging macrohabitat also occurred, probably as a result of rising water levels. It is tempting to correlate these observations: however, many unknown factors, for example food resources or weather conditions on the breeding grounds, may well have influenced the condition of migrants at Lake Abert in 1983. Myers (1983) and others have emphasized the importance of the migration period and of migratory habitats in the year-round ecology of water-dependent birds and cited the need for further studies in this area. However, just as studies of breeding or wintering birds cannot describe the entire life history strategy of a species, neither do studies of the migration period. The physiological and habitat requirements of migratory birds have evolved within the context of their annual cycle of reproduction-migration-wintering. Studies such as the one reported here, which focus on a short time period, will necessarily be limited in the scope of conclusions that can be made as to the impacts of this period on the year-round ecology of the

species. The fall migration of north-temperate breeding birds studied in this investigation may well be a bottleneck in the ultimate survival of those species. However, information on foraging ecology during the migration season will be of greater value if viewed within the context of each species' year-round ecology.

VII. LITERATURE CITED

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VIII. APPENDICES

Appendix 1. Results of statistical comparisons between 1982 and 1983 of foods consumed by birds during fall migration, Lake Abert, Oregon.

Prey Category	Bird Species						
	NOPH ¹	AMAV	WIPH	EAGR	RBGU	NOSH	CAGU
Brine shrimp, adult	NS ²	NS	NS	NS	NS	*	NS
Brine shrimp, juvenile	NS	NS	NS	NS	--	*	--
Brine shrimp, cyst	NS	NS	--	NS	--	**	--
Alkali fly, adult	NS	NS	NS	NS	NS	--	NS
Alkali fly, larvae	*	NS	NS	*	NS	NS	NS
Alkali fly, pupae	NS	NS	*	NS	NS	*	**
Long-legged fly, adult	NS	NS	NS	NS	--	--	--
Long-legged fly, larvae	*	NS	NS	NS	NS	NS	NS
Other fly, adult	NS	--	--	NS	--	--	NS
Other fly, larvae/pupae	*	NS	NS	NS	NS	NS	NS
Amphipod	--	NS	--	--	NS	--	--
Beetle	NS	*	NS	NS	NS	--	NS
Seeds	--	NS	--	--	--	NS	--
Water flea	--	NS	--	--	--	NS	--

¹ NOPH = Northern phalarope, AMAV = American avocet, WIPH = Wilson's phalarope, EAGR = Eared grebe, RBGU = Ring-billed gull, NOSH = Northern shoveler, CAGU = California gull.

² NS = No significant year-to-year change at $p = 0.05$

* = Significant change at $p = 0.05$

** = Significant change at $p = 0.01$

Appendix 2. Index of visual estimates of fat reserves of migratory birds, Lake Abert, 1982 and 1983.

Area	Visual Estimate of fat	Score
Subcutaneous (at pectoral muscle)	none	1
	thin	2
	moderate	3
	thick	4
	very thick	5
Intestinal	none	1
	strips present	2
	fat in patches	3
	intestines visible but encased in fat	4
	intestines obscured, encased in fat	5
Cardiac	none	1
	heart 10% covered	2
	heart 25% covered	3
	heart 50% covered	4
	heart encased in fat	5