AN ABSTRACT OF THE THESIS OF

Ned H. Euliss, Jr. for the degree of Doctor of Philosophy
in Wildlife Science presented on October 11, 1989
Title: Assessment of Drainwater Evaporation Ponds as Waterfowl Habitat in the San Joaquin Valley, California.
Redacted for privacy
Abstract approved: ______________________
Robert L. Jarvis

During 1982 through 1984 on drainwater evaporation ponds in the Tulare Lake Drainage District (TLDD), California I examined: 1) diets of northern pintails (*Anas acuta*), green-winged teal (*A. crecca*), northern shovelers (*A. clypeata*), and ruddy ducks (*Oxyura jamaicensis*), 2) the ecology and standing crop of aquatic invertebrates and plants, and 3) the proximate composition of waterfowl carcasses in the southern San Joaquin Valley, California. The intent was to assess the quality of drainwater evaporation ponds as waterfowl habitat.

Animal foods dominated the diets of all waterfowl species examined with midge (Chironomidae) larvae, water

boatmen (Corixidae), rotifers (Rotatoria), and copepods (Copepoda) forming the bulk of the dietary biomass. Waterfowl diets were unique for each duck species and each bird opportunistically foraged on the most abundant foods given their behavioral and morphological attributes.

Waterfowl foods produced in TLDD evaporation ponds came from species-poor assemblages of biota, dominated by aquatic invertebrates. The salt marsh corixid (*Trichocorixa reticulata*) and a midge (*Tanypus grodhausi*) were the most abundant invertebrates, forming 44.9% and 51.4% respectively, of all biota (dry weights) sampled. Regression models constructed for the corixid and the midge indicted that electrical conductivity and julian date were important regulators of their populations in TLDD evaporation ponds.

Proximate composition of waterfowl carcasses and diets differed among duck species and appeared to reflect unique requirements of each species life style. Of the 2 body components examined, lipids were the most variable and appeared to change temporally in relation to needs of individual species for energy stores or insulation. Proximate composition of ruddy duck and northern shoveler diets were stable whereas those of northern pintails varied to accommodate temporally changing nutritional requirements.

Assessment of Drainwater Evaporation Ponds as Waterfowl Habitat in the San Joaquin Valley, California

by

Ned H. Euliss, Jr.

A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed October 11, 1989

Commencement June, 1990

APPROVED:

Redacted for privacy

Professor of Wildlife in charge of major

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

Date Thesis is presented October 11, 1989

ACKNOWLEDGEMENTS

I wish to thank my graduate committee members, David S. Gilmer, Robert L. Jarvis, E. "Chuck" Meslow, Lorraine T. Miller, John A. Ruben, and David R. Thomas for their cheerful guidance and critical review of this thesis.

Steven Hall, Gary Rose, Joe Jaynes, Fred Scott, and Ed Snapp of the Tulare Lake Drainage District and Nick Gruenberg and Butch Brisco of Don Jackson Farms permitted access to the study areas, provided copies of field data, and commented on annual reports. Their willingness to cooperate will do much to further our knowledge of drainwater evaporation ponds and permit wise use of them in the future.

Many individuals provided much appreciated assistance and support: Ken Proctor of Wasco Union High School and Vic Winkler of Zoecon, Inc. made office and laboratory space available; Ted Murphy and Al Tanabe of California State College at Bakersfield provided dissection scopes and access to drying ovens and analytical balances; Frank Adams and Leta Wong of Oregon State University provided proximate analyses of duck carcasses; Thomas Charmley (Manager, Kern National Wildlife Refuge) provided full use of the refuge's shop facility and provided excellent support; Bill Asserson, Bob Huddelson, Ralph Labrum, Jim

Marchesini, and Ed Smith of California Department of Fish and Game provided temporary housing and much appreciated assistance with field work.

I would like to acknowledge the excellent work provided by field and laboratory assistants, Curt Charmley, Steve Holland, Kate Nippolt, Jim Marchesini, Kitty McCauley, John Griffith, Steve Kupillas, and especially Holly Coe for keeping myself and this study organized. Special thanks go to my good friend, Ted Barber, for his help collecting ducks from dusk to dawn and other "odd jobs" for which only a friend would volunteer.

I am indebted to Northern Prairie Wildlife Research Center and the U.S. Fish and Wildlife Service (Region 1) for funding this research and the Oregon Cooperative Wildlife Research Unit for administrative support. I am especially grateful to Dave Gilmer, for his confidence and for assistance in all aspects of this project. Valuable statistical support from Chip Harvey, Doug Johnson, and Terry Shaffer of Northern Prairie Wildlife Research Center is greatly appreciated.

I am especially appreciative of my friend and major professor, "Bob" Jarvis, for his advice, support, and assistance during this study. His ability to view complex phenomenon in simple outlines did much to maintain my enthusiasm and continues to be an inspiration.

Lastly, I would like to thank my family for their understanding, support, and assistance during this study. I am especially appreciative of my wife, Betty, for giving me time off from parental chores to complete class work and write this thesis.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Table Page

ASSESSMENT OF DRAINWATER EVAPORATION PONDS AS WATERFOWL HABITAT IN THE SAN JOAQUIN VALLEY, CALIFORNIA

I. INTRODUCTION

Effective waterfowl management requires a thorough knowledge of each species life cycle requirements. Advances over the last decade have provided a better understanding of anatid breeding biology, but wintering biology has only recently received consideration. This oversight was the result of past assumptions that wintering habitat was not limiting and played little role in the reproductive efforts of waterfowl. However, recent studies indicate that wintering habitat may play a substantial role in the breeding ecology of puddle ducks (anatini) (Heitmeyer and Fredrickson 1981, Krapu 1981). The wintering period is critical because it affects the physiological condition of ducks returning to nesting areas. Consequently, reproductive success on breeding grounds may be more closely related to wetland conditions on wintering areas than previously believed (Heitmeyer and Fredrickson 1981). In mallards (Anas platyrhynchos) the first clutch is usually the largest (Batt 1979, Krapu and Doty 1979), and most of the lipid requirements for this first clutch come from endogenous reserves obtained on wintering and/or migration areas (Krapu 1981).

An understanding of diets in winter in relation to nutritional requirements is of importance to waterfowl managers. Most early studies of food habits were based on gizzard analyses (Bartonek 1968), but this procedure yields biased results because of differential digestion of food items (Swanson and Bartonek 1970). Additionally, most early studies did not measure the availability of foods in habitats where ducks were collected and little was learned of the relative selectivity of food items by waterfowl. Recently, more comprehensive studies of waterfowl diets utilizing improved techniques have mostly been concentrated during the breeding season (Bartonek 1968, Bartonek and Hickey 1969, Bartonek 1972, Dirschl 1969, Drobney 1980, Krapu 1974a, Krapu 1974b, Krapu and Swanson 1975, Landers et al. 1977, Reinecke and Owen 1980, Serie and Swanson 1976, Sugden 1973, Swanson and Bartonek 1970, Swanson and Sargeant 1972, Swanson and Meyer 1973, Swanson et al. 1974a, Swanson et al. 1974b, Swanson et al. 1977, Swanson 1977b, and others). Most of these studies indicate a dietary shift from plant to animal foods during the breeding season, particularly in egg-laying hens and in ducklings. Prior to the use of these improved food habits techniques (Swanson and Bartonek 1970), most ducks were considered to be largely vegetarian (Cottam 1939, Martin and Uhler 1939). Apparently the high energetic demands of hens and ducklings during this stressful period (i.e. the energetic costs of egg-laying and the rapid growth of ducklings) require protein that cannot be satisfied through a diet of plant foods alone (Drobney 1980, Krapu 1974a, Krapu and Swanson 1975, Sugden 1973, Swanson and Meyer 1973). Additionally, the importance of animal foods to brooding mallards has been stressed through the hens preference for marshes heavily populated with invertebrates (Talent et al. 1982). The acquisition of invertebrate foods from breeding marshes may be related to body size. Large bodied and early nesting anatids such as arctic nesting geese (Branta canadensis and Anser caerulescens), eiders (Somateria mollissima), and mallards obtain sufficient endogenous reserves from nonbreeding areas to supply most of the nutrients required for the first clutch of eggs (Ankney and MacInnes 1978, Korschgen 1977, Krapu 1974a, Krapu 1981, McLandress and Raveling 1981, Raveling 1979a, Raveling 1979b, Ryder 1970). However, smaller and later nesting species such as shovelers (Anas clypeata) and wood ducks (Aix sponsa) apparently forage before and during egg-laying to obtain the necessary nutrients for successful reproduction. The smaller size of these anatids may preclude storage of sufficient reserves to produce the first clutch of eggs (Afton 1979, Drobney 1980). In any case, invertebrate foods rich in protein are necessary for ducklings and brooding hens.

Preliminary work, employing improved techniques, on wintering waterfowl ecology focused on food habits (Beam and Gruenhagen 1980, Connelly and Chesemore 1984, Euliss and Harris 1987, Miller 1987, Pederson and Pederson 1983). These studies indicate that invertebrate foods, mainly chironomid midges (Chironomidae), form substantial portions of the diets of wintering waterfowl. Although those studies provided new information concerning the role of invertebrates for wintering ducks, many other aspects of wintering ground ecology need investigation. Wintering areas may be important in maintaining physical condition for optimal reproduction, but information pertaining to the winter nutritional requirements of waterfowl and the capability of wintering habitats to provide required food resources is lacking. At the present time, there is scant information pertaining to the nutritional requirements of anatids during the nonbreeding period (Fredrickson and Drobney 1979, Prince 1979), and there is little information available concerning the quantity, quality, and availability of foods in habitats provided by wintering areas. Studies designed to provide this information are needed for effective waterfowl management.

Habitat for wintering waterfowl is deteriorating or being lost at an alarming rate (Tiner 1984) and remaining wetlands must be made more productive in order to compensate for previous losses (Bellrose and Low 1978). Wetland loss and degradation has been extensive in California where over 94% of the wetlands available prior to the 1850's have been lost (U. S. Fish and WIldlife Service 1978). Historically, the largest single block of wetlands in California was in the southern San Joaquin Valley where over 250,000 ha of shallow wetlands were located in the Tulare Lake and Buena Vista Lake Basins. These wetlands now have been totally converted to agricultural fields because soils and climate in the area are conducive to the production of economically valuable crops.

Soils in the Tulare Lake Basin (TLB) are saline and under traditional irrigation practices, salts concentrate in upper soil profiles and frequently limit plant growth. To reduce salt accumulation and enhance agricultural production, subsurface irrigation drainage systems have been installed to wash excess salts from upper soil profiles and remove them from irrigated fields. Water from drained fields is high in salts. Drainwater also contains heavy metals and other environmental contaminants (Presser and Barnes 1985) associated with embryonic mortality and abnormalities in water birds (Ohlendorf et al. 1986a, 1986b, 1987). Presently, the only acceptable means of disposing of subsurface drainage water in the TLB is by evaporation in shallow ponds. Present waterfowl use in the TLB is confined to habitats provided by Kern National Wildlife Refuge (NWR), private duck clubs, water storage basins, flooded agricultural fields, and evaporation ponds.

Evaporation ponds support large numbers of wintering and migrating waterfowl and shorebirds in the TLB. There are about 1,300 ha of evaporation ponds in the basin with increases likely because volume of high salinity subsurface drainwater from irrigated farmland continues to increase, posing major disposal problems for the agricultural enterprise (Hanson 1982). An estimated 26,000 ha of new or restored wetlands can be developed from irrigation drainwater in the San Joaquin Valley (San Joaquin Valley Interagency Drainage Program 1979). However, waterfowl managers know very little about the potential of these areas to provide a suitable environment for wintering waterfowl. Although the salt load of drainwater is high (up to 300 mmhos/cm^2 EC), preliminary evaluation indicates that it has potential for marsh management (Ives et al. 1977).

Waterfowl management on most wintering and migration areas is directed towards the production of plants with large seed crops, such as alkali bulrush (Scirpus maritimus), common barnyardgrass (Echinochloa crusgalli), swamp timothy (Heleochloa schoenoides), and domestic grains. Although these plants produce large amounts of forage, the ability of these manipulated wetlands to supply the foods required to maintain a favorable nutrient and energy balance for waterfowl during the nonbreeding season has not been assessed. Further, there is no satisfactory method of comparing the value of these managed wetlands to each other or to other wintering ground habitats. As a result, wetland management is based on the subjectivity of local managers as modified by available personnel and cost limitations. Because wintering grounds are managed mainly for foods that waterfowl use to maintain a healthy nutrient and energy balance, a system is needed to enable managers to evaluate wetlands on their relative abilities to supply waterfowl with specific nutrients and gross energy via food resources.

One approach to evaluate wetlands on the basis of their ability to supply specific nutrients is to compare the nutrient composition of seasonally consumed foods to the body condition (protein and lipid reserves) of ducks during winter. An understanding of the seasonal trends in body condition in wintering waterfowl and the seasonal availability, use, and nutrient composition of waterfowl foods would permit an assessment of the value of various wetlands to wintering ducks. A knowledge of the seasonal abundance of food items in wintering ground habitats would then enable managers to evaluate wetlands based on the availability of nutrients to waterfowl during critical periods.

The overall goal of my research was to evaluate the potential of evaporation ponds in the TLB to provide foods capable of maintaining a favorable energy balance in wintering ducks. The foods that waterfowl consume from various wetlands all interact and ultimately determine the status of nutrient reserves in wintering waterfowl. Therefore, the role each wetland plays in maintaining these reserves may be evaluated through a comparison of the nutrient composition of seasonally available foods characteristic of individual wetlands and the status of body reserves in waterfowl.

This investigation provides baseline data on factors affecting waterfowl use of evaporation ponds in the TLB. These data are organized into chapters that address: 1) feeding ecology of waterfowl, 2) standing crops and ecology of aquatic invertebrates, and 3) body condition and nutrition of waterfowl.

II. STUDY AREA

The Tulare Lake Basin (TLB) forms the southern end of the San Joaquin Valley. Prior to the 1850's, this area contained a wetland complex that comprised over 250,000 ha (U. S. Fish and Wildlife Service 1978), forming the largest single block of wetland habitat in California. Today, essentially all of this habitat has been converted into agricultural fields.

Average annual rainfall in the TLB is about 15 cm. Nearly all precipitation falls between November and March, with long dry summers (Kahrl 1979). Agriculture is the primary industry in the basin. Major crops include cotton, barley, wheat, safflower, alfalfa, and grapes. Arid conditions necessitate irrigation of nearly all crops.

The basin comprises about 1,300,000 ha of the valley floor (U. S. Fish and Wildlife Service 1978). The work described in this thesis occurred within the Tulare Lake Drainage District (TLDD). The District is about 78,000 ha in size and contains large blocks of agricultural lands, evaporation ponds, and farming communities. The Kern-Pixley National Wildlife Refuges (NWR's) (6,000 ha) and about 2,400 ha of private duck clubs are situated in the basin and adjacent to the TLDD.

Evaporation ponds have been present in the TLB since 1980. I collected data from 3 evaporation pond systems (EPS) that contained either 4 or 10 interconnected ponds (18 ponds total); water flow was unidirectional within each EPS. There is no outflow in an EPS, resulting in a strong salt gradient; the salt load of each pond in the series is progressively higher than the preceding one. Average pond size is about 65 ha. Evaporation ponds are typically shallow (< 1 m) with gradually sloping sides and flat bottoms.

III. MATERIALS AND METHODS

Field Procedures

Pond Classification

Evaporation ponds examined in this study were classified according to their age (i.e. 7 ponds were established in January 1980, 8 in August 1981, and 3 in December 1982). Three ponds from each age group were selected for estimating seasonal and annual changes in standing biomass of plant and animal foods. Study units within each age group were selected on the basis of waterfowl use.

Duck Collecting Techniques

From September through March in 1982-84, actively feeding northern pintails, green-winged teal, northern shovelers, and ruddy ducks were collected from the EPS study units by shooting. An attempt was made to collect 20 birds of each species on a monthly basis and to collect equal numbers of each sex. Normally, several birds were collected simultaneously and in several instances, 2 or more species were collected together.

Different techniques were used to collect birds depending on the time of day. During diurnal periods, I allowed birds to actively forage for at least 10 minutes prior to collection. At nighttime, birds were collected as they flushed when illuminated with a spot light (Euliss 1984). I did not observe the feeding behavior of ducks at night but recent studies suggest that ducks feed mostly at night (Tamisier 1972, 1976, 1978/79, Euliss and Harris 1987) and the observation of foraging behavior was not necessary to obtain sufficient specimens suitable for food habits analysis (Euliss 1984).

Immediately following shooting, the esophageal contents of each duck was processed for food habits analysis. An incision was made from the mouth through the length of the neck and along the spine to about the kidneys to expose the esophagus and proventriculus. The esophageal/proventricular juncture was clamped with a hemostat to prevent food exchange. The esophagus was quickly removed and its contents flushed into a labeled specimen jar with 80% ethanol to prevent postmortem digestion (Dillery 1965). Only the esophageal contents were examined for food habits due to the differential passage rates of hard and soft foods through the digestive tract (Swanson and Bartonek 1970). Occasionally, the esophageal contents of birds would contain substantial amounts of blood. To prevent clots from forming, I flushed them with fresh water to dissolve potential clots and subsequently removed the water by screening (0.5 mm) prior to storage in ethanol.

Bird carcasses were weighed to the nearest gram, and sex and age determined by plumage characteristics (Carney 1964), and by presence or absence of a bursa. Duck carcasses were frozen within 12 hours after collection and stored frozen until laboratory work was performed.

Invertebrate and Plant Collecting Techniques

Standing biomass samples of aquatic plants and invertebrates were collected at random from transects established in designated study units every 3 weeks. Transects were established in each evaporation pond for collection of biota samples during 1982-83 and 1983-84. Because the dimensions of ponds varied, transects from different ponds were spaced different distances apart. In all cases, the length of each pond was subdivided so that equally spaced transects were established perpendicular to the longest dimension of the pond. The exact location where samples were collected was determined randomly on a microcomputer by generating a set of random numbers that represented the length of a given transect in meters. Samples of water column and benthic biota were obtained with samplers modified after the ones described by Swanson

(1978a, 1978b). Benthic samples were cleaned by removing small sediment particles by sieving with a 0.5 mm self-cleaning screen (Swanson 1977a). Separate water column and benthic samples were collected from each of 10 transects per pond in 1982-83 (i.e. 20 samples/pond; 10 benthic and 10 water column) and from 20 transects during 1983-84 (i.e. 40 samples/pond; 20 benthic and 20 water column). Increasing sample size was necessary to reduce large sample variance.

Assessment of the Abiotic Environment

Water depth, temperature, pH, electrical conductivity, and dissolved oxygen were determined when standing biomass samples were obtained. Each parameter was measured at the waters surface, at mid-depth, and at the bottom. Standard field meters were used to obtain all measurements.

Laboratory Procedures

Processing Esophagi and Standing Biomass Samples

Food items present in duck esophagi and standing biomass samples were sorted by hand and/or with a Chapman pump-powered aspirator (Euliss 1984). The weight of each taxon was determined to the nearest milligram with an analytical balance after drying to a constant weight at 55-60 C in a drying oven.

Food items separated from esophagi and standing biomass samples were identified using guides by Hitchcock and Chase (1950), Usinger (1956), Mason (1957), Ward and Whipple (1959), Martin and Barkley (1961), Grodhaus (1967), Munz and Keck (1973), Merritt and Cummins (1984), Pennak (1978), and Borror et al. (1981). Seeds of questionable identity were sent to the California Department of Food and Agriculture for identification. G. Grodhaus of the California Department of Public Health and G. Lamberti from Oregon State University identified several invertebrates and verified the identity of other invertebrate taxa.

Processing Duck Carcasses for Proximate Analysis

Duck carcass homogenates were prepared in our laboratory and submitted to the Department of Agricultural Chemistry at Oregon State University for proximate determinations of lipid and protein content. Duck carcasses were prepared by plucking while partially frozen except that remiges were removed with clippers. Feet and bills were removed and discarded. Carcasses were ground in a commercial meat grinder; specimens were kept frozen with dry ice. Ground tissues were placed in a blender along with sufficient water to insure good adhesion and blended thoroughly. The amount of water added was recorded and proximate determinations corrected accordingly. Two samples from each bird were submitted for analysis. Lipids were extracted using a Soxlet apparatus and Kjeldahl nitrogen determinations were used to determine total protein using a 6.25 conversion factor (Horowitz 1970:16,127).

Statistical Procedures

All data collected in this study were entered into computer databases using RBase 5000 (Microrim 1985) and analyzed using standard statistical procedures (SAS Inst. 1985). Hypotheses tested and statistical techniques utilized are outlined in the following chapters. All tests were evaluated at the 0.05 significance level.

IV. WATERFOWL FEEDING ECOLOGY

Introduction

Wetland habitats for wintering waterfowl are deteriorating or being lost at a rapid pace (Tiner 1984). Wetland losses of 94% over areas historically present in California's Central Valley has been a result of rich soils and desirable climate for production of agricultural crops. Particularly hard hit has been the southern San Joaquin Valley where about 250,000 ha of shallow wetlands in the vicinity of the Tulare Lake and Buena Vista Lake Basins have been converted into agricultural fields (Gilmer et al. 1982). Soils and climate in the area are conducive to the production of cotton, alfalfa, safflower, and barley. However, soils are saline and under traditional irrigation practices, salts concentrate in upper soil profiles and frequently limit plant growth. To reduce salt buildup and enhance agricultural production, farmers have installed subsurface irrigation drainage systems that wash excess salts from upper soil profiles and remove them from irrigated fields. Water from drained agricultural fields is high in salts and contains heavy metals and other environmental contaminants (Presser and Barnes 1985). Presently, the only acceptable means of disposing of subsurface drainwater in the Tulare Lake

Basin (TLB) is by evaporation in shallow ponds. Present waterfowl use in the area is confined to habitats provided by the Kern National Wildlife Refuge (NWR), private duck clubs, water storage basins, flooded agricultural fields, and evaporation ponds.

Large numbers of wintering and migrating waterfowl and shorebirds have been observed on evaporation ponds but the potential of the areas to provide a suitable environment is unknown. There are presently about 1,300 ha of evaporation ponds in the TLB alone.

The objective of this chapter is to report the diets of several species of waterfowl that use evaporation ponds to describe the foods that are utilized from these newly created wetlands. Study birds were selected on the basis of frequent use of evaporation ponds and to represent a divergence in feeding habits. Northern pintails (*Anas acuta*) and green-winged teal (*A. crecca*) were selected because they represent large and small dabbling ducks, respectively. Northern shovelers (*A. clypeata*) were selected because of their filter-feeding habit and ruddy ducks (*Oxyura jamaicensis*) because they dive for foods in deeper portions of the ponds.

Study Area

This study was conducted on drainwater evaporation ponds operated by the Tulare Lake Drainage District (TLDD) in Kings and Kern Counties, California. The evaporation ponds examined during this study were built in 1980 and consisted of 3 evaporation systems (EPS) that collectively contained 18 separate ponds. An EPS consisted of a series of interconnected ponds with unidirectional water flow, except in terminal ponds that lacked an outlet. Average pond size was about 65 ha. Ponds were generally < 1 m deep with gradually sloping sides and flat bottoms. Drainwater entering an EPS was about 5-10 mmhos/cm^2 EC but increased steadily in successive ponds due to evaporation and frequently exceeded 300 mmhos/cm^2 EC in terminal ponds.

Diversity of aquatic plants and invertebrates was low relative to surrounding freshwater wetlands but those taxa present were abundant. Widgeongrass (_Ruppia maritima_) was common in ponds having 40-75 mmhos/cm^2 EC and horned pondweed (_Zanichellia palustris_) was occasionally observed in less saline ponds but was never very abundant. Midge larvae and corixids comprised the bulk of the foods available. Only 2 species of midge larvae were observed; _Tanypus grodhausi_ was the most common. Similarly, the bulk of the corixid biomass was formed by _Trichocorixa_ reticulata although another taxa (Corisella spp.) was infrequently present during the spring. Additionally, copepods (Copepoda), rotifers (Rotatoria), and brine fly larvae (Ephydridae) were seasonally abundant and were utilized by ducks.

Average annual rainfall was about 15 cm and nearly all precipitation fell between November and March with long dry summers (Kahrl 1979). Agriculture is the primary industry in the basin. Major crops include cotton, barley, wheat, safflower, alfalfa, and grapes. Arid conditions necessitate that nearly all crops be irrigated.

Materials and Methods

Ducks were shot from September through March, 1982-84, during diurnal and nocturnal periods. During the day, ducks were shot after observing them feed for $\geq$ 10 min. At night, birds were illuminated with a 12-volt floodlight and shot as they flushed without observing feeding behavior (Euliss 1984). Duck esophagi were immediately removed and their contents preserved in 80% ethanol (Swanson and Bartonek 1970). Food items collected from duck esophagi were sorted into taxonomic groupings, dried to a constant weight at 55-60 C in a drying oven and weighed to the nearest milligram on an analytical balance. Food items were identified using guides provided by Martin and Barkley (1961), Grodhaus (1967), Pennak (1978), and Merritt and Cummins (1984).

Food data were summarized as aggregate percent (Swanson et al. 1974a) dry weight. Only birds that contained at least 0.005 g were used in statistical analyses. A General Linear Models (GLM) procedure (SAS Inst. 1985) was used to identify factors most affecting food habits data. Because foods consumed from evaporation ponds by study birds were mostly invertebrates, aggregate percent dry weight of total invertebrates consumed was used as the dependent variable in an ANOVA to evaluate the effect of explanatory variables: month, year, bird age, period (diurnal versus nocturnal), and age of EPS. To compensate for unequal variances, an arcsin transformation (Snedecor and Cochran 1980:290-291) was performed on aggregate percent dry weight data. A GLM ANOVA was also used to assess differences in usage of specific foods among duck species and orthogonal contrasts (Snedecor and Cochran 1980:226-228) were used to evaluate seasonal changes in waterfowl consumption of specific foods. Depths recorded at each feeding zone where birds were collected required a square root transformation (Snedecor and Cochran 1980:288-290) and transformed data were tested for differences among duck species using a Student-Newman-Keuls (SNK) multiple comparison test.

Results

ANOVA results from the GLM indicated that year and month were the most important independent variables affecting consumption of invertebrate foods. For pintails, these 2 variables accounted for half the variation in total invertebrate consumption ($R^2 = 0.50$) with year ($P < 0.05$) and month ($P < 0.01$) having a significant effect. The best model for northern shovelers was similar with year ($P < 0.01$) and month ($P < 0.05$) both significantly affecting consumption of total invertebrates although they explained little of the overall variation ($R^2 = 0.16$). Ruddy duck consumption of invertebrates was extremely variable and the best 2-way model involved month and habitat ($R^2 = 0.09$) where only the effect of habitat was significant ($P < 0.05$). However, the model using year and month explained only slightly less variation ($R^2 = 0.07$) with only year showing a significant effect ($P < 0.05$). Because the differences were slight the model of year and month was adopted in order to be consistent and to facilitate comparisons among duck species. The effect of these independent variables was controlled by partitioning Type III sums of squares and examining for main effects in all subsequent analyses. Food habits data collected for green-winged teal were too few for analysis.

Food habits

I collected 58 northern pintails, 12 green-winged teal, 105 northern shovelers, and 185 ruddy ducks from the TLDD study ponds (Table 1). Within duck species, diets were similar among sex, age, time of collection (diurnal versus nocturnal), and age of pond ($P > 0.05$) with only year and month having a significant effect on the total dry weight of invertebrates consumed. Thus, data were analyzed while controlling for effects of year and/or month, where appropriate, in the following analyses.

The esophagi of 58 northern pintails contained 49.5% plant seeds and 50.5% animal matter (Table 1). Midges (39.4%) and widgeongrass nutlets (34.6%) were the most important foods and they were found in 55.2% and 44.8% of all pintails examined, respectively. Foods of additional importance were water boatmen (5.9%) and seeds from miscellaneous plants (14.9%), mostly terrestrial species that either grew along levees or that grew in the area prior to the pond construction and flooding. These 4 foods formed nearly 95% of the diet of pintails.

Only 12 green-winged teal were collected from the TLDD evaporation ponds and their esophagi contained 21.4% plant seeds and 78.6% animal matter (Table 1). Copepods (24.1%), midges (23.2%), water boatmen (21.9%) were the

Table 1. Aggregate percent dry weights of major food items found in northern pintail, green-winged teal, northern shoveler, and ruddy duck esophagi collected from agricultural drainwater evaporation ponds in the San Joaquin Valley, California, during September through March, 1982-83 and 1983-84.

	Waterfowl species			
Food item	PINT (N=58)	TEAL (N=12)	SHOV (N=105)	RUDD (N=185)
Plant				
Widgeongrass	34.6	7.5	1.5	2.6
Other (16 items)	14.9	13.9	6.0	7.2
Total plant matter	49.5	21.4	7.5	9.8
Animal				
Seed shrimps		9.0	0.5	
Copepods		24.1	15.2	
Rotifers			20.4	
Midges	39.4	23.2	4.5	49.7
Brine flies	2.3	tr[a]	tr	3.7
Water boatmen	5.9	21.9	51.6	36.0
Water boatmen eggs	2.7			0.7
Other (7 items)	0.2	0.2	0.3	
Total animal matter	50.5	78.6	92.5	90.1

PINT = Northern pintails, TEAL = Green-winged teal, SHOV = Northern shoveler, and RUDD = Ruddy ducks.

[a] tr = < 0.5%

most commonly consumed foods. Foods of lesser importance in the diet were: widgeongrass nutlets (7.5%), miscellaneous seeds (13.9%) mostly from terrestrial plants, and seed shrimps (9.0%). Nearly 100% of the diet was formed by these 6 foods.

The esophagi of 105 northern shovelers contained 7.5% plant seeds and 92.5% animal matter (Table 1). Water boatmen (51.6%), rotifers (20.4%), and copepods (15.2%) were the most commonly consumed foods although midges (4.5%) and miscellaneous seeds (6.0%) were also of dietary importance. These 5 foods formed nearly 98% of the diet of shovelers.

Ruddy duck esophagi collected from the TLDD study sites contained 9.8% plant seeds and 90.1% animal matter (Table 1). Midges (49.7%) and water boatmen (36.0%) were the 2 most commonly consumed foods although miscellaneous seeds (7.2%) were also consumed. Nearly 93% of the diet observed in the ruddy duck sample was formed by these 3 foods.

Most food items were of common importance to all waterfowl species examined except that copepods and seed shrimps were consumed only by northern shovelers and green-winged teal and rotifers were consumed only by shovelers. Water boatmen eggs were consumed only by pintails and ruddy ducks with pintails ($F = 9.55$, $P < 0.01$) consuming more than ruddy ducks. All ducks consumed widgeongrass nutlets with pintails ($F = 20.06$, $P < 0.01$) consuming significantly more than all other species. All birds used midge larvae but the greatest consumption was by ruddy ducks ($F = 27.89$, $P < 0.01$). Brine flies were also used by all duck species, however, no significant difference in usage was observed among species ($F = 1.60$, $P = 0.20$). Water boatmen were important foods to all duck species but shovelers relied on them more than other ducks ($F = 3.42$, $P < 0.05$). Seed shrimp and copepod usage was confined to green-winged teal and shovelers but no statistical comparisons were made because of small sample sizes for green-winged teal. Rotifers were used exclusively by shovelers and they formed an important proportion of the seasonal diet.

Seasonal Trends

Although the food habits of all waterfowl species contained common elements, there were generally unique seasonal patterns among species. The diets of northern pintails changed from mostly plant foods in fall to mostly animal foods in March (Figure 1). Pintails consumed significantly more plant foods ($F = 28.16$, $P < 0.01$) than either northern shovelers or ruddy ducks and widgeongrass nutlets was the most commonly consumed plant food. Midges

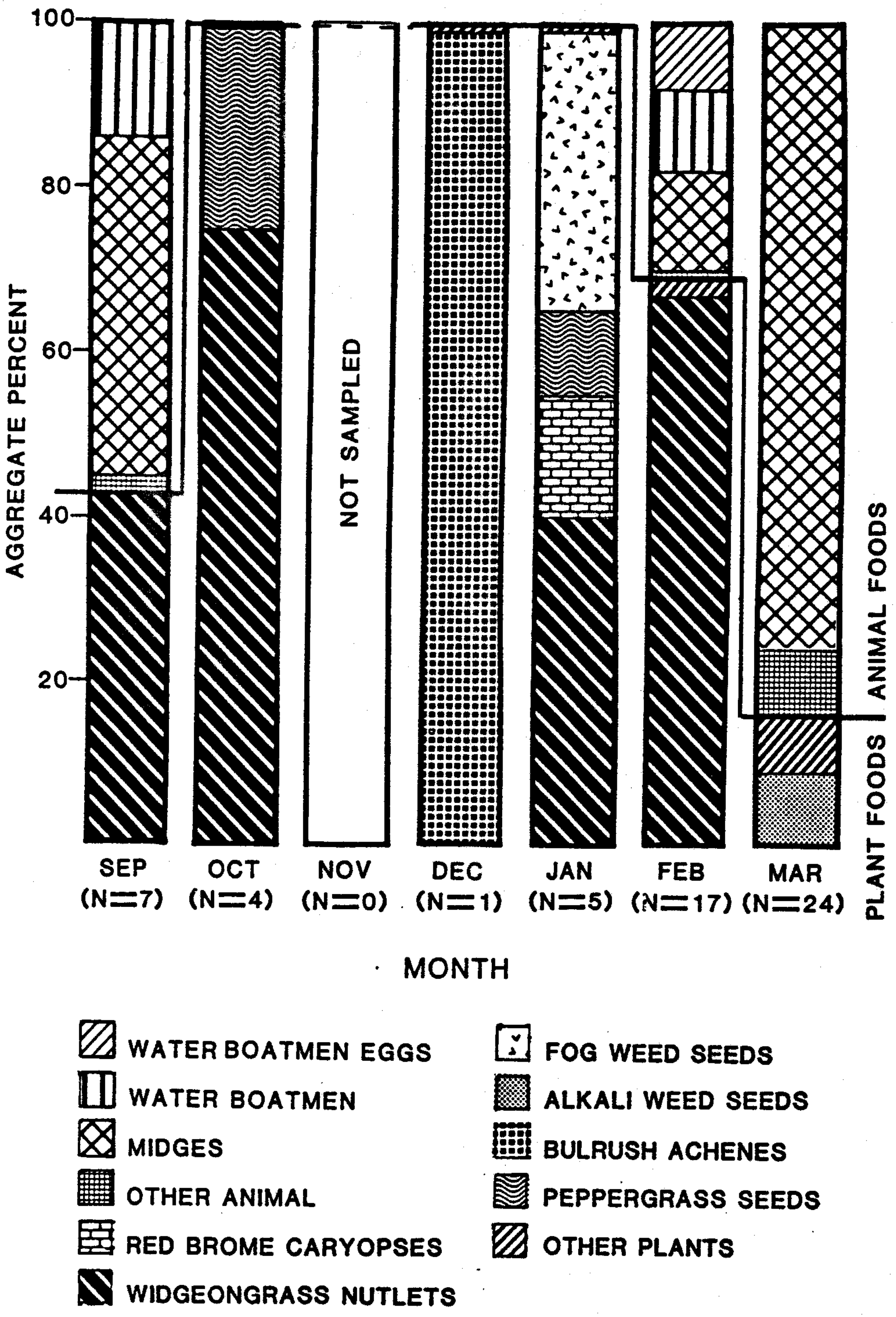

Figure 1. Seasonal food habits of northern pintails collected from agricultural drainwater evaporation ponds in the San Joaquin Valley, California, during September through March, 1982-83 and 1983-84.

were important pintail foods that were consumed mostly during September, February and March with no strong pattern of seasonal usage evident among months (T = 1.73, P = 0.09). Seeds of miscellaneous plants were also consumed during October through January, although use of the ponds by pintails was low during that time period (H. Coe, pers. comm.) and relatively few birds were available to collect for food habits analysis. Water boatmen were consumed by pintails with no clear seasonal use pattern detected (T = -0.34, P = 0.73).

Aquatic invertebrates dominated the diets of northern shovelers during all months of the study (Figure 2). Water boatmen, rotifers, and copepods formed 70-90 % of the foods consumed each month with distinct seasonal use patterns observed for individual food items. Water boatmen use declined seasonally with significant decreases occurring in January (T = -2.87, P < 0.01), February (T = - 3.15, P < 0.01), and March (T = -8.48, P < 0.01). Shoveler usage of rotifers was also strongly seasonal with significantly higher consumption occurring in January (T = 5.16, P < 0.01), February (T = 3.44, P < 0.01), but not in March (T = 0.16, P = 0.88). Although copepods were consumed during both January and March, only the consumption in March was a significant increase over preceding months (T = 19.48, P < 0.01). Midges were used as foods by shovelers to a lesser extent than found for

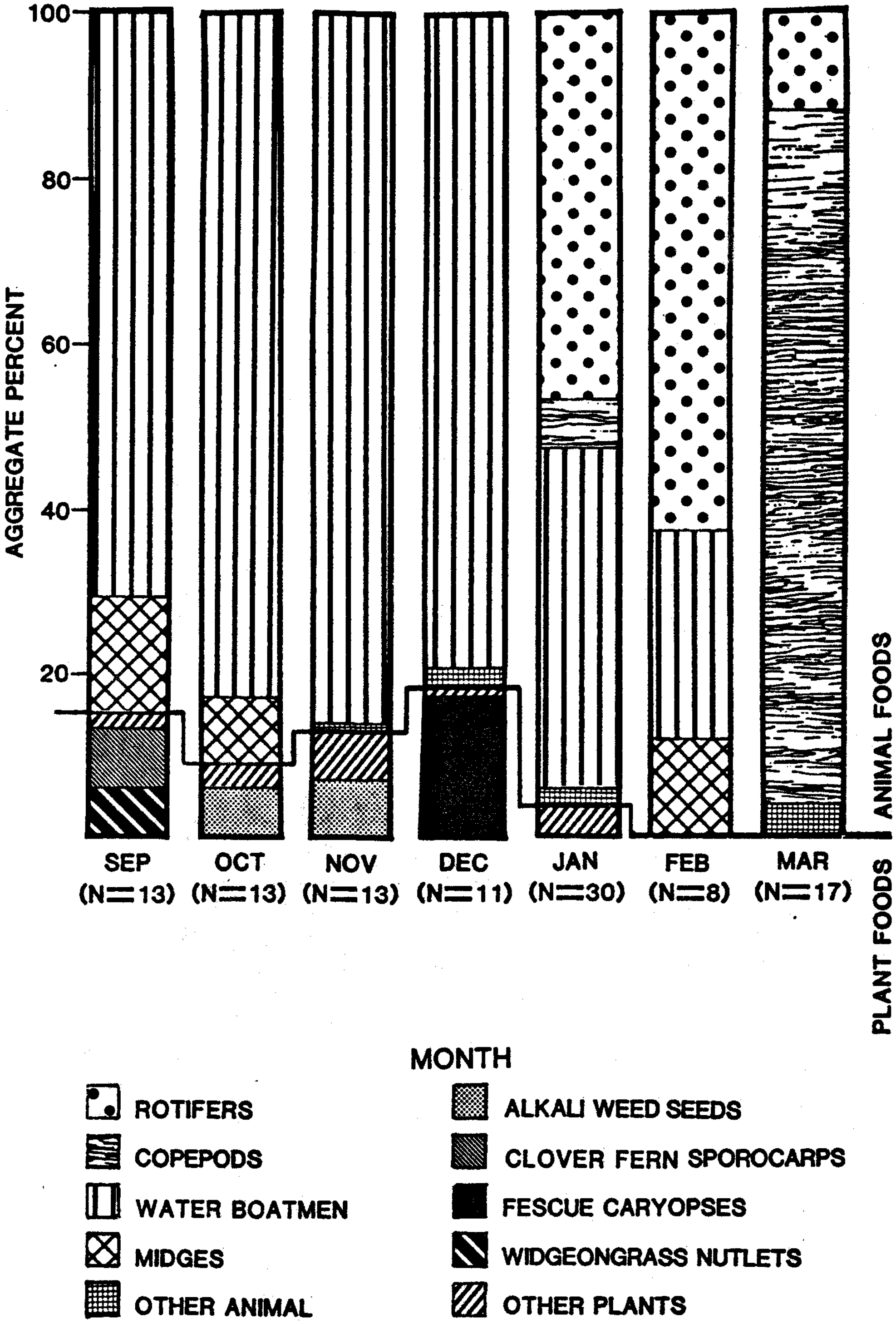

Figure 2. Seasonal food habits of northern shovelers collected from agricultural drainwater evaporation ponds in the San Joaquin Valley, California, during September through March, 1982-83 and 1983-84.

either pintails or ruddy ducks (Table 1) and no clear seasonal pattern was observed ($T = -0.25$, $P = 0.81$). Miscellaneous plant seeds formed 5-20% of the monthly diet from September through January with 100% of the diet being composed of invertebrates during February and March. Rotifers were unique food items for shovelers and copepods were shared in common only with green-winged teal (Table 1).

Diets of ruddy ducks also varied seasonally and as for shovelers, were composed mostly of animal foods (Figure 3). Midges and water boatmen formed the bulk of the diet during all months examined with a heavier reliance on water boatmen occurring during September through January with consumption in both February ($T = -4.28$, $P < 0.01$) and March ($T = -4.94$, $P < 0.01$) representing significant declines over previous months. Midges were consumed most heavily during the later half of the wintering period with significant increases over previous months occurring in February ($T = 2.83$, $P = 0.01$) and March ($T = 4.35$, $P < 0.01$). Ruddy ducks made little use of other foods although brine flies and seeds of miscellaneous plants were consumed.

One major factor influencing the diets of each respective species relates to water depths in the unique zones each duck species exploited while foraging. To examine this depth relationship, a multiple (LSD)

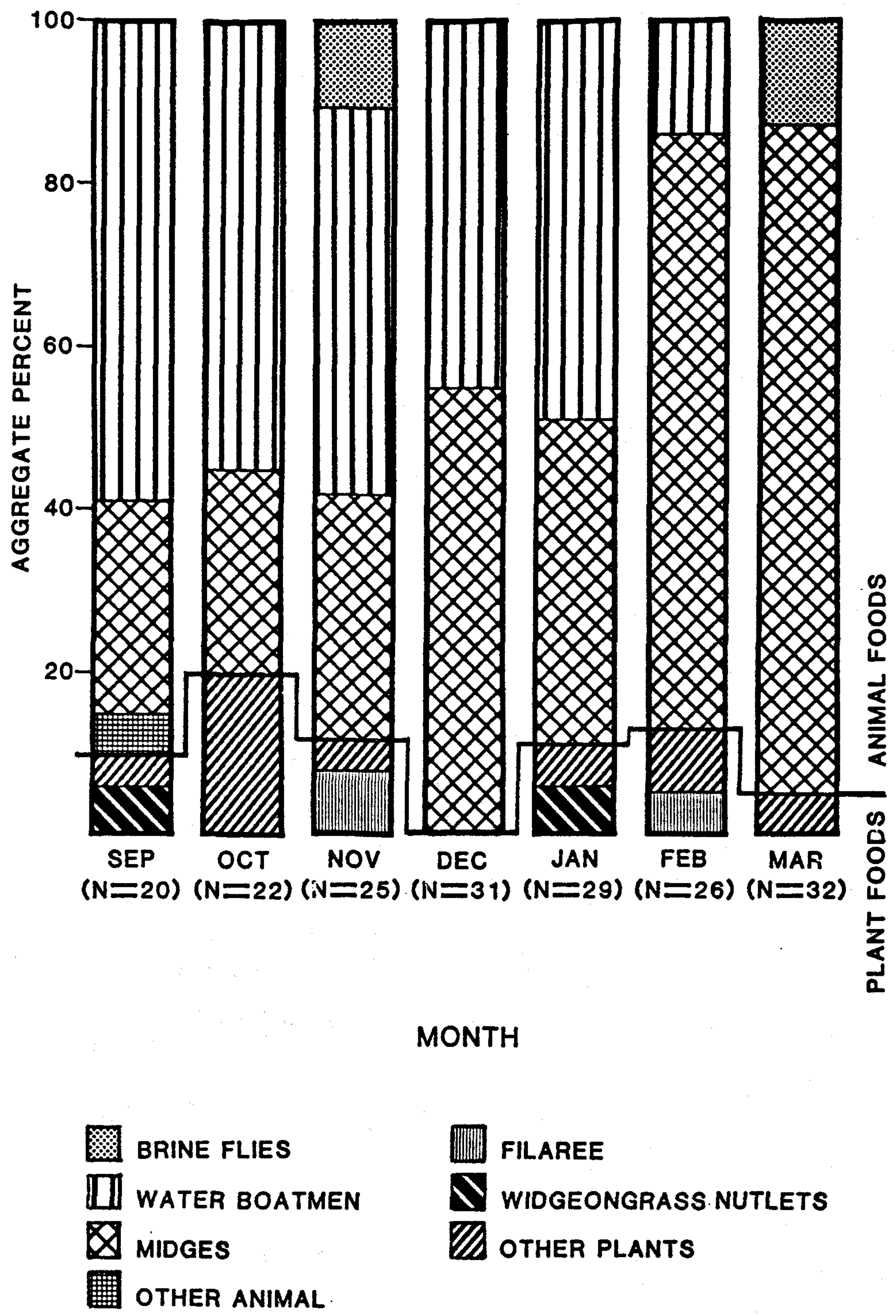

Figure 3. Seasonal food habits of ruddy ducks collected from agricultural drainwater evaporation ponds in the San Joaquin Valley, California, during September through March, 1982-83 and 1983-84.

comparison was used to evaluate species differences among feeding depths recorded for each duck species examined. Mean water depths at sites where ducks were feeding of 2.8, 1.7, 4.9, and 9.5 cm were recorded for pintails, green-winged teal, northern shovelers, and ruddy ducks, respectively. These differences among feeding depths recorded for all species were highly significant ($P < 0.05$) with each duck occupying water zones of different depths from other species.

Discussion

Food habits and foraging strategies

Most food items identified during this study were important to all duck species examined, but the proportionate usage of individual foods varied among duck species. Widgeongrass nutlets, midges, and water boatmen were the most commonly consumed foods. However, rotifers which were not consumed by other ducks, were important foods of shovelers; copepods were consumed only by shovelers and green-winged teal. Several previous studies have indicated that green-winged teal can forage efficiently on small food items (Euliss 1984) and, although less well studied for food habits, northern shovelers and other filter-feeding anatids also consume very small food items (Bellrose 1978, Crome 1985). Both pintails and green-winged teal dabbled for foods along pond margins in shallow water areas optimal for their body size; ruddy ducks foraged in deeper water areas by diving. Thus it appeared that each duck species exploited foods from the TLDD study ponds that were most easily obtainable given their morphological and behavioral attributes.

Pintails and green-winged teal mainly dabbled for foods in water areas optimal for their body size with 2.8 and 1.7 cm mean feeding depths recorded for each duck species, respectively. This difference was highly significant ($P < 0.05$) and as noted by Euliss and Harris (1987), probably represents a major habitat partitioning factor influencing the diets of these 2 species. The similarity in food habits of these 2 duck species has been noted by other authors (Glasgow and Bardwell 1962, McGilvrey 1966, Tamisier 1976, Euliss and Harris 1987). While similarity in food habits is difficult to document in this study because of small sample sizes for green-winged teal, basin morphology of the TLDD study sites suggests that the habitat is suboptimal for both species and as such likely affects the low usage patterns observed for both birds (H. Coe, pers. comm.). The TLDD study sites are characterized by gently sloping sides and flat bottoms with average depths of approximately 1 m. Average feeding depths recorded for pintails and green-winged teal during this study were similar to those reported by Euliss and Harris (1987). Thus, water depths on the study area were generally too deep for both anatids and feeding was restricted to shallow areas along pond margins. Over the 6 year period from 1981 through 1987 only 4% of the pintails and 3.7% of the green-winged teal population in the TLB were censused from the TLDD evaporation ponds during winter (Barnum and Euliss, in prep.). Pintail usage of the study sites was confined mostly to fall and spring months with little use occurring during winter (H. Coe, pers. comm.). Animal foods were heavily used during both time frames and the seasonal patterns observed may relate to protein requirements of feather molt (Heitmeyer 1988) and reproduction (Krapu 1979, 1981). Thus, the importance of TLDD ponds to pintails and green-winged teal may relate to the abundance and high availability of animal foods during time periods when their dietary requirement for animal proteins is high.

Northern shovelers and ruddy ducks consumed similar proportions of animal foods, although seasonal usage patterns were different (Figures 2 and 3). Both birds showed strong seasonal usage of corixids with significantly more being consumed early in the winter period than late winter to early spring. Consumption of corixids by shovelers decreased significantly in January, February, and March over preceding months. Somewhat later, usage of corixids by ruddy ducks decreased significantly in February and March over usage observed earlier in the season. For ruddy ducks, this decrease in consumption of corixids was offset by a corresponding and significant seasonal increase in the consumption of midges during February and March. Northern shovelers offset the decrease in consumption of water boatmen by significantly increasing consumption of rotifers in December and February and in use of copepods during March. Because of their extremely small size, neither rotifers nor copepods were consumed by ruddy ducks during this study.

The period of heavy use of water boatmen by both northern shovelers and ruddy ducks identifies a time frame of potential overlap for the same food resource, especially in fall and winter when both birds rely heavily on that food. However, both birds rely on this food only during periods when water boatmen were extremely abundant; numbers of individuals often exceeded 200,000 individuals/m^2 at specific sites within ponds. While water boatmen have been reported as important foods of shovelers (Martin et al. 1951), ruddy ducks are considered mostly as predators of midge larvae (Siegfried 1973, Gray 1980). Thus, what may appear as potential overlap may instead be an opportunistic response by ruddy ducks to an extremely abundant food. Filtering appears more adaptive and efficient in capturing small swimming prey, including corixids, whereas diving for foods along sediment interfaces appears to be more profitable in obtaining midges and other less mobile prey items. Overlap thus appears to occur only during periods of extreme abundance when the prey base is probably sufficient to accommodate the dietary needs of both ducks.

Food Usage

Food availability and the nutritional needs of each waterfowl species appear to be prime factors influencing food usage given the behavioral and morphological differences of individual duck species. Similar conclusions have been reached by Beam and Gruenhagen (1980), Connelly and Chesemore (1980), Pederson and Pederson (1983), Euliss and Harris (1987), and Miller (1987). In the present study, all duck species were highly opportunistic and foraged heavily on foods that were concentrated in some fashion or another. Because emergent vegetation was lacking on the TLDD study area, wind was an important factor in concentrating floating foods along windward shores and making them readily available to feeding ducks. The activities of redheads (*Aythya americana*) and American wigeon (*Anas americana*) feeding on widgeongrass in the study ponds resulted in many plants being uprooted and extensive windrows of plants accumulated along windward shores in some ponds in the study area. Widgeongrass nutlets attached to plants in windrows were attractive to pintails and they responded to the enhanced availability by feeding on nutlets from windrowed plants.

Wind also altered the availability of several invertebrate taxa in the ponds. Pupae of midges, ephydrids, and other diptera float to the waters surface just prior to emergence of adults. Newly emerged adults are extremely vulnerable to predation until their wings dry and they are capable of flight. Green-winged teal, northern shovelers, and northern pintails were observed to opportunistically modify their feeding habits to take advantage of this phenomenon and foraged on these insects as they concentrated on the waters surface. Wind made exploiting freshly emerged diptera adults even more profitable by concentrating them in windrows along windward shores. Ducks were observed to orient themselves on windward shores when foraging and one male pintail observed feeding in this manner had consumed nearly 27,000 freshly emerged midges. During periods of peak emergence of insects, it was not uncommon to find several hundred to several thousand newly emerged adults of midges and other diptera in the esophagi of all 3 waterfowl species. Only ruddy ducks were not observed to exploit food from the surface of the water.

The availability of several invertebrate foods was also enhanced by numerical abundance. Rotifers consumed by northern shovelers during this study may be the smallest foods consumed by North American waterfowl. Other filter-feeding anatids such as the pink-eared duck (Malacorhynchos membranaceus) can feed efficiently on foods as small as 110 um (Crome 1985); rotifers (Keratella) consumed by northern shovelers in this study averaged only about 100 um (Hutchinson 1967). Lamellae spacing can be adjusted to facilitate filtering different sized foods (Zweers 1980). However, adjusting lamellae gaps to filter extremely small foods would be costly and would not be worthwhile unless they were sufficiently abundant to offset the energetic expense. Although rotifer populations were not quantified during this study, they were often so abundant they discolored the water. Shoveler esophagi collected at such times frequently contained several million rotifers and one bird consumed over 55 million.

The 2 most abundant foods in the TLDD ponds were corixids and midges, both of which were abundant and constituted a readily available food source. Collectively, both taxa were observed to exceed 400,000 individuals/m^2 at certain sites within TLDD ponds. The importance of these 2 insects to all duck species was likely influenced by their abundance and availability.

Seasonal use of animal foods to satisfy protein requirements for optimal reproduction (Krapu 1979, 1981) and for feather molt (Heitmeyer 1988) was well illustrated by pintail usage of the study sites. Even though overall use by pintails of TLDD ponds was low, use increased during fall and spring (H. Coe, pers. comm.); times that corresponded well with a high seasonal requirement for animal foods in waterfowl diets (Krapu 1979, 1981, Heitmeyer 1988). Thus, the value of these areas to pintails and other dabbling ducks is strongly seasonal, occurring during time periods when animal proteins are required dietary items.

Conclusions

Evaporation ponds in the San Joaquin Valley will continue to attract large numbers of ducks, shorebirds, and related water birds because of abundant food production and the availability of large areas that provide sanctuary. Wetlands productive of invertebrates are well suited to ducks such as shovelers and ruddy ducks that consume large quantities of animal foods throughout their annual cycles. Additionally, evaporation ponds provide ready sources of protein-rich invertebrate foods that are required by dabbling ducks to satisfy protein requirements during reproduction and feather molt. However, questions raised at the Kesterson NWR concerning the effect of environmental contaminants on water birds, including waterfowl, need to be addressed. If contaminant issues can be resolved, these areas are productive and can provide valuable feeding and resting areas for waterfowl in California. Further, present management of the areas (e.g. maintaining water depths of about 1m) could be modified to make the areas more attractive to dabbling ducks by lowering water levels to enhance the availability of invertebrate foods (Euliss and Grodhaus 1987).

V. AQUATIC INVERTEBRATE ECOLOGY

Introduction

Wetland habitats for wintering waterfowl are deteriorating or being lost at a rapid pace (Tiner 1984). In California's Central Valley, 94% of the historical wetlands have been converted to cropland because of rich soils and desirable climate. In the southern San Joaquin Valley, about 250,000 ha of shallow wetlands in the Tulare Lake and Buena Vista Lake Basins have been converted into agricultural fields. Soils are saline and under traditional irrigation practices, salts concentrate in upper soil profiles and frequently limit plant growth. To reduce salt buildup and enhance agricultural production, farmers have installed subsurface irrigation drainage systems that wash excess salts from upper soil profiles and remove them from irrigated fields. Water from drained agricultural fields is high in salts and is known to contain heavy metals and other environmental contaminants (Presser and Barnes 1985).

Because of the effectiveness of subsurface drainage in reducing salt loads in upper soil profiles, an increasing number of farms are converting to this system, posing major disposal problems for the agricultural enterprise (Hanson 1982). In some locations, as much as 1 ha of evaporation pond may be required for every 5 ha of drained agricultural field (Hanson 1982). Approximately 1,300 ha of evaporation ponds are present in the Tulare Lake Basin (TLB) alone. Potentially, as much as 26,000 ha of new or restored wetlands could be developed from irrigation drainwater in the San Joaquin Valley (San Joaquin Valley Interagency Drainage Program 1979) if contaminant issues can be resolved. However, waterfowl managers know very little about the potential of these areas to provide a suitable environment for waterfowl. Although the salt load of these areas is high (up to 300 mmhos/cm^2 EC), preliminary evaluation indicates they have potential for wetland management (Ives et al. 1977).

Evaporation ponds attract waterfowl and an understanding of factors that contribute to the attractiveness of these areas will permit wise management of such ponds in the future. Evaporation ponds provide relatively large undisturbed areas for resting, but they support a low diversity of waterfowl food plants; most ponds are devoid of hydrophytes except widgeongrass (Ruppia maritima) and horned pondweed (Zanichellia palustris). Diversity of aquatic invertebrates is also poor but certain species are very abundant.

Recent studies have stressed the dietary value of aquatic invertebrates to waterfowl wintering in California (Beam and Gruenhagen 1980, Connelly and Chesemore 1980, Pederson and Pederson 1983, Euliss and Harris 1987, Miller 1987) and my preliminary examination indicated that aquatic invertebrates were a major component of the diets of waterfowl on evaporation ponds. This chapter assesses the standing biomass of aquatic invertebrates and environmental factors regulating their abundance in evaporation ponds in the TLB.

Study Area

This study was conducted on agricultural drainwater evaporation ponds operated by the Tulare Lake Drainage District (TLDD) in Kings and Kern Counties, California. The evaporation ponds studied consisted of 3 systems containing 4 or 10 interconnected ponds (18 ponds total). Water flow was unidirectional and the terminal pond in each system lacked an outlet. Water flowing into an evaporation pond system (EPS) was approximately 5-10 $mmhos/cm^2$ EC but increased in successive ponds due to evaporation and frequently exceeded 300 $mmhos/cm^2$ EC in terminal ponds. Average pond size was 65 ha with shallow water depths (< 1 m), gradually sloping sides, and flat bottoms.

Hypersaline waters of TLDD evaporation ponds supported abundant but species-poor assemblages of plants and animals. Widgeongrass was the most abundant hydrophyte, but formed dense stands only in ponds having approximately 40-70 mmhos/cm^2 EC; most ponds were devoid of hydrophytes. Levees were vegetated with salt tolerant species, including iodine bush (Allenrolfea occidentalis), fivehook (Bassia hyssopifolia), fog weed (Atriplex argentea), and red brome (Bromus rubens). Aquatic invertebrates were also poorly diverse with the vast majority of the biomass being represented by the salt marsh corixid (Trichocorixa reticulata) and a chironomid midge (Tanypus grodhausi). Brine flies (Ephydridae), copepods (Copepoda), and rotifers (Rotatoria) were also present and seasonally reached concentrations high enough to become important waterfowl foods.

Average annual rainfall in the TLB was approximately 21 cm and nearly all precipitation fell between November and March with long dry summers (Kahrl 1979). Maximum summer temperatures often reached 43 C and minimum temperatures of 0 C only lasted a few hours on the coldest winter days. Soil reaction varied from neutral to strongly alkaline, often limiting production of agricultural crops. More detailed descriptions of soils and climate of this area can be found in U.S. Fish and Wildlife Service (1961) and Kahrl (1979).

Materials and Methods

Standing biomass samples were collected from 9 separate evaporation ponds out of 18 total in 3 EPS's. Study ponds were selected on the basis of bird use and also divergence in salt loads. Sampling in 1982-83 began in October and continued through March, and in 1983-84 from September through March. Equally spaced transects were established in each study pond and standing crop samples were collected from them every 3 weeks. Because the dimensions of ponds varied, transects from different ponds were spaced different distances apart. In all cases, the length of each pond was subdivided so that equally spaced transects were established perpendicular to the longest dimension of the pond. The exact location where samples were collected was determined randomly on a microcomputer by generating sets of random numbers that represented the length of a given transect in meters. Samples of water column and benthic biota were obtained with samplers modified after the ones described by Swanson (1978a, 1978b). Benthic samples were cleaned by removing small sediment particles by sieving with a self-cleaning screen (0.5 mm mesh) (Swanson 1977a). Separate water column and benthic samples were collected from each of 10 transects per pond in 1982-83 (i.e. 20 samples per pond every 3 weeks; 10 benthic and 10 water column) and from 20 transects during 1983-84 (i.e. 40 samples per pond every 3 weeks; 20 benthic and 20 water column). Increasing sample size was necessary to reduce large sample variance.

Invertebrates were enumerated, sorted into taxonomic groupings, and identified from guides provided by Usinger (1956), Ward and Whipple (1959), Grodhaus (1967), Pennak (1978), Borror et al. (1981), and Merritt and Cummins (1984), dried to a constant weight at 55-60 C and weighed to the nearest mg on an analytical balance.

Water depth, temperature, electrical conductivity, turbidity, and dissolved oxygen were measured at each sample station during each sample period. Each parameter was measured at the waters surface, mid-depth, and at the bottom. Standard field meters were used to obtain all measurements except that secchi disc readings were used to index turbidity. Day length information was obtained from the National Weather Service in Bakersfield, California. Julian date variables were constructed for each sampling period to reflect the number of days past summer and winter solstices.

A General Linear Model (GLM) (SAS Inst. 1985) was employed to examine relationships of invertebrate dry weights and numerical counts to explanatory variables. A model was fit to the best relationship and residuals of significant models were plotted against other independent variables to explore additional relationships. Further, interactions among variables included in models and with other candidate variables were also examined until no further significant variables or interactions were detected. Standardized regression coefficients were used to evaluate the relative contribution of explanatory variables in models (Snedecor and Cochran 1980:357). Because salt loads in the TLDD evaporation ponds progressively increase and thus alter the habitat temporally, descriptive methods were used to construct regression and ANOVA models.

Independent variables collected at 3 water depths (electrical conductivity, water temperature, and dissolved oxygen) were analyzed as repeated measures (Milliken and Johnson 1984:351-362) to detect significant differences among depth strata. Huynh-Feldt probabilities (Huynh and Feldt 1970) were interpreted because the assumption of compound symmetry condition of covariance matrices was not appropriate. Electrical conductivity of mid-depth and at the bottom were averaged to produce a compound variable to explain occurrence of natural logs (ln) of dry weights and numerical count data for the salt marsh corixid.

A natural log transformation was used for invertebrate abundance and dry weight data because of highly skewed distributions. Invertebrates were not present in all samples and the data contained many zero values. Because natural logs of zero values cannot be taken, a small quantity was added to each observation before taking natural logs. The quantity added was equal to 1 X 10^{-p} (C. Harvey, pers. comm.), where p = the maximum number of digits (excluding 0) to the right of the decimal place observed in the untransformed data.

Results

Abiotic environmental variables

During both years combined, dissolved oxygen ($F = 50.97$, $P < 0.01$) and water temperature ($F = 8.36$, $P < 0.01$) decreased significantly with increasing depth whereas electrical conductivity ($F = 16.45$, $P < 0.01$) increased significantly (Table 2). Some differences were also apparent between the 2 years. During the 1982-83 field season, study ponds were significantly deeper ($t = 4.86$, $P < 0.01$), had lowered surface electrical conductivity values ($t = -7.29$, $P < 0.01$), and had cooler surface waters ($t = -2.00$, $P < 0.05$) than during 1983-84 (Table 3). However, no significant differences ($P > 0.05$) were observed for air temperatures between the 2 years.

The 1982-83 field season was marked by unseasonal flooding and was significantly wetter than the 1983-84 field season. This condition resulted in deeper pond levels, cooler surface waters, and lowered electrical

Table 2. Means and significant differences found among 3 water depth profiles for electrical conductivity, water temperature, and dissolved oxygen, agricultural drainwater evaporation ponds, Tulare Lake Drainage District, California, 1982-84.

	Water Depth		
Variable	Surface[a]	Middle	Bottom
Electrical conductivity	32.31*	40.74***	41.19
Dissolved oxygen	12.86***	12.17***	10.51
Water temperature	15.81*	15.09**	14.29

[a] Asterisks denote level of significance between depth and mean of deeper water column level: single (*) = $P < 0.01$; double (**) = $P < 0.001$; and triple (***) = $P < 0.0001$

Table 3. Comparisons of means of environmental variables collected from drainwater evaporation ponds, Tulare Lake Drainage District, California, 1982-84.

	1982-83			1983-84		
Variable[a]	N	Mean	Std Dev	N	Mean	Std Dev
DO (Top)	0			66	12.86	3.95
DO (Mid)	0			66	12.17	3.77
DO (Bot)	0			62	10.51	3.76
Turbidity	0			75	0.19	0.09
Temp (Top)**	50	14.74	5.25	75	16.52	5.56
Temp (Mid)	0			66	15.10	4.40
Temp (Bot)	0			62	14.29	3.72
Air temp	50	17.00	5.48	81	18.06	6.77
EC (Top)***	50	20.06	12.00	75	40.48	17.19
EC (Mid)	0			57	40.74	16.88
EC (Benthic)	0			57	41.19	17.28
Depth***	50	82.53	29.09	81	60.57	22.35

[a] Asterisks denote level of significance of difference between field seasons: double (**) = $P < 0.001$ and triple (***) = $P < 0.0001$

conductivity values of surface waters relative to 1983-84 (Table 3). These 3 variables may explain why models differed somewhat between years, as determined during subsequent analyses using field season as a separate explanatory variable.

Invertebrate standing crop

The salt marsh corixid and the midge, Tanypus grodhausi dominated the biomass of both water column and benthic communities, respectively. Collectively, they accounted for 96.3% of all dry weights observed with T. grodhausi (51.4%) forming the largest proportion (Table 4). Further, 99.2% and 74.2% of all samples collected contained the salt marsh corixid and T. grodhausi, respectively. Standing crops for the corixid ranged from zero to 2.830 g dry wt/m^2 ($\bar{x}$ = 0.354, SE = 0.05) with mean abundances ranging from zero to 11,857 individuals/m^2 ($\bar{x}$ = 1,487, SE = 217)(Table 5). Standing crop of mean dry weights for T. grodhausi ranged from zero to 9.353 g dry wt/m^2 ($\bar{x}$ = 0.405, SE = 0.105) with mean abundances ranging from zero to 45,278 individuals/m^2 ($\bar{x}$ = 3,026, SE = 536). Some ponds averaged 60,207 individuals/m^2 and nearly 34 g dry wt/m^2 of aquatic invertebrates when they were sampled with individual samples ranging much higher. Taking high sample values and high variances as realistic and as

Table 4. Biomass of individual invertebrate taxa collected from 132 habitat samplings, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

	Biomass g/m^2				
Taxa	RANGE	MEAN	SE	Percent	Percent Occurrence
Trichocorixa reticulata	0-2.830	0.354	0.050	44.9	99.2
Tanypus grodhausi	0-9.353	0.405	0.105	51.4	74.2
Copepoda	0-0.257	0.009	0.003	1.1	33.3
Cladocera	0-0.223	0.002	0.002	0.3	4.5
Ostracoda	0-0.156	0.001	0.001	0.1	2.3
Dytiscidae	0-1.093	0.008	0.008	1.0	0.8
Other animals and plants (9 items)	0-0.328	0.009	0.042	1.1	18.9

Table 5. Abundance of individual invertebrate taxa collected from 132 habitat samplings, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

	Individuals/m^2				
Taxa	RANGE	MEAN	SE	Percent	Percent Occurrence
Trichocorixa reticulata	0-11,856.940	1,487.298	217.007	32.4	99.2
Tanypus grodhausi	0-45,277.722	3,026.195	535.622	65.9	74.2
Copepoda	0-1,468.303	63.777	19.137	1.4	33.3
Cladocera	0-1,439.095	10.941	10.902	0.2	4.5
Ostracoda	0-64.534	0.512	0.489	tr[a]	2.3
Dytiscidae	0-1.246	0.009	0.009	tr	0.8
Other animals and plants (9 items)	0-100.520	2.064	0.840	tr	18.9

[a] tr = < 0.1%

indicating normal clumped distributions of aquatic invertebrates (Elliott 1977), as many as 400,000 individuals/m^2 and up to 77 g dry wt/m^2 were available at certain sites within ponds. Mean values were more conservative with slightly over 4,590 individuals/m^2 and 0.788 g dry wt/m^2 of biomass available from all taxa.

Factors regulating invertebrate populations

Development of meaningful regression models for certain aquatic invertebrates in TLDD evaporation ponds was hindered by a high proportion of zero observations of miscellaneous taxa and very small dry weights in samples. However, meaningful descriptive regression models were constructed for the salt marsh corixid and for the chironomid, *T. grodhausi*; these 2 taxa formed a large proportion of all invertebrate taxa sampled and were the most heavily utilized waterfowl foods from the TLDD evaporation ponds (Euliss, unpubl. data.).

Chironomid (*Tanypus grodhausi*)

A simple regression model containing benthic EC was developed that explained 60% of the variability in biomass of *T. grodhausi*. The form of the relationship was (Table 6):

Table 6. Regression model for natural logs of chironomid dry weights, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

Variable[a]	df	Regression Coefficient	SE	P value	Standardized Regression Coefficient
Intercept	1	-1.267	1.031	0.2245	
EC (Bottom)	1	-0.209	0.023	0.0001	-0.77

[a] R^2 for overall model= 0.60

Ln Dry Weight = -1.267 -0.209(Benthic EC).

Numerical abundance for _T_. _grodhausi_ was explained well (R^2 = 0.82) by pond position, field season, and julian date. There was a significant interaction between pond position in an EPS and julian date: the effect of julian date on chironomid abundance depended on the pond position and the effect of pond position on chironomid abundance depended on the day of the field season (Table 7).

The salt marsh corixid

The salt marsh corixid occurred in all but one sample but only 57 observations were available for analysis due to missing data for mid-depth and benthic EC, both of which when averaged were important in the regression model. Julian date and EC were the most important variables accounting for variability of biomass and abundance of corixids.

A regression model including julian date and EC was developed that significantly explained the biomass of corixids (R^2 = 0.86) in the TLDD study ponds (Table 8). Averaged values for mid-depth and benthic EC had a unimodal effect, reaching a maximum effect at 53.5 mmhos/cm^2 EC as revealed by the first derivative test on

Table 7. ANOVA model for natural logs of chironomid abundance, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

Variable[a]	df	Mean Square	P value
Intercept	1	0.415	0.0641
Pond location	8	3.245	0.0001
Field season	1	2.879	0.0034
Julian date	1	8.089	0.0001
Julian date x Pond location	8	2.166	0.0001

[a] R^2 for overall model = 0.82

Table 8. Regression model for natural logs of corixid dry weights, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

Variable[a]	df	Regression Coefficient	SE	P value	Standardized Regression Coefficient
Intercept	1	-2.058	1.390	0.1447	
Julian date	1	-0.061	0.004	0.0001	-0.77
EC	1	0.322	0.058	0.0001	1.67
EC^2	1	-0.003	0.001	0.0001	-1.38

[a] R^2 for overall model = 0.86

the model adjusted for the effect of julian date. The form of the overall relationship for biomass of corixids was (Table 8):

$$\text{Ln dry weight} = -2.058 + 0.322(\text{EC}) - 0.003(\text{EC})^2 - 0.061(\text{Julian date}).$$

Standardized regression coefficients computed for each variable in the model indicated that EC was more important than julian date. A one standard deviation change in EC would result in a 1.67 unit change in the ln of corixid dry weights, whereas, a change of the same magnitude in julian date would change ln of corixid dry weights by only 0.77.

The best model for abundance of corixids was similar to the model for biomass. This model was (Table 9):

$$\begin{aligned}\text{Ln counts} = 0.866 &+ 0.147(\text{EC})\\ &- 0.001(\text{EC})^2\\ &+ 0.078(\text{Julian date})\\ &- 0.001(\text{Julian date})^2\\ &+ 0.000004(\text{Julian date})^3\end{aligned}$$

All variables but Julian date were significant (Table 9).

Standardized regression coefficients computed for variables in the model indicated that julian date was a

Table 9. Regression model for natural logs of corixid abundance, Tulare Lake Drainage District drainwater evaporation ponds, California, 1982-84.

Variable[a]	df	Regression Coefficient	SE	P value	Standardized Regression Coefficient
Intercept	1	0.866	2.109	0.6832	
Julian date	1	0.078	0.059	0.1942	2.06
Julian date^2	1	-0.001	0.001	0.0231	-7.77
Julian date^3	1	0.000004	0.0000015	0.0080	5.06
EC	1	0.186	0.027	0.0001	1.57
EC^2	1	-0.001	0.0003	0.0003	-1.30

[a] R^2 for overall model = 0.87

more important factor regulating numbers of corixids than EC. A one standard deviation change in julian date would result in a 2.06 unit change in ln of corixid numbers whereas a change of the same magnitude for EC would result in only a 1.57 unit change in the ln of corixid numbers.

Discussion

Invertebrate standing crop

Dry weight and abundance data collected for aquatic invertebrates and plants indicated that the TLDD drainwater evaporation ponds contain a species poor assemblage of biota. The salt marsh corixid and the midge, Tanypus grodhausi, dominated the biomass of all animals and plants recovered from habitat samplings. Collectively, those 2 taxa accounted for 96.3% of the biomass and 98.3% of all individual organisms collected (Tables 4 and 5). Moreover, the salt marsh corixid and the midge, Tanypus grodhausi, were present in 99.2% and nearly 75% of all sample replicates. All other taxa accounted for < 1.2% of the biomass and < 1.5% of the individual organisms collected. Despite this low diversity, standing biomass was high with an average of over 9 g dry wt/m^2 of Tanypus grodhausi and about 3 g dry wt/m^2 of the salt marsh corixid available in certain ponds at optimal periods (Table 4). Kimerle and Anderson (1971) reported that the midge, *Glyptotendipes barbipes*, had a annual production rate of 162 g dry wt/m^2 in a sewage lagoon in Oregon. Their estimate is the highest rate of secondary production reported in the literature (Benke 1984) although their weekly standing biomass estimates ranged from 2.16-45.13 g dry wt/m^2 with a mean value of 19.1 g dry wt/m^2. Several other investigators have reported high secondary production rates of over 50 g dry wt/m^2 (Maitland and Hudspith 1974, Lindegaard and Jonasson 1979, Morgan et al. 1980) but those high rates of secondary annual production were largely due to high standing crops (> 10 g dry wt/m^2) rather than high turnover rates (Benke 1984). Such poor diversity and high secondary production characterize other artificially enriched man-made environments such as sewage lagoons (Kimerle and Anderson 1971).

Factors regulating invertebrate populations

Chironomid (*Tanypus grodhausi*)

A simple regression model was developed that accounted for 60% of the variation in ln of dry weight biomass of *Tanypus grodhausi*. Backflushing with estuarine water is the most frequently used method of controlling their populations in sewage stabilization lagoons in the San Francisco Bay area (G. Grodhaus, pers. comm.). The fact that different salt species (or other factors) may limit their populations on TLDD evaporation ponds is reasonable because of strong divergence in salt species composition between fresh and seawater (Wetzel 1983) with the former being noticeably low in NaCl, a dominant oceanic salt.

The regression model developed for abundance of Tanypus grodhausi abundance data differed from the one developed for biomass because none of the measured environmental variables accounted for much of the variability in the data set. Because classification variables were more important in the GLM, it is reasonable to conclude that either unmeasured variables or variables that were not measured accurately enough, influenced the abundance of chironomids to a greater extent than the variables considered in this study.

The salt marsh corixid

The best regression model produced to describe corixid biomass included an averaged mid-depth/benthic EC variable and julian date. Although this corixid is adapted to cope with hypersaline water (Usinger 1956), EC was the most important variable in the model in its negative quadratic form with most corixid biomass occurring at 53.5 mmhos/cm^2

but declining on either side of this optimal value. Julian date was also significant but its standardized regression coefficient indicated that it was less important than EC.

The regression model constructed for corixid abundance also contained EC and julian date variables. However, standardized regression coefficients indicated that julian date was more important than EC in explaining abundance data for the corixid. While the result may appear contradictory to the biomass model, the 2 are complimentary and provide more insight into the ecology of the corixid when considered simultaneously. Corixids first respond to julian date by initiating a cohort that is large in number but small in biomass. Later, as individuals grow in size and biomass increases, EC becomes more important than julian date because there is an optimal value of EC for this species. Both the biomass and abundance regression models indicate that osmotic and seasonal factors affect corixid populations.

Electrical conductivity values of mid-depth and those at the bottom produced the best EC variable when averaged. The averaged variable also best portrays the ecological scenario because this corixid spends most of its time in those strata; surface waters were also used but only briefly when these invertebrates surface for air.

Conclusions

Waterfowl food items in TLDD evaporation ponds came from species-poor assemblages of biota, dominated by animal foods. The only important waterfowl food plant observed in habitat samplings was widgeongrass. The quantities observed were small and this food was not an important dietary item of ducks within the ponds sampled for food items during this study. However, several ponds included within the TLDD evaporation pond systems supported stands of widgeongrass but none of these ponds were assessed for standing biomass in this study. The ponds that supported widgeongrass generally had conductivity values of 40-70 mmhos/cm^2 EC. Because the salt loads in TLDD evaporation ponds increase annually as each basin accumulates more salts, suitable habitat for widgeongrass should increase each year, but salt loads in ponds will probably exceed this species' tolerance range eventually. Invertebrates were more diverse than plants and were present over a greater range of salt concentrations. However, diversity was extremely low with 96.3% of the dry weight standing crop from a single species of corixid and a single species of chironomid.

Estimates for both biomass and invertebrate abundance indicated that TLDD evaporation ponds were productive of aquatic invertebrates sought out by waterfowl as food items. Standing biomass in sample replicates for the corixid ranged from 0 g dry wt/m^2 to 2.83 g dry wt/m^2 with abundances ranging from 0 individuals/m^2 to 11,857 individuals/m^2. Estimates for <u>Tanypus</u> <u>grodhausi</u> were similar with dry weights ranging from 0 to 9.353 g dry wt/m^2 and abundances ranging from 0 to 45,278 individuals/m^2. Collectively, > 60,000 individuals/m^2 and about 14 g dry wt/m^2 were available as food for ducks in certain pond locations during peak periods. The high standing crop of waterfowl foods, the large open configuration of evaporation ponds and the low level of human disturbance all contribute to high use by birds. Further, usage may intensify during certain times of the year when animal foods are required in waterfowl diets as a source of essential amino acids during the reproductive season (Krapu and Swanson 1975, Krapu 1979 and 1981) or during the feather molt (Heitmeyer 1988). Water entering TLDD evaporation ponds first percolates through upper soil profiles in fertile agricultural fields and is undoubtedly high in plant nutrients that contribute to the high standing crops observed in evaporation ponds.

The environment provided by TLDD evaporation ponds was found to be extremely harsh. Hypersaline waters of the evaporation ponds was a dominant factor influencing macroinvertebrate populations with a salt gradient starting at about 20% sea strength (10 mmhos/cm^2 EC) and extending to about 5 times more concentrated (300 mmhos/cm^2 EC) than sea water in terminal ponds. This harsh salt gradient likely restricted the number of pioneering taxa to a few specialists that have the osmotic capability. I feel this is the primary factor influencing the low biotic diversity observed during this study. All species observed were not present in all ponds in the salt gradient, except the salt marsh corixid, a species known for its tolerance to hypersaline waters in commercial salt evaporation facilities in the San Francisco Bay area (Usinger 1956). Because of the strong seasonal synchrony of most insects, it was not surprising that julian date as well as EC explained most of the variability observed in the dry weight data set ($R^2 = 0.86$). However, salt tolerance of salt marsh corixids may be limited. The model indicated greatest biomass at 53.5 mmhos/cm^2 EC (approximately sea strength) with decreases above and below that level. Despite the implications of the model, corixids tolerated salt loads well in excess of sea strength and were commonly observed in ponds at EC's in excess of 300 mmhos/cm^2. Although data was not collected from ponds that exceeded about 70 mmhos/cm^2 EC, massive windrows of carcasses, some 20m x 5m x 0.2m were observed along windward shores following apparently normal population crashes. Although corixids were important foods to waterfowl during this study, windrows of the dead insects were never observed to be utilized by ducks.

Environmental parameters regulating the abundance of chironomids were far less clear than for corixids. Significant regression models were developed for biomass and for abundance. The regression model using only benthic EC accounted for 60% of the variation in dry weight biomass of T. grodhausi and was expected because this species is sensitive to salt concentrations. The importance of julian date to the abundance model was anticipated because of the marked seasonality of most aquatic invertebrates, but pond position and field season aided very little in interpretation. Other environmental parameters may be reflected in these classification variables that produced a significant GLM but aided very little in detecting the specific environmental parameters involved. Thus, other environmental parameters that influence chironomid populations in TLDD evaporation ponds may have existed but they were either not measured or were not measured precisely enough for their effect to be detected.

Concentrations of specific salts or salt species ratios may offer potential for subsequent research on factors regulating standing crops of T. grodhausi. This species is controlled (removed) in sewage lagoons by flushing with NaCl-rich estuarine water (G. Grodhaus, pers. comm.). During this study, T. grodhausi was observed in ponds having salt concentrations higher than those used to control their populations elsewhere. The TLDD evaporation ponds and other inland water bodies are lower in NaCl than seawater but have much higher concentrations of calcium, magnesium, and potassium salts (Wetzel 1983). The interactions of these salts on survival and production of chironomids may have had a substantial regulatory effect on populations but that interaction was beyond the scope of this study.

TLDD evaporation ponds support large standing crops of invertebrates important as waterfowl foods. In addition, saline tolerant widgeongrass grew profusely in some ponds, presumably where salt loads were optimal for this species. Evaporation ponds continually accumulate salts and the communities they support will show a gradual successional change to more hypersaline forms as EPS's age. Although age of pond was not a significant factor influencing biota in this study, the ponds were studied for only 2 years. If markedly different biotic communities occur in succession as salinity increases, different kinds of water birds may be attracted to the ponds. Availability of potential foods to foraging birds may be quite different than the availability of organisms in the present community, which may strongly affect the attractiveness of these drainwater ponds to water birds. Nutrient-rich waters from drained agricultural fields will enhance productivity, regardless of successional state and large open expanses of water will continue to provide sanctuary and refuge from human disturbance.

VI. BODY CONDITION AND NUTRITION OF WATERFOWL

Introduction

The status of nutrient reserves in waterfowl has received much attention in relation to the use of body reserves for egg production on northern breeding marshes (Korschgen 1977, Ankney and MacInnes 1978, Krapu 1979, Raveling 1979a, Raveling 1979b, Krapu 1981, Ankney 1984). Less attention has been focused on the role of body reserves on survival and fitness of waterfowl on wintering or migration areas. Prior to the 1980's, wintering waterfowl were largely considered to be vegetarians (Cottam 1939, Martin and Uhler 1939, and others). Grains and other vegetable foods are rich in carbohydrates that easily convert to body fats for insulation and energy stores. However, recent studies have demonstrated that aquatic invertebrates constitute a substantial portion of the diet of ducks wintering in California (Beam and Gruenhagen 1980, Connelly and Chesemore 1980, Pederson and Pederson 1983, Euliss and Harris 1987, Miller 1987). Invertebrates are high in protein and cannot be converted to body fats as efficiently as most plant foods. However, invertebrates are rich in proteins that contain dietary essential amino acids. Protein is important to waterfowl during reproduction for synthesis of egg proteins (Krapu

1979, 1981). Some protein is also required during winter to supply amino acids for feather molt (Heitmeyer 1988). However, consumption of invertebrates during winter in California seems far in excess of that needed to provide amino acids for feather replacement.

Diets of waterfowl wintering in California vary considerably according to species and time of year. In the southern end of the Central Valley in the immediate vicinity of the Tulare Lake Basin (TLB), northern pintails consume mostly plant seeds while feeding in seasonally flooded wetlands with less than 35% of the diet being composed of animal foods (Euliss and Harris 1987). In that study, northern pintails showed strong seasonal usage patterns with invertebrates significantly increasing in the diet during late winter and early spring. In contrast to northern pintails, ruddy ducks and northern shovelers feed extensively on aquatic invertebrates throughout the winter. In a concurrent investigation of waterfowl diets on agricultural drainwater evaporation ponds in the TLB, I found that over 90% of the diets of northern shovelers and ruddy ducks were composed of animal foods whereas diets of northern pintails contained approximately equal portions of plant and animal foods (Euliss, unpubl. data).

Agricultural developments, while enhancing the abundance of carbohydrate-rich plant foods, have decreased acreages of wetlands and abundance of natural foods such as aquatic invertebrates and native plant seeds. Levees and other flood control devices have eliminated spring flooding that historically inundated areas of uplands and hence exposed seed crops and terrestrial invertebrates to migratory birds during spring migration. Thus, both the mixture of available foods and their temporal availability have been altered by agricultural development. This change may be especially important in the Central Valley of California where only 6% of the original wetlands remain and 60% of the waterfowl in the Pacific Flyway winter (U. S. Fish and Wildlife Service 1978).

This study was conceived to determine trends in body composition of waterfowl wintering in the TLB in relation to the nutritional composition of foods available to and consumed by waterfowl from agricultural drainwater evaporation ponds and other surrounding habitats. I believe this approach provides an evaluation of these newly created wetlands on the basis of (food habits) waterfowl energetics in winter and nutrition rather than on traditional evaluations of habitat quality based on bird use. Evaluations based on bird use may fall short of providing adequate evaluations because birds require a variety of habitat types in winter (Tamisier 78/79), each of which are used at different times of the day or night and for entirely different reasons. Thus, evaluations based strictly on duck use may fail to address critical aspects of waterfowl ecology.

Study Area

This study was conducted on drainwater evaporation pond systems (EPS) operated by the Tulare Lake Drainage District (TLDD) in Kings and Kern Counties, California. The evaporation ponds I examined were first built in 1980 and consisted of 3 EPS's that collectively contained 18 pond units. Average pond size was about 65 ha. Individual ponds were generally < 1 m deep with gradually sloping sides and flat bottoms. Drainwater entering an EPS was generally around 5-10 mmhos/cm^2 EC. However, high evaporation rates resulted in conductivity in excess of 300 mmhos/cm^2 EC.

Diversity of aquatic plant and invertebrate foods was low in comparison to surrounding freshwater wetlands but those taxa present were often highly abundant. Corixids and chironomid larvae comprised the bulk of the invertebrate foods available during most time frames and comprised over 97% of the available dry weight biomass (Euliss, unpubl. data). Additionally, copepods, rotifers, and brine fly larvae (Ephydridae) were seasonally abundant and were utilized by ducks. Widgeongrass (_Ruppia maritima_) and horned pondweed (_Zanichellia palustris_) were occasionally observed but were not very abundant. Average annual rainfall was about 21 cm and nearly all precipitation fell between November and March with long dry summers (Kahrl 1979). Agriculture is the primary industry in the basin. Major crops include cotton, barley, wheat, safflower, alfalfa, and grapes. Arid conditions necessitate that nearly all crops be irrigated.

Materials and Methods

During September through March, 1983-84, northern pintails (Anas acuta), northern shovelers (A. clypeata), and ruddy ducks (Oxyura jamaicensis) were collected by shooting on evaporation ponds, and from waterfowl hunters on the Kern National Wildlife Refuge (NWR). Food habits of waterfowl wintering on evaporation ponds and the temporal availability of waterfowl foods produced in evaporation ponds were determined concurrently in separate investigations of food habits and standing crop of waterfowl foods produced in evaporation ponds. Birds were grouped into 3 time periods: (1) fall migration (September and October), (2) winter (November - January), and (3) spring migration (February - March).

Specimens were prepared for proximate analyses by plucking feathers from partially frozen carcasses; remiges and rectrices were cut flush with the skin with shears. The bills and feet were removed and the carcass was weighed prior to sectioning into pieces and grinding in a commercial meat grinder. Ground material was reweighed, placed in a blender along with a known quantity of water, and blended to a consistent homogenate. Duplicate 20 g samples of homogenate from each bird were analyzed by the Department of Agricultural Chemistry, Oregon State University. Fat content was determined by ether extraction over a 22 hour period in a Soxlet apparatus and Kjeldahl nitrogen was determined and converted into crude protein by multiplying by 6.25 (Horowitz 1970: 16, 127). Proximate composition of waterfowl food items was obtained from published analyses and were used to estimate the nutritional composition of waterfowl diets on evaporation ponds. Nitrogen Free Extract (NFE), protein, and fat was taken as a proportion of aggregate percent dry weight (Swanson et al. 1974a) of individuals food items prior to averaging to get a mean contribution for each nutrient during each time period. The use of mean percents avoids the bias that results when a small number of birds consume large a quantity of an abnormal food. The difference between the collective proportions of NFE, protein, and fat represent water, ash, and fiber.

A condition index based on wet weights of fat was used to examine for trends within and among duck species. The index was used because percentages of fat and protein are interdependent and because it compensated for structural size variations among birds (Johnson et al. 1985). Although dry weights are normally preferred, there is little variation in water content on a fat-free basis (Raveling 1979a, Ringelman and Szymczak 1985).

Protein weight in grams was used to assess influence of explanatory variables within duck species (Miller 1985). Because of great size variation among the 3 waterfowl species examined, protein weights were used only for comparisons within species. Comparisons among species were based on the condition index.

Proximate data on waterfowl carcasses were analyzed using SAS software (SAS Inst. 1985). Frequency distributions based on weight of carcass, fat, condition index, and protein were plotted against normal distribution curves and tested for normality using the Kolmogorov-Smirnov Goodness of fit test (Zar 1974:54-56) and were similar to a normal distribution ($P > 0.05$). Hence, untransformed data were used for further analysis. A General Linear Model (GLM) was used to evaluate the effect of explanatory variables: species, sex, age, time period, and all possible interaction variables on weights of carcass, protein, and on the condition index of Johnson et al. (1985). Because of unbalanced ANOVA cells, least-squares estimates of marginal means (LSM's) were used to estimate class means and to locate differences in the explanatory variables (SAS Inst. 1985).

Results

Ruddy Ducks

Carcass weights

Overall, carcass weights of ruddy ducks of the various sex and age classes were significantly different (F = 5.61, $P < 0.01$) during the 3 time periods (Table 10). Carcass weights in winter (November - January) were significantly higher than weights observed during spring (February - March) ($P < 0.01$) but were similar ($P > 0.06$) during fall (September - October). The overall effect of time period was significant in the model (F = 3.99, $P < 0.05$). Age of bird also had a significant effect (F = 18.98, $P < 0.01$) on weight; immature birds of both sexes were lighter than adults of either sex class.

Protein

Protein content of ruddy duck carcasses varied among the various sex and age classes (Table 10) and the overall GLM was significant (F = 6.80, $P < 0.01$). Age of bird (F = 26.22, $P < 0.01$), the interaction of sex x age (F = 13.3, $P < 0.01$) and the interactions of time period x sex x age (F = 3.41, $P < 0.05$) were all significant

Table 10. Mean weight (sd) of whole carcasses, protein and fat of ruddy ducks collected from Tulare Lake Drainage District evaporation ponds, 1983-84, Kings and Kern Counties, California.

		PERIOD DURING WINTER		
SEX/AGE	Constituent	SEP-OCT gms	NOV-JAN gms	FEB-MAR gms
Males				
	N	4	19	12
Adult	Carcass	532(28)	563(80)	531(55)
	Protein	92(4)	95(11)	104(10)
	Fat	17(15)	72(56)	47(33)
	N	8	14	1
Immatures	Carcass	489(66)	479(58)	419
	Protein	76(7)	86(8)	67
	Fat	22(31)	32(24)	26
Females				
	N	5	18	6
Adult	Carcass	532(61)	542(57)	439(32)
	Protein	88(6)	86(8)	93(7)
	Fat	39(39)	77(38)	25(15)
	N	7	8	6
Immatures	Carcass	443(31)	467(36)	451(19)
	Protein	82(14)	83(6)	91(5)
	Fat	10(9)	37(22)	35(19)

explanatory variables. Adults had significantly higher ($P < 0.01$) protein weights than immatures, probably reflecting larger body sizes of adults rather than specific age related phenomenon. Similarly, there were significant time period x sex interactions with males collected during winter containing more protein than males during fall ($P < 0.05$) or females during winter ($P < 0.05$). Likewise, females in spring had more protein than either males in fall ($P < 0.05$) or females in winter ($P < 0.05$). The time period x sex x age interaction was even more complicated with 30 of the 66 possible combinations being significant (Table 11). The most striking difference found was that adult males in spring contained significantly more protein (103.5 gms) than all other time period x sex x age combinations (66.5-94.8 gms) ($P < 0.01$ to $P < 0.05$) (Table 10, 11). Conversely, immature males in spring contained the least protein (66.5 gms) of all time period x sex x age combinations except in fall when immature males and immature females had the same ($P > 0.30$) protein content (Table 11).

Fat

Wet weights of fat, like those of carcass weights, appeared heaviest in winter although weights of the various sex and age classes varied considerably (Table

Table 11. Significant differences found for grams of protein among time period x sex x age combinations in ruddy ducks collected from drainwater evaporation ponds in the Tulare Lake Basin, California, 1983-84.

		Significant differences found for combinations[a]										
Combination	id	2	3	4	5	6	7	8	9	10	11	12
Period[b] I												
Males												
Adults	1	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns
Immatures	2		*	ns	*	*	*	ns	*	ns	*	*
Females												
Adults	3			ns	ns	ns	ns	ns	*	*	ns	ns
Immatures	4				*	ns	ns	ns	*	ns	*	ns
Period II												
Males												
Adults	5					*	*	*	*	*	ns	ns
Immatures	6						ns	ns	*	*	ns	ns
Females												
Adults	7							ns	*	*	ns	ns
Immatures	8								*	ns	*	ns
Period III												
Males												
Adults	9									*	*	*
Immatures	10										*	*
Females												
Adults	11											ns
Immatures	12											

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[a] * indicates significant differences of $P < 0.05$

[b] Period I = Sep - Oct; Period II = Nov - Jan; Period III = Feb - Mar

10). The overall GLM for condition index was significant ($F = 3.84$, $P < 0.01$) with time period being the only significant ($F = 8.22$, $P < 0.01$) variable in the model. Ruddy ducks were significantly fatter during winter than during other time periods ($P < 0.01$).

Northern Shovelers

Carcass weights

Carcass weights of northern shovelers were variable but no clear pattern could be discerned (Table 12). The overall GLM for carcass weight was significant ($F = 4.27$, $P < 0.01$), but none of the explanatory variables were significant. Sex approached significance ($F = 3.90$, $P = 0.052$) with males weighing slightly more than females.

Protein

Protein weight of carcasses of northern shovelers indicated that males had more protein than females (Table 12). The overall GLM was significant ($F = 8.56$, $P < 0.01$) and sex ($F = 16.03$, $P < 0.01$) was the only significant explanatory variable in the model; males contained significantly more protein than females ($P < 0.01$), probably reflecting the larger body size of males.

Table 12. Mean weight (sd) of whole carcasses, protein and fat of northern shovelers collected from Tulare Lake Drainage District evaporation ponds, 1983-84, Kings and Kern Counties, California.

SEX/AGE	Constituent	PERIOD DURING WINTER SEP-OCT gms	 NOV-JAN gms	 FEB-MAR gms
Males				
	N	12	14	12
Adult	Carcass	621(57)	605(42)	605(48)
	Protein	91(9)	98(4)	95(8)
	Fat	25(19)	34(20)	51(29)
	N	0	6	0
Immatures	Carcass		604(33)	
	Protein		101(4)	
	Fat		27(17)	
Females				
	N	2	5	2
Adult	Carcass	595(17)	521(61)	557(1)
	Protein	80(9)	83(3)	88(4)
	Fat	29(19)	26(14)	82(6)
	N	10	15	7
Immatures	Carcass	576(43)	542(57)	548(28)
	Protein	85(8)	85(7)	85(4)
	Fat	24(12)	37(23)	60(19)

Fat

Proximate analyses of northern shovelers indicated that fat content increased temporally (Table 12). The GLM using the condition index based on fat was significant (F = 5.21, P < 0.01) with time period (F = 13.88, P < 0.01) and sex (F = 6.85, P < 0.01) both affecting fatness of birds. Fat content steadily increased seasonally with all 3 time periods significantly different from each other. Females had significantly more fat than males.

Northern Pintails

Carcass weights

Carcass weights of adult northern pintails tended to decline seasonally with males weighing more than females during all time periods (Table 13). The GLM used for northern pintails differed from the one used for ruddy ducks and northern shovelers because only adult birds were included in the sample; suboptimal production by pintails resulted in few immatures in the population of wintering birds. The overall GLM was significant (F = 15.05, P < 0.01) with sex (F = 36.25, P < 0.01) and time period (F = 6.58, P < 0.01) significantly influencing carcass weights. Adult males (983 ± 14 gms) were significantly heavier than

Table 13. Mean weight (sd) of whole carcasses, protein and fat of northern pintails collected from Tulare Lake Drainage District evaporation ponds, 1983-84, Kings and Kern Counties, California.

		PERIOD DURING WINTER		
SEX/AGE	Constituent	SEP-OCT gms	NOV-JAN gms	FEB-MAR gms
Males				
	N	10	16	15
Adult	Carcass	1085(63)	976(81)	889(76)
	Protein	168(13)	162(15)	197(20)
	Fat	188(72)	139(70)	76(57)
	N	0	0	0
Immatures	Carcass			
	Protein			
	Fat			
Females				
	N	2	5	7
Adult	Carcass	809(179)	835(107)	754(124)
	Protein	130(4)	139(21)	139(17)
	Fat	140(54)	144(65)	90(58)
	N	0	0	0
Immatures	Carcass			
	Protein			
	Fat			

females (799 ± 27 gms). Carcasses of both sexes were significantly lighter in the spring than in the winter and fall. Fall and winter carcass weights were not different for both males and females.

Protein

Weight of protein in adult northern pintails differed between sexes (Table 13) and the GLM model was significant ($F = 5.12$, $P < 0.01$) with sex ($F = 22.97$, $P < 0.01$) being the only significant explanatory variable. As occurred for shovelers, larger bodied males contained significantly more protein than females ($P < 0.01$).

Fat

Fat weights of northern pintails paralleled the trend observed for carcass weights, with birds steadily losing fat after their arrival in the fall until the spring migration period (Table 13) and the overall GLM model was significant ($F = 2.45$, $P < 0.05$), however none of the explanatory variables were significant.

Species Differences in Condition Index

Using only adult birds, a GLM was performed to evaluate the affect of species, sex, and time period of collection on fat content as measured with the condition index. The overall model was significant ($F = 4.64$, $P < 0.01$) with species ($F = 13.80$, $P < 0.01$) and species x period interaction ($F = 5.27$, $P < 0.01$) being the only 2 significant variables. Condition indices of ruddy ducks and northern shovelers were similar ($P > 0.05$) and both were significantly lower than of northern pintails. Several species x time period interactions were also significant (Table 14). Northern pintails had more fat than northern shovelers during fall and winter, but not ($P > 0.05$) during spring when fat content of pintails decreased and fat content of northern shovelers increased. Pintails also had more fat than ruddy ducks during fall, but the 2 species were not significantly different ($P > 0.05$) during the winter and spring periods.

Nutritional Composition of Diet on Evaporation Ponds

Ruddy ducks

Ruddy ducks fed heavily on aquatic invertebrates (84-92%) from drainwater evaporation ponds and the seasonal

Table 14. Significant differences found among condition indices of species x time period combinations for ducks collected in the Tulare Lake Basin, California, 1983-84.

		Significant differences found for combinations[a]							
Combination	id	2	3	4	5	6	7	8	9
Ruddy ducks									
Period[b] I	1	*	ns	ns	ns	ns	*	*	*
Period II	2		*	*	*	ns	ns	ns	ns
Period III	3			ns	ns	ns	*	*	ns
Northern shovelers									
Period I	4				ns	*	*	*	*
Period II	5					*	*	*	*
Period III	6						ns	ns	ns
Northern pintails									
Period I	7							ns	*
Period II	8								*
Period III	9								

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[a] * indicates significant differences of $P < 0.05$

[b] Period I = Sep - Oct; Period II = Nov - Jan; Period III = Feb - Mar

reliance on specific foods varied seasonally (Figure 4, Euliss unpubl. data). Chironomids increased in the diet seasonally (from 25.4-77.8%) while corixids decreased (56.3-6.5%). However, when food items were expressed in nutritional terms from published analyses (Table 15) the composition of the diet changed little among the 3 periods, < 60% was protein, about 4% was fat, and 5-9% was NFE.

Northern shovelers

Northern shovelers also foraged heavily on invertebrate foods (98-99%) from evaporation ponds and like ruddy ducks, there were significant changes in the usage of specific food items, seasonally (Figure 5, Euliss unpubl. data). Corixids formed < 75% of the diet in the fall and winter; copepods (42%), and rotifers (37%) formed the bulk of the diet in spring. Nutrient composition of the diet changed little among the 3 periods, about 60% was protein, about 4% was fat and about 7% was NFE, and NFE decreased to about 1% in spring.

Northern pintails

In contrast to ruddy ducks and northern shovelers, northern pintails fed more on plant seeds, although there

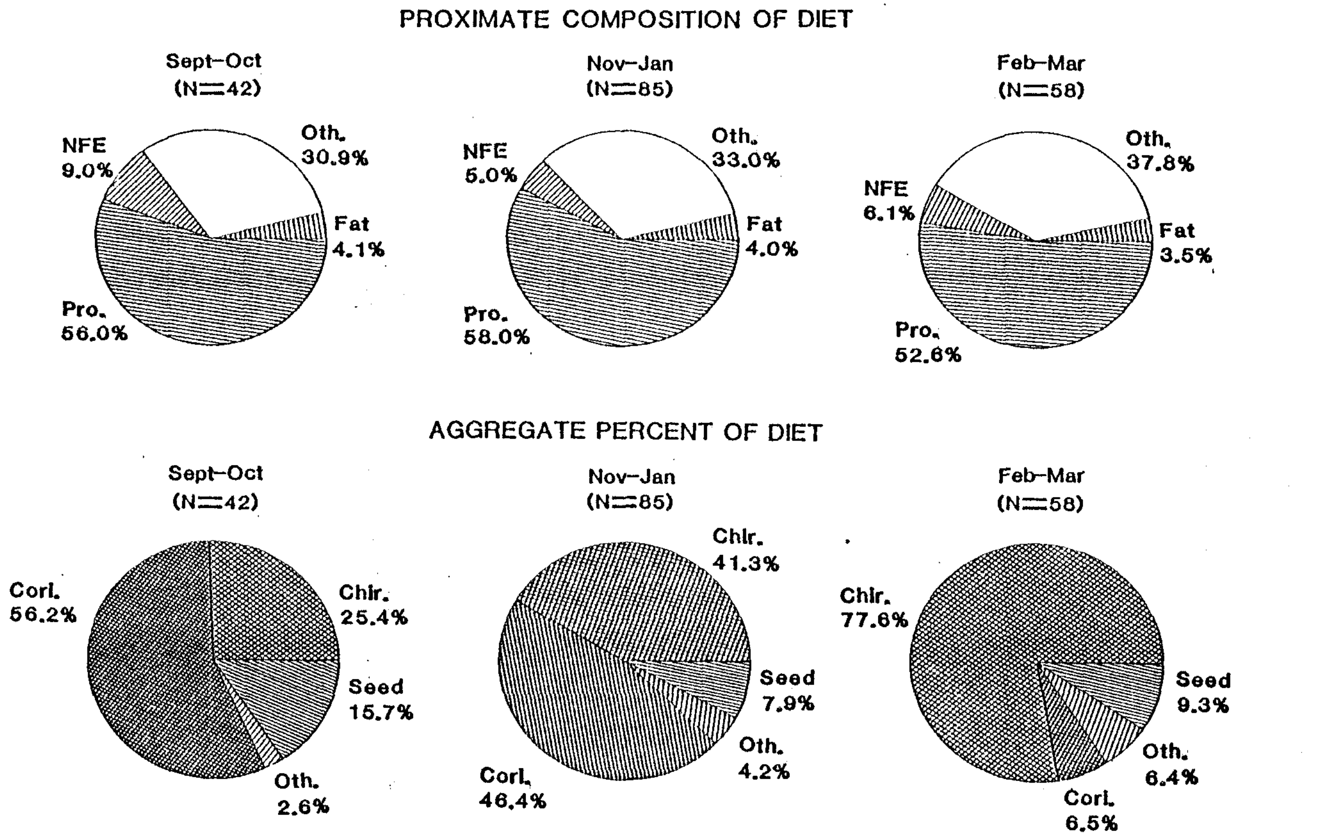

Figure 4. Aggregate percents and proximate composition of the diets of ruddy ducks on agricultural drainwater evaporation ponds, Kings and Kern Counties, California, 1982-84.

Table 15. Nutritional composition of waterfowl foods.

	Proximate composition (%)						
Food item	Pro	Fat	NFE	Fiber	Ash	Kcal/gm	Authority
Plant							
Echinochloa crusgalli	12.1	3.4	42.7	26.2	6.8		Spinner and Bishop 1950
Echinochloa crusgalli	9.7	1.4	40.5	22.2	26.2		Bardwell et al. 1962
Echinochloa crusgalli						4.422	Kendeigh and West 1965
Echinochloa crusgalli						4.695	Cummins and Wuycheck 1971
Barley	13.7	2.1		4.7	2.2		Sugden 1971
Wheat	15.4	1.9		3.6	2.1		Sugden 1971
Wheat	18.5	1.9	73.7	4.1		3.780	Sugden 1973
Fall rye	13.7	2.1		3.7	1.8		Sugden 1971
Terrestrial grasses						4.357	Cummins and Wuycheck 1971
Upland plant seeds						4.539	Cummins and Wuycheck 1971
Grand mean	13.9	2.1	52.3	10.7	7.8	4.359	
Animal							
Cladocera						4.955[a]	Cummins and Wuycheck 1971
Cladocera	31.7	2.1	1.7	13.8	50.7	2.630	Sugden 1973
Copepoda						5.741[a]	Cummins and Wuycheck 1971
Corixidae	71.1	5.0	0.8	18.4	4.7	5.109	Reinecke and Owen 1980
Corixidae	64.4[a]					5.122	Driver et al. 1974
Chironomidae larvae						5.209[a]	Cummins and Wuycheck 1971
Chironomidae larvae						5.410[a]	Driver et al. 1974
Aquatic invertebrates						4.229	Cummins and Wuycheck 1971
Grand mean	55.7	3.6	1.3	16.1	27.7[b]	4.880	

[a] Represents mean values given for several species.

[b] Value inflated due to high ash content of Cladocera.

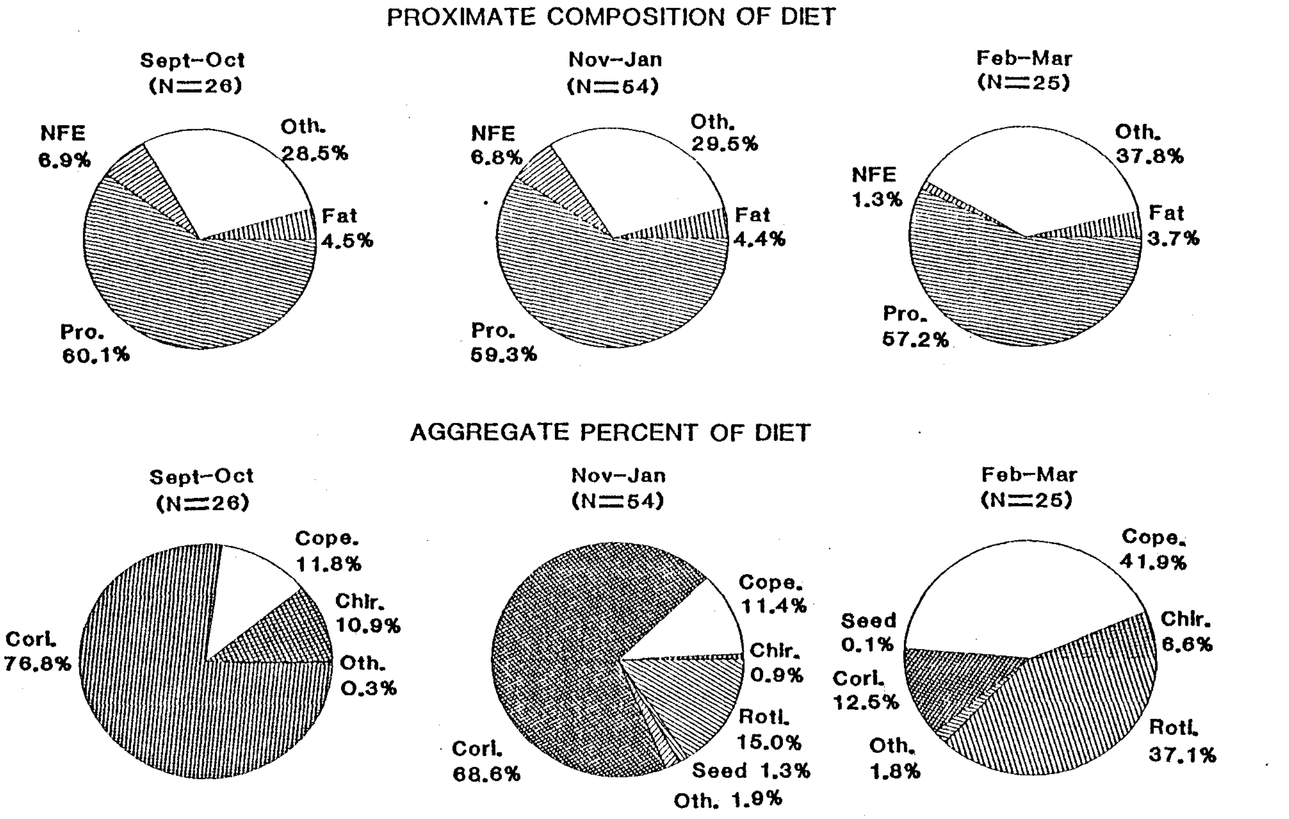

Figure 5. Aggregate percents and proximate composition of the diets of northern shovelers on agricultural drainwater evaporation ponds, Kings and Kern Counties, California, 1982-84.

was significant variation in the diet with invertebrates significantly increasing during fall and spring (from < 30-57%) (Figure 6, Euliss unpubl. data). My estimates of the proximate composition of the diets of northern pintails also differed from the patterns observed for other duck species with different nutrients varying in importance among time periods. NFE was a primary component of the diet during all time frames (23-52%) although it appeared to form a larger proportion during winter and protein content was highest during fall (26%) and spring (38%).

Discussion

Carcass Composition

Ruddy ducks

Proximate composition of ruddy duck carcasses differed from the patterns observed for northern pintails and northern shovelers, probably reflecting unique requirements of their aquatic life styles and for a reproductive cycle that differs from that of most North American waterfowl (Bellrose 1978). Most notable differences were patterns of lipid accumulation and a significant increase in the protein content of adult males during spring.

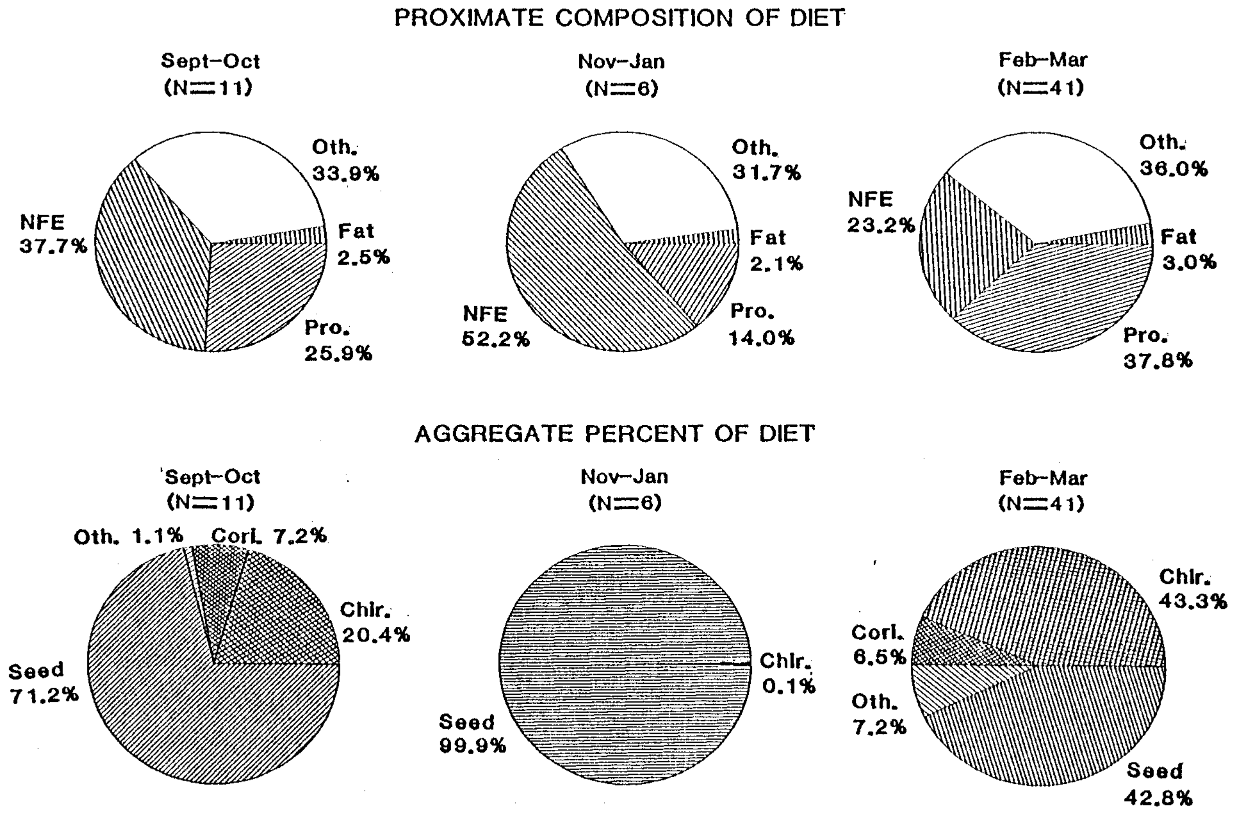

Figure 6. Aggregate percents and proximate composition of the diets of northern pintails on agricultural drainwater evaporation ponds, Kings and Kern Counties, California, 1982-84.

Carcass weights of ruddy ducks were significantly higher in winter relative to other time frames. As expected, weights of adults and immature birds were significantly different with adults outweighing immatures. That difference, however, was most likely related to structural size differences of adult versus immature birds rather than specific age related differences. Lipids were by far the most variable body component but only time period was identified as a significant variable in the GLM for condition index. In that analysis, birds of all sex and age groups, were in significantly better condition during winter than during other time periods. Although temperatures are mild during winter in California relative to many wintering areas, the value of increased insulation provided by elevated endogenous lipids may be of great value to ruddy ducks because they are almost exclusively aquatic (Bellrose 1978). Further, ruddy ducks are the most northerly distributed of the tropical stiff-tailed ducks (oxyurini). The accumulation of insulative fat during winter may enable the ruddy duck to winter further north than other oxyurids.

Protein content of ruddy ducks revealed an interesting pattern that was not observed in either northern pintails or northern shovelers. When all sex and age classes were combined, there were no significant changes in protein content of ruddy ducks across seasons. However, the overall GLM revealed that age of bird as well as interactions of sex x age and time period x sex x age were significant variables explaining trends in protein weights. The differences of sex and age were observed with the larger bodied males and adults containing more protein than smaller bodied females or immatures. As with weights of the carcass and fat content, those differences probably reflect size differences of the different sex and age classes rather than actual sex or age related differences. However, no comparable condition indices have been developed for protein that allow an investigator to account for size variation among individuals.

The interaction term of time period x sex x age on protein weights of ruddy ducks was complicated with 30 out of 66 possible combinations (45.5%) being significant (Table 12). Excluding the 1 immature male in spring, 12 of 23 significant differences (52%) referred to adult males in spring. Eleven other differences were also observed (Table 12). In all 12 cases, adult males in spring contained more protein than other sex x age x time period combinations.

The ecological relevance of adult males increasing protein may relate to feather molt, hypertrophy of musculature for spring migration and/or for courtship displays. Male ruddy ducks undergo a complete body molt in February and March (Bellrose 1978) and the protein requirements of feather development are high (Heitmeyer 1988). However, the buildup of endogenous protein to satisfy protein demands of the molt have not been demonstrated for other species of molting waterfowl (Newton 1968, Ankney 1979, Raveling 1979a, Ankney 1984, Heitmeyer 1985, Mainguy and Thomas 1985, Heitmeyer 1988) nor was it observed for other duck species in this investigation.

Although not studied in detail, many biologists feel the ruddy duck is sedentary during winter and may need well developed breast muscles only during migration. Ruddy ducks are seldom observed flying (Bellrose 1978) and hypertrophy of muscle mass to facilitate spring migration may partially explain the significant increase in protein by adult males in the spring just prior to migration. However, neither adult nor immature females gained protein content from the winter to the spring period, yet they migrate along with the males.

Male ruddy ducks have elaborate, vigorous, repeated courtship displays consisting of rapid head bobbing while holding the tail erect and running rushes across the waters surface (Johnsgard 1965). These displays contrast with the normal placid activity patterns of ruddy ducks and may require hypertrophy of some muscles during the courtship phase of reproduction. Perhaps the increased protein content I observed on the wintering grounds during spring was related to courtship activities during and just after spring migration. However, only male ruddy ducks of the species of waterfowl so far investigated undergo a complete body molt in spring and that may also be related to the increase in protein content I observed.

Northern shovelers

Proximate carcass composition of northern shovelers also differed from the other duck species examined. Although none of the explanatory variables explained carcass weights, the GLM based on the condition index of Johnson et al. (1985) indicated that both time period and sex affected the observed patterns of lipid accumulation. Fat steadily increased from fall to spring in both males and females, and females had more fat than males during all time frames. The unusually protracted spring migration of shovelers (Bellrose 1978) may represent an adaptation to exploit invertebrate abundance during late winter and early spring on wintering and staging areas.

The seasonal increase in fat by both sex and age classes of northern shovelers is likely a result of enhanced abundance and fat content of food items. Zooplankton populations escalate in late winter and early spring in response to increasing ambient temperatures and blooms of phytoplankton (Wetzel 1983). In response to the elevated temperature and food availability, the clutch size and the rate of egg production increase in zooplankton such as Cladocera, Copepoda, and Rotatoria (Wetzel 1983). Lipid levels in zooplankton would increase because of the lipid content of the eggs (Cummins and Wuycheck 1971). Dietary fat converts to endogenous fat more efficiently than from dietary carbohydrates; conversion from dietary protein to endogenous fats is least efficient. Over 90% of the diet of shovelers was animal matter and hence less than 7% of the diet was carbohydrate (Euliss, unpubl. data). A protracted spring migration by northern shovelers would maximize access to invertebrates that are at their seasonal high in number and fat content to facilitate spring lipogenesis.

The higher fat content of females than males is likely related to biological events of reproduction. While endogenous fats are insufficient to satisfy all the lipid requirements of a full clutch of eggs in small bodied waterfowl (Afton 1979, Drobney 1980), they would be of value in satisfying partial requirements and the storage of some endogenous fats would offset the exogenous requirements after arrival on breeding areas. Further, males may spend more time courting in February and March and less time feeding than females as has been observed for northern pintails (Miller 1985). Thus, the higher energy costs of courting and reduced foraging probably also contribute to the lowered body fat of males.

Northern pintails

Proximate composition of northern pintails followed a trend that was nearly opposite that observed for northern shovelers. Pintails lost weight and fat content after their arrival in the fall (Table 14). The GLM for adults indicated that both sex and time period significantly influenced carcass weights. Body weights of both sexes declined from winter to spring, indicating a general decline in body condition.

The decrease in fat content in spring appeared contrary to the biological needs of pintails. Endogenous fats accumulated from wintering or migration areas supply the lipid requirement for egg production in large ducks such as mallards and northern pintails (Krapu 1979, 1981). Thus, I expected fat reserves to increase temporally as I noted for northern shovelers and as Miller (1986) noted for northern pintails in the Sacramento Valley, California. However, Miller (1986) observed that during dry years fat content declined between February and March, which he related to food shortages because of reduced areas of wetlands. During this study, waterfowl foods in the TLB may have been reduced because flooding the year (1982-83) previous to this study reduced agricultural production during the study and because below normal precipitation reduced the number of seasonal wetlands. In addition, the TLB is a relatively isolated block of waterfowl habitat and birds must fly a considerable distance before reaching the area. Northern pintails are one of the first waterfowl to migrate northward with many birds wintering in California south of the TLB and in Mexico (Bellrose 1978). The closest wetland complex south of the TLB is the Salton Sea, some 200 miles to the south. Energy expenditures for flight from southerly areas may also reduce fat loads of northern pintails migrating through the TLB during spring.

The GLM for protein weights of northern pintails was similar. Although the overall model was significant, the only significant explanatory variable was sex with larger bodied males having more protein than females. Again, probably a structural size difference rather than a sex related difference of biological relevance. Development of a non-biased index for protein similar to the condition index based on fat developed by Johnson et al. (1985) is needed to account for size variations among birds.

Lipid Accumulation Patterns among Species

Considering only adult birds, the GLM used to evaluate different temporal patterns of lipid accumulation among duck species was significant with both species and a species x time period interaction as significant variables in the model. Despite the seasonal decrease in fat in northern pintails they were fatter and had a higher condition index than ruddy ducks and northern shovelers. However, the condition index of northern pintails was similar to northern shovelers during the spring when pintails lost fat content and shovelers gained fat. Also, ruddy ducks increased fat content in winter to levels similar to those of pintails

Each duck species demonstrated unique seasonal patterns of condition index. Pintails are the most mobile and have the most varied diet of the 3 species (Bellrose 1978). The mobility would also allow them to be opportunistic foragers but would require fat reserves to successfully search for abundant food resources. The continuous loss of fat reserves by pintails during the winter may reflect the cost of a highly mobile, opportunistic foraging strategy, especially during years of below average wetland conditions in a semi-arid environment. In wet years, pintails apparently gain body condition (Miller 1986).

In contrast to pintails, ruddy ducks are largely sedentary during winter and have a restricted diet. Ruddy ducks have reduced protein content in winter, perhaps associated with their sedentary life style. Ruddy ducks increased their fat reserves in winter but those reserves may serve an insulative function in this semi-tropical species.

Like ruddy ducks, northern shovelers have a restricted diet but they are more mobile. Seasonally increasing fat content of shovelers may be related to elevated energy value of animal foods during spring and\or hyperphagy because spring lipogenesis to increase endogenous lipids to offset costs of reproduction is adaptive.

Nutritional Composition of Diet on Evaporation Ponds

Ruddy ducks

Ruddy ducks foraged mostly on aquatic invertebrates and even though use of specific food items varied seasonally, the nutritional composition of the diet was relatively stable (Figure 4). On a dry weight basis, protein formed over 50% of the diet with fat and NFE forming 9-13%. From my estimate of the proximate composition of the diet, there did not appear to be an increase in NFE in the diet during winter that would have contributed to the significant increase in endogenous fats of ruddy ducks. Hyperphagia seems the most likely explanation for the increase in endogenous fats during winter.

Northern shovelers

Northern shovelers also foraged mostly on aquatic invertebrates and the significant changes observed in use of specific foods did not appear to alter the nutritional composition of the diet among time periods (Figure 5). The apparent increase in fiber, ash, and water during spring may be an artifact because rotifers and copepods dominated the diet in that period; there are no published reports of the proximate composition of those 2 foods. For those, my estimates were based on the grand mean of all reported analyses of aquatic invertebrates (Table 15). The significant increase in endogenous fats of northern shovelers during spring in the TLB cannot be explained from a change in the diets observed on evaporation ponds. Because northern shovelers make more extensive use of other wetland types in the TLB than do ruddy ducks (Barnum and Euliss, in prep.), use of foods from other habitats that are high in NFE and fat or hyperphagia may explain the significant seasonal increase in endogenous fat.

Northern pintails

Northern pintails forage mostly on plant foods in the TLB (Euliss and Harris 1987, Euliss unpubl. data) and drainwater evaporation ponds are one of the poorest pintail habitats in the area (Barnum and Euliss, in prep.), probably because of the low availability of plant seeds and deep water. Low use of evaporation ponds by pintails also influenced the small number of birds collected but the overall diet of birds collected from evaporation ponds still reflected their general food usage patterns (Figure 6). Protein content of the diet during fall and spring was high relative to the content during winter. The relatively high protein content in the fall may be related to the prealternate molt; protein for feather synthesis are apparently derived from dietary input (Newton 1968, Ankney 1979, Raveling 1979, Ankney 1984, Heitmeyer 1985, Mainguy and Thomas 1985, Heitmeyer 1988). The high protein content of the diet in spring may be associated with the prebasic molt of hens (Heitmeyer 1988) and with reproduction (Krapu 1979, 1981) of birds nesting in the area.

Conclusions

Waterfowl wintering or migrating through the TLB are dependent on the various types of wetlands in the area to maintain body condition that is optimal for survival given the unique strategy of each species. For species such as ruddy ducks and northern shovelers that normally consume large quantities of animal foods throughout their life cycles, the habitats provided by drainwater evaporation ponds are especially attractive because they produce large standing crops of aquatic invertebrates (Euliss unpubl. data). Further, drainwater evaporation ponds will attract waterfowl that consume less animal matter, such as northern pintails, when their dietary requirements for protein are high. Feather synthesis requires large amounts of dietary protein (Ankney 1984, Heitmeyer 1985, Heitmeyer 1988) and the abundance of invertebrates in drainwater evaporation ponds attracts northern pintails in the fall if other wetlands in the TLB cannot supply the proteins required for the prealternate molt. Moreover, ducks nesting in the area will be attracted to the ponds during early spring because of protein requirements of egg production and for the prebasic molt of hens (Heitmeyer 1988). Because foods available to waterfowl from evaporation ponds are mostly invertebrates, ducks such as pintails, that depend on plant foods for lipogenesis are likely to depend less on evaporation ponds than species such as shovelers that are specialists on animal foods. Preservation of the long term integrity of waterfowl habitat in the TLB need to consider the availability of carbohydrate-rich foods from wetlands such as flooded grain fields or seasonal wetlands that provide natural plant seeds to birds that have high dietary NFE demands.

Farming trends have long affected the quantity and quality of waterfowl habitat in the TLB. Prior to agricultural development, the area was the site of the largest wetland complex in California (250,000 ha; U. S. Fish and Wildlife Service 1978). However, because of desirable soils and climate, the TLB was totally reclaimed (except during extreme flood years) for agricultural production. The soils are, however, saline and under traditional irrigation practices, salts accumulate in upper soil profiles and frequently limit production of agricultural crops. Farmers have long integrated salt management schemes into farming operations and more efficient means of improving agricultural production are always being sought out and implemented. One method of removing salts from upper soil profiles was a process known as preirrigation. In this practice, agricultural fields are flooded to a depth of 3-8 cm for periods of a month or more to allow salts in the soil to dissolve in the overlaying water. The water plus dissolved salts is then drained from the agricultural field. Because many cereal grains are produced in the TLB, many of the preirrigated fields contain waste grains that are attractive to waterfowl as food items. Barnum and Euliss (in prep.), found that preirrigated grain fields were the most important habitat for pintails in the TLB. However, preirrigation is rapidly being replaced with subsurface drainage systems because they are more efficient at removing salts and enhancing agricultural production. Drainwater evaporation ponds are the terminal sumps for water from subsurface drain systems. Thus, the availability of invertebrate-rich evaporation ponds is increasing as the availability of carbohydrate-rich preirrigated grain fields is decreasing.

Historically, flood waters filled the Tulare Lake to capacity in late winter and early spring providing seasonal inundation of uplands that contained various moist soil and upland plant seeds and terrestrial invertebrates. Because of seasonal drawdowns, oxidative processes occurred each summer to maximize availability of plant nutrients required for optimal production of phytoplankton and its associated invertebrate community. The result would have been to enhance the availability of both plant and animal foods during the spring when birds require carbohydrate-rich foods for lipogenesis or exogenous proteins for reproduction or feather molt. Initial development of the area by agriculture reduced the quantity of these natural wetlands that supplied a diversity of food items to waterfowl and replaced them with cereal grains high in carbohydrates. The extent to which those early agricultural practices altered species composition of waterfowl using the area historically is unknown but it seems intuitive that birds such as pintails and other ducks that feed heavily on plant seeds may have found the area more attractive after modification by farmers than under pristine conditions. Native seed crops are presumably less productive than domestic grains and, historically, they occurred only around the fringes of the Tulare Lake in shallow water or in areas of seasonal inundation. After agricultural development, grains were available in preirrigated fields that would have been under 20 feet or more of water prior to human influence. Agricultural developments over the last decade are causing opposite trends with the creation of large expanses of evaporation pond systems and the development of newer harvest techniques that reduce the availability of harvested grains to waterfowl. In the process of washing salts from a field equipped with subsurface drains, water is not on the field long enough to attract waterfowl. Further, with the exception of geese, waterfowl do not field feed in the TLB as they have been observed to do at other locales. The extent to which the lowered availability of preirrigated grain fields and an increasing availability of evaporation ponds will alter species composition of waterfowl in the TLB is unknown, but a decreased availability of grains and an increased availability of animal foods might suggest that it would shift the composition to favor species such as ruddy ducks and northern shovelers that rely heavily on animal foods.

The attractiveness of the area to granivorous species such as pintails would be reduced. Managers may need to provide seasonal wetlands in spring to provide carbohydrate-rich seeds for some waterfowl, such as northern pintails, to compensate for declines in the availability of cereal grains.

VII. CONCLUSIONS

Evaporation ponds were found to attract waterfowl in the Tulare Lake Basin (TLB) because of abundant foods and large areas for sanctuary. Water from drained agricultural fields is used to fill evaporation ponds and it is highly saline and contains heavy metals and other contaminants associated with embryonic mortality and deformity in water birds (Ohlendorf et al. 1986a, 1986b, 1987). Biologists are concerned about the sublethal effects of contaminants on water birds, including possible reproductive impairment on northern breeding areas as well as enhanced susceptibility to diseases but as yet no investigations to evaluate sublethal effects have been initiated.

Biotic diversity in evaporation ponds was low but those taxa present were highly abundant and produced large standing crops of potential waterfowl foods. The only hydrophyte observed regularly in evaporation ponds was widgeongrass (_Ruppia maritima_) and it was present only in ponds where EC values were 40-70 mmhos/cm^2. Invertebrates dominated the biomass produced in evaporation ponds and the diversity was low with over 96% of the biomass being formed by the salt marsh corixid (_Trichocorixa reticulata_) and a chironomid (_Tanypus grodhausi_). Those 2 taxa were present in 99.2% and 74.2%, respectively, of all samples collected during the course of this investigation. At least 22 additional taxa of plants and animals were also present but they collectively accounted for < 4% of the biomass and < 2% of the number of individual plants and animals observed. Standing crops of 10 g dry wt/m^2 are considered high (Benke 1984) and up to 9.4 g dry wt/m^2 of chironomid larvae and 2.8 g dry wt/m^2 of corixids were observed during this investigation.

Fat reserves of waterfowl in the TLB showed temporal patterns that were unique for each waterfowl species examined. Ruddy ducks were fattest in winter when ambient temperatures were coolest. Fat reserves of northern shovelers increased from fall to spring while those of northern pintails decreased. Ruddy ducks and northern shovelers had a restricted diet composed mostly of animal foods. Because neither species consumed significant quantities of plant foods, it is unlikely that dietary carbohydrates were a significant nutrient affecting buildup of endogenous lipids. Instead, hyperphagy and/or exploitation of invertebrates when they were fattest (i.e. invertebrates carrying egg sacs high in lipids) may explain how lipogenesis was facilitated. Northern pintails consume substantial quantities of invertebrates during winter in California but they rely most heavily on plant seeds, reflecting a more granivorous life style than ruddy ducks and northern shovelers. In contrast to ruddy ducks and shovelers, pintails altered the nutrient composition of their diets seasonally in such a way that critical nutrients for feather molt, mobility, and reproduction were met. Protein requirements for feather molt and reproduction are easily obtained by pintails from evaporation ponds because of high standing crops of aquatic invertebrates but they must rely on other habitats in the TLB to obtain plant seeds high in Nitrogen Free Extract (NFE).

Waterfowl wintering in or migrating through the TLB are dependent on the various types of wetlands in the area to maintain body condition that is optimal for survival given the unique strategy of each species. For species such as ruddy ducks and northern shovelers that normally consume large quantities of animal foods throughout their life cycles, the habitat provided by drainwater evaporation ponds are especially attractive because they produce large standing crops of aquatic invertebrates. Because foods available to waterfowl from evaporation ponds are mostly invertebrates, ducks such as pintails that depend mostly on plant seeds for nutrients are likely to depend less on evaporation ponds than species such as ruddy ducks and shovelers that are specialists on animal foods.

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The extent to which the lowered availability of preirrigated grain fields and an increasing availability of evaporation ponds will alter species composition of waterfowl in the TLB is unknown, but a decreased availability of grains and an increased availability of animal foods might suggest that it would shift the composition to favor species such as ruddy ducks and northern shovelers that rely heavily on animal foods. The attractiveness of the area to granivorous species such as pintails would be reduced. Managers may need to provide seasonal wetlands to provide carbohydrate-rich seeds for some waterfowl species such as northern pintails to compensate for declines in the availability of cereal grains.

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