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UNIVERSITY OF SAN DIEGO

San Diego

**Time-activity and energy budgets of Eared Grebes (*Podiceps nigricollis*) at
Salton Sea**

A thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science in Marine Science

By

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2017

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Acknowledgments

I would like to thank Dr. Hugh Ellis and the rest of my committee, Dr. Ellen Freund and Tom Anderson, as well as Annette Henry, for thoroughly reading through and contributing to my thesis, to make it the best that it can be. I truly appreciate all of their insights.

I would like to thank the Valentine Eastern Sierra Reserve and the University of San Diego Marine Science Program for funding the travel and lodging expenses for this project. Additionally, I would like to thank the Valentine Eastern Sierra Reserve and the Sonny Bono Salton Sea National Wildlife Refuge for giving me lodging while I was doing my fieldwork.

Specifically, I would like to thank Tom Anderson (at Salton Sea), for providing me with information about the grebes at Salton Sea, and for helping me collect pile worms. I would also like to thank Joe Jehl and Sean Boyd (at Mono Lake) for providing me with information about when the grebes arrived and migrated from my study areas. I would also like to extend my gratitude to the High Sierra Brine Shrimp Fishery for graciously donating brine shrimp for my project.

I would like to thank both the undergraduate (Chyna Gray, Brent Allman, Kathryn Silverman, and Valerie Thorngren) and graduate students (Alli Yoshida and Branda Cook) in Dr. Ellis's lab for assisting me with collecting my observational data, as well as, accompanying me on the long drives up to Mono Lake, which I would not have been able to do without them. I would also like to

thank Annette Henry and the USD Biology department for lending me their spotting scopes and tripods.

I would like to thank all of the Marine Science graduate students for all of their friendship, and giving me the needed breaks while I was analyzing my data and writing my thesis. I would also like to thank Starla Tudor for giving me excellent job experience during my time here.

Lastly, I would also like to thank my family for being an amazing set of sounding boards for me to bounce ideas off of, and for being willing to read through my thesis. I cannot even begin to thank them enough for all of their support and guidance.

Table of Contents

<u>List of Tables</u>	ix
<u>List of Figures</u>	x
<u>Abstract</u>	xi
<u>Chapter 1: Introduction</u>	1
General Biology of Eared Grebes	1
Eared Grebe Migration and Range in Western North America	2
Salton Sea	5
Mono Lake	6
Great Salt Lake	7
Time-Activity Budgets	7
Scan Sampling	8
Focal Animal Sampling	10
Determining Energy Budgets	10
Objectives	11
<u>Chapter 2: Methods</u>	13
Study Sites	13
Salton Sea	13
Mono Lake	13
Eared Grebe Observational Methods	18
Focal Animal Sampling	19
Scan Sampling	20
Time-Activity Data Collection	20

Salton Sea	20
Mono Lake	21
Prey Collection	21
Bomb Calorimetry	21
Energy Budgets	22
Data Analysis	23
<u>Chapter 3: Results</u>	25
Salton Sea Focal Animal Time-Activity Data	25
Daily Changes During each Observational Period	25
Behavioral Trends	30
Actual Time Spent in Each Behavior	35
Focal Animal Energy Budgets	35
Energy Expenditure at Salton Sea	35
Prey Item Caloric Value	42
Salton Sea Daily Food Requirements	42
Scan and Focal Animal Sample Comparison at Mono Lake	47
<u>Chapter 4: Discussion</u>	52
Salton Sea	52
Phenology	52
How Grebes Spend Their Time at Salton Sea	53
Changes in Energy Budgets Across Season	53
Comparisons with Grebes Elsewhere	57
Time-Activity Budgets at Other Lakes	57

Energy Budgets of Grebes at Other Lakes	57
Energy Budgets of Other Waterbirds	65
Methodological Assessment	65
Comparison of Focal Animal and Scan Sampling	65
Caveats and Considerations for the Future	71
<u>Literature Cited</u>	73
<u>Appendix A:</u> Observation dates for scan and focal animal samples	81
<u>Appendix B:</u> Salton Sea time-activity budgets for late February, early April, and late April	84
<u>Appendix C:</u> Mono Lake time-activity and energy budgets	90

List of Tables

Table 3.1: Salton Sea Focal Animal Sample N-values	26
Table 3.2: Behavior at Salton Sea by Time of Day	31
Table 3.3: Behavioral Energy Costs	40
Table 3.4: Caloric Value of Prey	45
Table 3.5: Salton Sea Prey Item Intake	48
Table 4.1: Salton Sea Eared Grebe Energy Budgets	55
Table 4.2: Time-Activity Budget Comparison	58
Table 4.3: Daily Energy Expenditure of Waterbirds in the Literature	68
Table A-1: Observation Dates (2014)	82

List of Figures

Figure 1.1: Eared Grebe Migration	3
Figure 2.1: Salton Sea Study Sites	14
Figure 2.2: Mono Lake Study Sites	16
Figure 3.1: Salton Sea Time-Activity Budgets (Early March and Late March)	28
Figure 3.2: Salton Sea Behavioral Trends During Morning, Midday, and Afternoon	33
Figure 3.3: Salton Sea Behavioral Trends for the Entire Day	36
Figure 3.4: Actual Time Spent in Each Behavior	38
Figure 3.5: Salton Sea 24-Hour Energy Expenditure	43
Figure 3.6: Mono Lake Focal and Scan Sample Comparison	50
Figure 4.1: Eared Grebe Energy Budgets	62
Figure 4.2: Daily Energy Expenditure of Waterbirds in the Literature	66
Figure B-1: Salton Sea Time-Activity Budgets (Late February)	86
Figure B-2: Salton Sea Time-Activity Budgets (Early April and Late April)	88
Figure C-1: Mono Lake Time-Activity Budgets (Late August and Mid- October)	92
Figure C-2: Mono Lake 24-Hour Energy Expenditure	94

Abstract

Time-activity budgets are a widely accepted way of approximating the daily energy expenditure of many species, including waterbirds. Time-activity budgets can be determined through the use of observational methods, such as focal animal or scan sampling. For this study, focal animal sampling was determined to be the most accurate way to study Eared Grebes (*Podiceps nigricollis*) as they frequently disappear from view when diving. Grebes were observed mainly at their post-wintering stopover site Salton Sea, where I determined their time-activity and energy budgets with a spotting scope having a functional range of 600 m. At Salton Sea, Eared Grebes were observed during five trips from late winter (February) to early spring (April) 2014. These observation periods were broken down into morning, midday, and afternoon to evaluate how their behavior changed by time of day. During the fall sampling period, both focal animal and scan samples were taken at Mono Lake in order to evaluate the two observational methods. Scan sampling underestimated diving behavior, because it was not possible to know how many grebes were under the water at any given time. Focal animal sampling during daylight hours were converted to energy budgets using energy equivalents developed for Eared Grebes previously by Ellis (1994).

An unknown proportion of the grebe population stops at Salton Sea and is able to put on fat before continuing their migration. Because these birds feed underwater at Salton Sea, dive bouts were used as a measure of feeding activity. Dive bout behavior was highest when the grebe population, at Salton Sea, was

composed of those still arriving from the south (in February). This behavior decreased throughout the period of time that the population was observed. The decrease in dive bout behavior is likely attributed to the increasing proportion of the grebe population preparing to migrate. When grebes dived less, they spent more time surface swimming and resting, which increased from February through April. The amount of time grebes spent preening did not change among the five observational periods.

It is assumed that post-wintering Eared Grebes arrive at Salton Sea in waves at differing times, except when the majority of grebes are either arriving (late winter) or preparing for departure (April). As a result, there can be a variety of physiological states represented in individuals during the same time period. The grebes expended a similar amount of energy throughout each observational period even though they have different patterns of behaviors, which may be explained by their non-synchronous arrival times. Assuming that grebes spend most of their time at night resting, the 24-hour daily energy budget ranged from 2.36 to 2.49 times Basal Metabolic Rate (BMR). The daily energy budget of Salton Sea grebes was slightly lower than those of other waterbirds found in the literature.

Chapter 1: Introduction

General Biology of Eared Grebes

The Eared Grebe (*Podiceps nigricollis*) is a small diving waterbird that thrives in hypersaline lakes. Eared Grebes can spend up to ten months of each year completely flightless, while they are on the water (Cullen et al. 1999; Jehl et al. 2003). During these flightless periods they often dive for food, typically aquatic invertebrates (Cullen et al. 1999) or, rarely, small fish (Jehl and McKernan 2002; pers. obs.). Eared Grebes undergo body composition changes associated with a shift to or from migratory behavior. This happens several times during their annual cycle. When the grebes arrive at a lake, for purposes of staging or use as an extended stopover site, their pectoral muscles atrophy and their digestive organs increase in size as they begin feeding (Jehl 1997). Conversely, when they prepare to migrate, which occurs without feeding (Jehl and Henry 2010), they increase muscle mass of organs needed for flight (breast, heart) and decrease the size of their digestive tract. These changes constitute one of the most dramatic body composition reorganizations known in migratory birds (Jehl 1997).

One of the cues for the grebes to start preparing to migrate during post-breeding staging is a decrease in density of their prey items. This was initially documented by Jehl (1988) for grebes at Mono Lake during their post-breeding (fall) staging period. When the adult brine shrimp population dropped below 3000 shrimp/m² (or approximately 176 shrimp/m³, assuming a mean depth of 17 m according to Jehl 1988), the grebes could no longer dive for food efficiently

and about 70% of the population migrated within two weeks. When the brine shrimp density declines to the aforementioned threshold, the grebes depart on the next leg of their migratory route, following another body composition change, toward their southern wintering grounds (primarily the Gulf of California). In 1988 this threshold was not reached in late fall at Mono Lake and the grebes did not depart until February (Jehl 1988). At Salton Sea, however, their cue to migrate might be more related to breeding because their main prey items there, pile worms (*Neanthes succinea*), are reproducing fairly constantly and presumably maintaining their numbers (Carpelan and Linsley 1961).

Eared Grebe Migration and Range in Western North America

In western North America, Eared Grebes frequent hypersaline lakes along the Pacific Flyway, a migration route used by numerous species of birds. Following breeding in late spring and early summer, most Eared Grebes in North America migrate to either Mono Lake, California, or Great Salt Lake, Utah, where they begin arriving in late July and stage until sometime in the fall, depending on prey availability (Jehl 1988). It is on these staging lakes that Eared Grebes prepare for their winter migration south (Jehl and Henry 2010; Fig. 1.1) by molting their flight feathers and increasing their body fat content (Jehl 1988). Most Eared Grebes winter in the Gulf of California (Cullen et al. 1999). In late winter to early spring (February to April), they migrate to Great Salt Lake with an unknown proportion of them using Salton Sea, California as an extended stopover site to replenish their energy stores (Anderson et al. 2007; Yoshida 2016). At Great Salt Lake, courtship and presumably pair formation occurs (Caudell and

Figure 1.1: **Eared Grebe Migration:** Map of the Western United States indicating the migration routes that Eared Grebes take between wintering grounds and staging lakes (from Jehl 1996 and Jehl et al. 1999 and 2003). Figure created in ArcGIS.

Eared Grebe Migration in North America

Prepared by: Samantha San Francisco, July 13, 2016
Data Source: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Conover 2006). From Great Salt Lake they disperse to various wetlands in the northwestern United States and southwestern Canada to breed.

For the purposes of this thesis, a grebe is described as staging when it spends a longer period of time fattening, and undergoing a wing molt (Mono Lake) or preparing to breed (Great Salt Lake), depending on the time of year. On the other hand, a grebe at a stopover site (Salton Sea) spends a shorter period of time fattening and does not molt or engage in breeding behavior.

Salton Sea

Some Eared Grebes stop at Salton Sea for unknown durations from late February through early April, during their vernal migration. While there, they undergo a body composition shift characteristic of grebes switching from a flighted to a purely aquatic condition (Jehl 1997). At the Salton Sea they increase their fat reserves before undergoing another change in body composition and continuing their vernal migration northward. How the grebes partition their time at Salton Sea has never been documented.

At Salton Sea the main prey of the Eared Grebes is pile worms, although during this study a grebe was observed (pers. obs.) eating a fish, likely tilapia (*Oreochromis mossambicus*). The pile worms are typically found in the sediments 2 - 12 m below the water surface (Kuhl and Oglesby 1979; Detwiler et al. 2002). They are found in high densities almost year-round mainly within 1 km of the shoreline (Kuhl and Oglesby 2002); however, at depths greater than 2 m their densities dramatically decline from late spring to summer (Anderson et al. 2007). This decline in density is primarily due to low oxygen levels in the

sediment (Anderson et al. 2007). While the pile worms reproduce all year at Salton Sea, they undergo two main spawning periods: one in the late spring and the other during the fall, when adult worms migrate to the surface of the water column to release their gametes (Detwiler et al. 2002). Pile worm spawning takes place in the few hours directly following sunset (Carpelan and Linsley 1961).

Mono Lake

At least a million grebes use Mono Lake as a post-breeding staging ground, beginning in July and peaking in September or October, depending on the year (Boyd and Jehl 1998). While at Mono Lake, their primary prey is brine shrimp (*Artemia monica*), however, they also feed on the pupae and larvae of brine flies (*Ephydra hians*) (Jehl 1988). The grebes prepare to leave Mono Lake when the adult brine shrimp population decreases below a threshold value (Jehl 1988).

Two generations of brine shrimp occur each year at Mono Lake. The first typically hatches from overwintering cysts in early March and matures in late May. This generation of brine shrimp gives rise to a second generation, which remains until they produce overwintering cysts (Dana et al. 1990). As a result, when the grebes arrive at Mono Lake in July, there is a high density of brine shrimp that will not be replenished during the rest of the summer and fall. In the fall, the brine shrimp population is an important food resource for the Eared Grebes, as well as other waterbird species, including California Gulls (*Larus californicus*), Ruddy Ducks (*Oxyura jamaicensis*), Wilson's Phalaropes (*Phalaropus tricolor*), and Red-necked Phalaropes (*Phalaropus lobatus*; Jehl

1988).

Like the brine shrimp, brine flies are an important food source to many different bird species at Mono Lake, in addition to the Eared Grebe. Brine flies and their pupae are present in high densities during the late summer, and decline into the fall (Jehl 1988). Brine fly adults submerge themselves in order to lay their eggs. Brine fly pupae are attached to submerged shoals of tufa, which are calcium carbonate structures that are formed via underwater seepages.

Great Salt Lake

Eared Grebes also migrate to Great Salt Lake during the post-breeding staging period. Roberts et al. (2013) report, from 1997-2012, well over a million grebes present during this time period, and sometimes more than double that number. A similar number of grebes also uses Great Salt Lake as a pre-breeding staging ground in the late spring (Caudell and Conover 2006).

The grebes at Great Salt Lake feed mainly on brine shrimp (*Artemia franciscana*). These brine shrimp reproduce mainly by giving birth to live shrimp during the grebes' pre-breeding staging period (Stephens 1999), thereby replenishing the brine shrimp population during the spring and early summer. This means that the grebes' food source does not run out during this time period. However, during the post-breeding staging period, in the fall, the grebes feed on the remaining brine shrimp population from earlier in the year (Caudell and Conover 2006).

Time-Activity Budgets

Time-activity budgets have been used to survey how species partition

time among different behaviors, most often during their breeding periods. Time-activity budgets have been constructed using tagging or telemetry for seabirds such as Common Murres (*Uria aalge*; Cairns et al. 1987) and South Georgian Shags (*Phalacrocorax georgianus*; Wanless et al. 1995), and for a wading bird, the Snowy Egret (*Egretta thula*; Macarrone et al. 2012). However, this is not a viable way of studying Eared Grebes because it requires the live-capture, and recapture, of individuals, nearly impossible in the huge groups of Eared Grebes in most areas. Alternatively, time-activity budgets can be determined by using observational methods such as scan sampling and focal animal sampling.

Scan Sampling

Scan sampling is an instantaneous sampling of what a group of individuals is doing at a particular instant in time (Altmann 1974). It is widely used as an observational method in order to survey the behaviors of a large part of a study population. Scan sampling is a technique that has not been standardized in the literature making it adaptive to the species being studied. This leads to a number of observational sampling methods and statistical evaluations that have been used.

Several waterbird studies use the entire flock in a single scan, which is only feasible when the species that is being studied occurs in small numbers. Variability among studies exists with respect to the length of time between each scan and in the number of consecutive scans (observation bout). Morton et al. (1989), looking at American Black Ducks (*Anas rubripes*), Goudie (1999), studying Harlequin Ducks (*Histrionicus histrionicus*), and Schummer and Eddleman (2003) reporting on American Coots (*Fulica americana*), all used a full

minute between each individual scan; however, the length of each observation bout ranged from 30 - 120 min. Also studying Harlequin Ducks, Adams et al. (2000) chose to use 15 s between each scan, and their observation bouts lasted 5 min. This was so they could more easily keep track of each individual in the flock being observed, as opposed to the more typical scan sample. Some studies also used the entire day as the length of the observation bout. Green et al. (1999) did a scan of the entire flock of White-headed Ducks (*Oxyura leucocephala*) every 15 min over the span of a 24 h period. Green and Hamzoui (2000) studying Marbled Teal (*Marmaronetta angustirostris*) and Boulkhssaim et al. (2006) working with Shelduck (*Tadorna tadorna*) made a scan of the flock every 30 min during the daylight hours.

Few of these studies (Goudie 1999; Green et al. 1999; Adams et al. 2000) had to consider individuals leaving the field of view due to diving. For flocks larger than 50 individuals, Green et al. (1999) estimated the total number of birds feeding by using the average length of a dive and of the inter-dive period and the number of birds observed in the inter-dive period. Adams et al. (2000) kept track of each individual for each observational bout and each group of birds sampled was very small (5 - 8 individuals).

Eared Grebes are gregarious birds; they are often found on a single lake in huge numbers, often in the hundreds of thousands (Jehl 1988) or millions (Boyd and Jehl 1998; Roberts 2013); subgroups may still number in the thousands. This makes it impossible to scan the entire flock or even smaller subgroups. Hepworth and Hamilton (2001), working on Pink-eared Ducks (*Malacorhynchus*

membranaceus), and Caudell and Conover (2006), studying Eared Grebes at Great Salt Lake, overcame this issue by specifically looking for smaller groups. Caudell and Conover (2006) were able to isolate groups of approximately 12 individuals as they observed grebes found close to the Antelope Island Causeway.

Focal Animal Sampling

Focal animal sampling is a continuous sampling method in which an individual is tracked for a pre-determined length of time or for as long as possible, and each behavior that the individual performs is recorded (Altmann 1974). Not only does this method take into account every behavior that the individual performs, but also how long each behavior is performed. It is necessary to follow many individuals in order to get an accurate representation of the behaviors of the entire population. This is also useful to determine the length of certain behaviors, such as dives and of the surface intervals of dive bouts (Nocera and Burgess 2002). Nocera and Burgess (2002) studied Common Loons (*Gavia immer*), which do not occur in very high numbers, unlike Eared Grebes.

Determining Energy Budgets

There are different methods that can be used in order to calculate an energy budget. A common method is to determine field metabolic rate (FMR) using isotopically labeled water. This technique requires the live capture of an individual and then recapture of that same individual 24 or 48 h after the labeled water has been injected. This proves to be nearly impossible in non-breeding birds such as grebes, because it is difficult to recapture them (Ellis and Gabrielsen 2002). Therefore, for this project, energy budgets were created through the use of

time-activity budgets (Conover and Caudell 2009), and were modified by me for this study to only include behaviors that had known energetic costs.

The energetic cost of most behaviors found in Eared Grebes on the water has been measured (Ellis 1994; Caudell and Conover 2009). This information, in conjunction with the time grebes spend in each behavior, can be used to determine how much energy grebes expend at a lake (i.e., their daily energy expenditure or DEE). Such an energy budget has never been constructed for Eared Grebes at the Salton Sea.

Objectives

The purpose of this study was to create the first analysis of Eared Grebes' energy costs at Salton Sea. To accomplish this, I have created a time-activity budget, based on behaviors with known energetic costs, of Eared Grebes at Salton Sea. The modified time-activity budget was converted to an energy budget. An energy budget should help determine the impact that Eared Grebes have on their prey, an idea previously addressed by Lovvorn and Gillingham (1996) looking at Canvasback Ducks (*Aythya valisineria*). Conversely, an energy budget may help to determine how environmental factors may impact the Eared Grebes.

The grebes' use of the Salton Sea was compared with their use of other areas at other times. To do that I compared my time-activity and energy budgets with those created by Caudell and Conover (2006) and Conover and Caudell (2009) for grebes staging at Great Salt Lake during the grebes' pre- and post-breeding staging periods respectively, and with fall staging grebes at Lake Abert

(Boula 1985). I have also made comparisons of energy budgets of waterbirds in general.

Chapter 2: Methods

Study Sites

Salton Sea

Salton Sea is located in the Colorado Desert of southern California (33°18'49", 115°49'00"; Fig. 2.1), the western portion of the larger Sonoran Desert. This large lake (889 km²) is a drowned basin with only agricultural water inputs from the surrounding areas (Glenn et al. 1999), as well as any direct precipitation. Due to the lack of any outlet, all water loss is through evaporation. This causes an increase in salinity (currently about 55 ppt according to USGS water monitoring, 2014), which exceeds that of the ocean (35 ppt). The Salton Sea was formed in 1905 when a levee on the Colorado River broke and flooded the basin. It has been important for various species of waterbirds since that time (Shuford et al. 2000 and 2002; Patten and Patten-Smith 2004). The maximum depth of Salton Sea is 13 m; however, during daylight hours the grebes are mainly found in waters of up to 2 m depth (within 1 km of the shore; Jehl and McKernan 2002), which is where the pile worm population is most dense (Detwiler 2002).

Mono Lake

Mono Lake (183 km²) is located in central California (38°01'00"N, 119°00'34"W), close to the border of Nevada (Fig. 2.2). The average depth of Mono Lake is currently 17 m, which is deeper than the depth range of the brine shrimp that grebes eat (6 m; Lenz 1984). The lake is fed by five freshwater streams, underwater seepages, and direct precipitation. Water loss from Mono Lake is solely through evaporation, which has resulted in an increase in salinity to

Figure 2.1: **Salton Sea Study Site:** Map of Salton Sea, CA showing the observation site, which was located at Rock Hill Trail (RHT; Red). Map taken from Google Maps.

Figure 2.2: **Mono Lake Study Sites:** Map of Mono Lake, CA showing the two observation sites. The northern site was located at Black Point (BP; Red) and the southern was located at South Tufa (ST; Purple). Map taken from Google Maps.

around 80 ppt. The salinity of Mono Lake was around 50 ppt in the 1940s. However, due to diversion of some of the freshwater inputs by the City of Los Angeles, the salinity almost doubled to 90 ppt, over the course of about 40 years (1941-1982) and the surface elevation of the lake dropped by 13 m. Starting in 1982 fresh water diversions were reduced and the salinity declined (Jehl 1988) until the recent drought (current salinity: 88 ppt according to the Mono Lake Committee, 2015). For many years, Eared Grebes have used Mono Lake as one of their post-breeding staging grounds from mid-July until their food runs out, in November or later. For at least the past three years, however, the majority of grebes have departed Mono Lake by late October (S. Boyd, pers. comm.) due to an early collapse of the brine shrimp population (J.R. Jehl, Jr., pers. comm.).

Eared Grebe Observational Methods

All grebe observations were conducted from the shoreline (at both lakes) using a spotting scope (20-60 x 78) on a tripod when birds were offshore between 100 m and 600 m. The four behaviors recorded during each observation were surface swimming, preening, dive bouts, and resting, because the energetic cost of these four behaviors are currently known. These behaviors are also the four most common behaviors performed by the Eared Grebe at Mono Lake and Salton Sea (Jehl 1988; Caudell and Conover 2006; and pers. obs.). Wing flapping occurred only when the grebes were preparing to migrate (Mono Lake: October). "Surface swimming" was defined as a grebe swimming across the surface of the water (including surface feeding). "Preening" is any maintenance done to the bird's feathers (i.e., straightening and oiling its feathers), which could include head

movement back to the uropygial or "preen" gland located at the base of the tail. A grebe was considered to be in a "dive bout" if an individual was observed diving under the surface or surfacing after a dive. The period of time between consecutive dives (mean = 14.4 s; range = 5-66 s) was also considered as part of a dive bout. A "resting" grebe was an individual on the surface that was stationary, with no apparent movement across the surface of the water and was not performing any of the aforementioned behaviors (Caudell and Conover 2006). If an individual grebe was observed performing two behaviors simultaneously (e.g., surface swimming and preening) the behavior that had the higher energetic cost was recorded.

Focal Animal Sampling

Individual Eared Grebes were observed at both Salton Sea and Mono Lake for as long as possible. There was a wide range in the length of each focal animal sample due to the fact that the grebes occur in large numbers at each lake and periodically disappear from view due to diving behavior. Grebes were observed at Salton Sea for 77.5 h on a total of 10 d from late February to mid-April, yielding 22.2 h of data. At Mono Lake, 34.7 h of observation over four days provided 12.1 h of catalogued behaviors. Individual grebes were observed using a spotting scope, and each focal animal sample was documented using a voice recorder. A focal animal recording was stopped if the grebe swam out of view or was joined by a group of diving grebes, which made it impossible to tell which grebe was being observed. The length of time that a grebe spent in each behavior

was divided by the length of the respective focal animal sample to give the percent of time spent in each behavior.

Scan Sampling

Scan sampling was initially attempted in this study. A subgroup of grebes (approximately four to six individuals) was monitored for each individual scan sample. Each scan sample was 30 min long, with a recording of the behavior of a small subgroup of grebes every minute. The Eared Grebes' behavior was recorded by tallying the number of individuals in the subgroup that were performing each behavior every minute, on the minute for the entirety of a scan sample (Altmann 1974). A single scan lasted no more than 10-15 s. Grebes observed for 34.7 h over four days at Mono Lake provided 12.2 h of scan data in late August, 2014 and 8.5 h in mid-October, 2014.

Time-Activity Data Collection

Salton Sea

Eared Grebes at Salton Sea were observed from the southern shoreline (Fig. 2.1) during five different observational periods. The focal animal sample observations occurred over the course of 2.5 months, from late February 2014 through late April 2014 (Table A-1). The majority of the focal animal samples were collected at the site located at the southern end of Salton Sea (Rock Hill Trail), because there were not a large number of grebes within scope range at the northern end of Salton Sea. The observational day typically began around sunrise, and continued until either the grebes swam out of view or sunset. Observations were stopped if the surface of the water became too choppy due to

high winds. The observational day was divided into three equal periods: morning, midday, and afternoon. The observational day got longer over the course of the study from late February to late April.

Mono Lake

Two trips were made to Mono Lake during the 2014 field season, one in late August and towards the end of the staging season in mid-October (Table A-1). During these two periods the grebes were observed using both focal animal and scan sampling. The majority of the observations were taken from the south site (South Tufa; Fig. 2.2). Both sites were sampled during late August. Observations were conducted only at the south site in mid-October. All observations began around sunrise and continued through sunset. Like with Salton Sea, the observational day was divided into the same three periods. The length of the day got shorter from late August to mid-October.

Prey Collection

Pile worms were collected at Salton Sea by using a large dip net to scoop up surface sediment. The pile worms were picked out of the sediment remaining in the net using tweezers. Brine shrimp used in calorimetry were donated by the brine shrimp fishery established at Mono Lake (High Sierra Brine Shrimp Company; Lee Vining, CA).

Bomb Calorimetry

A Parr 6200 Bomb Calorimeter was used to determine the caloric value of the grebes' prey items. Approximately 14 g of a prey species were weighed in a labeled crucible, and placed under a fume hood at room temperature (22.8 °C) to

air dry to constant weight. The drying process typically took three to four days and samples were weighed at least every 24 h. The dried samples were compressed into pellets weighing roughly 1 g each and were then immediately processed in the bomb calorimeter. This was done at least three times (see results: Table 3.4) with each prey species. A benzoic acid tablet was run as a standard at the beginning of each set of samples.

Energy Budgets

The data from the time-activity budgets (percent of time spent in each behavior category) were used to calculate the amount of energy that the grebes spent performing each behavior. In order to convert a time-activity budget into an energy budget, the known metabolic cost for each behavior (Ellis, 1994) was used. I converted the energetic cost of each behavior in mL O₂/(g · h) to kJ/(g · h), so that I could convert the observed time-activity budgets into energy budgets. In converting mL O₂ to SI units for basal metabolic rate, Ellis and Jehl (2003) used a respiratory quotient (RQ) of 0.71 in resting, post-absorptive Eared Grebes. They assumed that these grebes were utilizing fat reserves during metabolic measurements. However, there was no way to know in this study if the grebes were post-absorptive and RQ could not be determined. Therefore, I used an RQ of 0.80 as a conservative measure, for grebes utilizing protein from their diet (Koteja 1991), giving me a conversion factor of 20.35 mL O₂/kJ. If grebes were post-absorptive (preparing to depart) a more appropriate conversion factor would have been 19.8 mL O₂/kJ (Ellis and Gabrielsen 2003) that Ellis and Jehl used. If wrong, I have only created a 3% overestimate of energetic costs compared to the

lower RQ. Also, water temperature did not seem to have any effect on the basal metabolic rate of the grebes (Ellis and Jehl 2003). The average amount of time that the observed grebes spent performing each behavior (h) and the estimated weight of the grebes (g) at each time point was multiplied by the metabolic cost of each behavior ($\text{kJ/g} \cdot \text{h}$) (Wooley and Owen 1978), for each period of the day. This was done separately for each observational period, across the season, at Salton Sea.

The weights of grebes documented by Jehl (1997) were used in order to estimate the weight of the grebes over the period of time that they are at Salton Sea. The time-activity budget was then used to figure out the amount of energy that an Eared Grebe uses, on average, for each observational period at Salton Sea. These values are conservative as the cost of putting on fat (28 kJ/g of fat deposited; Kendeigh et al. 1977) was not accounted for because the grebes at Salton Sea do not put on fat at the same rate, since they arrive at different times. The caloric value of the prey items, assuming a metabolic efficiency of 80% for pile worms (Castro et al. 2008), was then used in order to determine the number of each prey item necessary to offset the average daily energy cost of the Eared Grebes.

Data Analysis

Non-parametric statistical tests were used to analyze the behavioral data (Adams et al. 2000). The Kruskal-Wallis test, which has been used in time-activity budget studies that use observational methods (Gauthier et al. 1988; Goudie 1999; Adams et al. 2000), was employed to test differences for each

behavior by time of day and by observational period. In order to maintain statistical independence and prevent pseudoreplication, a single focal animal sample was used as the sampling unit (Gauthier et al. 1988). Mann-Whitney U tests were used to evaluate the Kruskal-Wallis results with p-values ≤ 0.1 . Predetermined α -values (e.g., 0.05) were not used to set limits of significance (Hurlbert and Lombardi 2009); p-values ≤ 0.1 are noted. A power analysis, for use with non-parametric data sets, was performed on all of the time-activity budget data. The output from the power analysis test ranged from 0 to 1, with higher numbers indicating more power. A threshold of ≥ 0.8 was used for determining if data samples had sufficient size.

Chapter 3: Results

Salton Sea Focal Animal Time-Activity Data

Daily Changes During each Observational Period

There was a wide range (28 – 1119 s) in the length of each focal animal sample for each observational period at Salton Sea (Table 3.1). The percent of time spent resting, preening, surface swimming, and in dive bouts during the morning, midday, and afternoon for each observational period are presented along with the number of focal animal samples (N) per time of day in the tables beneath the time-activity budget graphs for March observations (see Fig. 3.1) where power analyses indicated sufficient sample sizes. Similar figures are presented in Appendix B for all other periods, which are not analyzed by time of day here due to low power analysis scores that indicate insufficient sample sizes. For all data with p-values ≤ 0.1 , the power analysis showed that there was a sufficient sample size, and the higher p-values (> 0.1) might be due to low sample size. Any differences in behaviors that produced values $p \leq 0.1$ are noted in red for each observational period (Table 3.2).

Early March

Surface swimming and preening did not vary with respect to time, however a Kruskal-Wallis test showed that there were differences (p-values ≤ 0.1) in dive bout behavior and resting. The grebes spent more time in dive bout behavior in the morning than during either midday ($p = 0.001$) or afternoon ($p = 0.014$; Fig. 3.1, Table 3.2). The percent of time spent resting was higher during midday than either morning ($p = 0.001$) or afternoon ($p = 0.015$).

Table 3.1: **Salton Sea Focal Animal Sample Times:** Mean ($\pm$ std. dev.) lengths of each focal animal sample occurring at Salton Sea in 2014. The range and number of focal animal samples, for each time period is also reported.

2014	Time (s)	Range (s)	N
Late Feb	547.47 ± 196.81	189-936	17
Early Mar	296.62 ± 183.71	66-919	65
Late Mar	312.31 ± 173.55	43-1119	93
Early Apr	331.10 ± 168.73	51-721	31
Late Apr	275.55 ± 157.92	28-756	44

Figure 3.1: Salton Sea Time-Activity Budgets (Early March and Late March):

The percent of time spent in each behavior during daylight for early March and late March at Salton Sea. Surface Swimming (SS): blue, Preening (P): red, Dive Bout (DB): green, and Resting (R): purple.

Early March (N)	SS ($\pm$ s.e.)	P ($\pm$ s.e.)	DB ($\pm$ s.e.)	R ($\pm$ s.e.)
Morning (N=13)	27.7 $\pm$ 8.7	5.3 $\pm$ 2.8	56.7 $\pm$ 11.0	10.3 $\pm$ 3.1
Midday (N=20)	38.3 $\pm$ 5.8	11.0 $\pm$ 4.5	17.6 $\pm$ 7.5	33.1 $\pm$ 5.2
Afternoon (N=32)	31.0 $\pm$ 5.3	19.4 $\pm$ 5.8	29.9 $\pm$ 7.4	19.9 $\pm$ 4.2

Late March (N)	SS ($\pm$ s.e.)	P ($\pm$ s.e.)	DB ($\pm$ s.e.)	R ($\pm$ s.e.)
Morning (N=32)	24.3 $\pm$ 4.0	22.5 $\pm$ 5.0	18.6 $\pm$ 4.8	34.6 $\pm$ 4.1
Midday (N=32)	31.7 $\pm$ 3.9	10.8 $\pm$ 3.7	13.6 $\pm$ 4.7	43.9 $\pm$ 4.6
Afternoon (N=29)	40.4 $\pm$ 4.6	19.4 $\pm$ 5.0	13.1 $\pm$ 4.5	27.1 $\pm$ 3.6

Late March

A Kruskal-Wallis test showed that there were differences ($p\text{-values} \leq 0.1$) in surface swimming, preening, and resting. The percent of time spent surface swimming increased from the morning through the afternoon ($p = 0.039$). The percent of time spent preening was lower ($p = 0.022$) during midday than in the morning. The percent of time spent in dive bout behavior did not vary with respect to time of day (Fig. 3.1). Resting varied throughout the day ($p = 0.029$) with an increase at midday compared to the afternoon ($p = 0.006$; Table 3.2).

Behavioral Trends Across each Observational Period

A power analysis for each behavior across all time periods gave values of 1 (for diving), 0.65 (surface swimming), 0.50 (resting), and 0.26 (preening). My comparisons for diving should not be influenced by sample size, however, those for preening, resting, and perhaps surface swimming might be. There was a general decrease in the percent of time spent in dive bout in the afternoon ($p = 0.042$). Conversely, there was a general increase in the percent of time that the grebes spent surface swimming and resting from late February through late April in both the morning (surface swimming: $p = 0.078$; resting: $p = 0.010$) and afternoon (surface swimming: $p = 0.044$; resting: $p = 0.006$). Differences in each of the behaviors throughout each observational period during midday (Fig. 3.2) were minimal.

Overall, the percent of time that the grebes spent surface swimming or resting varied inversely with the percent of time they spent in dive bouts throughout the daylight hours. Preening did not vary among each observational

Table 3.2: **Behavior at Salton Sea by Time of Day:** P-values for Kruskal-Wallis (KW) tests comparing grebe behavior in morning, midday, and afternoon during each observational period. Notable differences are shown in red. Mann-Whitney p-values are provided for Kruskal-Wallis tests that show a notable difference. For Kruskal-Wallis tests with high p-values, no Mann-Whitney test was conducted (indicated by dashes).

Late Feb	SS	P	DB	R
KW	0.294	0.271	0.691	0.230
Morn:Mid	--	--	--	--
Morn:After	--	--	--	--
Mid:After	--	--	--	--
Early Mar	SS	P	DB	R
KW	0.373	0.568	0.003	0.005
Morn:Mid	--	--	0.001	0.001
Morn:After	--	--	0.014	0.328
Mid:After	--	--	0.229	0.015
Late Mar	SS	P	DB	R
KW	0.039	0.079	0.429	0.029
Morn:Mid	0.183	0.022	--	0.179
Morn:After	0.016	0.412	--	0.231
Mid:After	0.135	0.214	--	0.006
Early Apr	SS	P	DB	R
KW	0.591	0.859	0.630	0.988
Morn:Mid	--	--	--	--
Morn:After	--	--	--	--
Mid:After	--	--	--	--
Late Apr	SS	P	DB	R
KW	0.365	0.444	0.179	0.301
Morn:Mid	--	--	--	--
Morn:After	--	--	--	--
Mid:After	--	--	--	--

Figure 3.2: **Salton Sea Behavioral Trends During Morning, Midday, and Afternoon:** Behavioral trends over the course of time that the grebes are at Salton Sea over each of the observed time periods. Error bars represent standard error. Colors as described in Figure 3.1.

period during the daylight hours (Fig. 3.3).

Actual Time Spent in Each Behavior During each Observational Period

The percent of time spent in each behavior was converted to hours, so that the data from the time-activity budgets could be used in creating an energy budget. From February to April, there is almost a three-fold decrease in the amount of time spent in dive bout behavior; while the amount of time spent surface swimming and resting roughly doubled during that same interval. The amount of time spent preening hardly changed during that same period (Fig. 3.4).

Focal Animal Energy Budgets

The energetic cost of each behavior (Table 3.3; Ellis 1994) was used in conjunction with the total number of hours spent in each behavior to determine the amount of energy expended per behavior for each observational period of the focal animal data set. The average mass of Eared Grebes reported by Jehl (1997) was used to determine the energy expenditure per bird for February (320 g), March (384 g), and April (411 g).

Energy Expenditure at Salton Sea

Eared Grebes are visual predators and are assumed not to feed in the dark. A 24-hour energy budget was created using the assumption that the grebes spend all their time at night resting (Jehl 1988; Caudell and Conover 2006). Based on my observations, the grebes swam out of my field of view at sunset. The distance that the grebes travelled was estimated by doubling the functional range of the scope (600 m). By using this estimate in conjunction with the average swimming speed of a Mallard duck (0.5 m/s; Prange and Schmidt-Nielsen 1970), I have

Figure 3.3: **Salton Sea Behavioral Trends for the Entire Day:** Behavioral trends over the course of time that the grebes are at Salton Sea over the entire day. Error bars represent standard error. Colors as described in Figure 3.1.

Figure 3.4: **Actual Time Spent in Each Behavior:** Total number of hours that the grebes spent in each behavior during each period that they were observed at Salton Sea. Tabular values are means $\pm$ s.e.

Observational Period	SS	P	DB	R
Late February (N=17)	2.74 ± 0.71	1.68 ± 0.71	4.80 ± 1.18	1.94 ± 0.58
Early March (N=65)	3.84 ± 0.42	1.65 ± 0.38	3.71 ± 0.59	2.60 ± 0.33
Late March (N=93)	3.92 ± 0.30	2.15 ± 0.33	1.86 ± 0.33	4.36 ± 0.31
Early April (N=31)	6.16 ± 0.55	1.75 ± 0.47	1.14 ± 0.48	3.80 ± 0.46
Late April (N=44)	5.08 ± 0.69	2.25 ± 0.60	1.63 ± 0.55	4.39 ± 0.56

Table 3.3: **Behavioral Energetic Costs:** Known energetic cost of each behavior ($\text{mL O}_2/\text{g} \cdot \text{h}$) compared to the basal metabolic rate of $1.212 \text{ mL O}_2/\text{g} \cdot \text{h}$ (Ellis and Jehl 2003). The energetic cost of each behavior is also presented in $\text{kJ}/\text{g} \cdot \text{h}$. The energetic cost presented for preening is the average of preening and vigorous preening, due to the different intensities of preening observed in the field.

Behavior	Known Energy Cost (mL O ₂ /g · h)	Known Energy Cost (kJ/g · h)	Multiple of BMR
Resting (on water)	2.048	0.0417	1.690
Preening	2.957	0.0603	2.440
Dive Bout	3.831	0.0780	3.161
Surface Swimming	4.539	0.0924	3.745

estimated that the grebes spend roughly 1.5 h swimming to (after sunset) and from (before sunrise) their roosting site, which is offshore somewhere. The remainder of the nighttime hours is assumed to be resting. The overall energy expenditure for a grebe of average mass (Jehl 1997) increased approximately 28% from late February (478.21 kJ/d) through late April (613.69 kJ/d), however the mass-specific energy expenditure varied only by 6% (a range of 1.46-1.54 kJ/g). The way that the energy was allocated per behavior varied considerably. Surface swimming and dive bouts can be evaluated together as locomotory activities. Doing this shows that these two behaviors dominate the energy expenditure in all of the observational periods. After early March the energy expended diving drops considerably, and is made up with an increase in surface swimming. In addition, the amount of energy used in resting stayed relatively constant after February, in spite of nighttimes getting shorter (Fig. 3.5).

Prey Item Caloric Value

The caloric value of the grebe prey, at both Salton Sea (pile worms) and Mono Lake (brine shrimp and brine fly pupae), was determined using bomb calorimetry. Although pile worms have considerably less energy density than brine shrimp and brine fly pupae, they are so much larger that their caloric value is nearly 30 times greater than either brine shrimp or brine fly pupae (Table 3.4).

Salton Sea Daily Food Requirements

The daily food requirement of a grebe was determined using the caloric value, of pile worms and the calculated energy expenditure for the 24-hour energy budget. The caloric value of the pile worms was adjusted for true digestibility

Figure 3.5: **Salton Sea 24-Hour Energy Expenditure:** Total energy expended per behavior (kJ/bird · d) as it changed over the course of time that the grebes are at Salton Sea, as well as total amount of energy expended (kJ/bird · d) for each observational period. Colors as described in Figure 3.1.

Table 3.4: **Caloric Value of Prey:** Mean ($\pm$ s.d.) caloric value of each prey item per gram, average dry weight (per individual), and mean caloric value per individual, for brine shrimp, brine fly pupae, and pile worms. The N-value is representative of the number of pellets that were analyzed per prey.

Prey (N)	Caloric Content	Average Dry Weight (g)	Caloric Content (kJ/individual)	Mean Individuals per Pellet
Brine Shrimp (N=7)	20.19 ± 0.54	0.001	0.02	80
Brine Fly Pupae (N=3)	17.90 ± 1.36	0.001	0.018	70
Pile Worms (N=4)	15.78 ± 1.88	0.037	0.584	26

(80%; Castro et al. 2008) to account for indigestible content. The total number of pile worms that an individual grebe would need to eat in a day to maintain weight ranged from 981 in late February to 1295 in early April (Table 3.5).

Scan and Focal Animal Sampling Comparison at Mono Lake

For the two observational periods at Mono Lake, both focal animal and scan sample observations were made, and are representative of the same time period. Here, the behavioral data from these two sampling methods were compared for the entire day. Surface swimming, preening, and resting were seen less in the focal animal samples than in the scan sample observations. On the other hand, diving was observed more in the focal animal samples (Fig. 3.6). During the focal animal observations, when a grebe was in the surface portion of a dive bout, it was noted which surface behavior it was performing. Using this information, it was determined that the grebes partitioned the amount of time spent in each behavior in the surface portion of a dive bout (surface swimming (Mean = 30.8%; Range = 3.3-89.4%; N = 109), preening (Mean = 3.9%; Range = 2.2-82.8%; N = 27), and resting (Mean = 65.3%; Range = 3.8-96.7%; N = 152)) consistently throughout all of the observational periods at Salton Sea and Mono Lake.

Table 3.5: **Salton Sea Food Intake:** Number of individual pile worms at Salton Sea that would need to be eaten in order to meet the daily energy expenditure using the caloric value that has been adjusted for digestibility (80%).

Observation Period	24-Hour Total: Resting at Night (kJ)	Pile Worm Caloric Value (kJ)		Food Intake
		Measured	Adjusted	
Late February	458.22	0.584	0.467	981
Early March	560.84			1201
Late March	535.80			1147
Early April	604.90			1295
Late April	596.36			1277

Figure 3.6: **Mono Lake Focal and Scan Sample Comparison:** Comparison of the focal animal and scan sample data sets for the entire day. Colors as described in Figure 3.1.

August 2014		
Behavior	Focal (%) N=67	Scan (%) N=730
Surface Swimming and Feeding	29.1 + 3.6	25.2 + 1.0
Preening	13.7 + 2.6	20.5 + 1.0
Dive Bout	27.4 + 4.0	10.0 + 0.6
Resting	29.8 + 3.2	44.3 + 1.2
October 2014		
Behavior	Focal (%) N=80	Scan (%) N=510
Surface Swimming and Feeding	20.4 + 3.0	28.0 + 1.2
Preening	18.6 + 3.2	19.3 + 0.8
Dive Bout	43.2 + 4.3	20.9 + 0.8
Resting	17.7 + 2.3	31.8 + 1.1

Chapter 4: Discussion

Salton Sea

Phenology

In the population censuses of Eared Grebes at Salton Sea (Jehl and McKernan 2002) showed the main influx of grebes occurred during February and March, and then the grebe population decreased dramatically around April. In February, the grebes at Salton Sea are mainly composed of birds that have recently arrived. By April the majority of the grebe population is preparing to migrate, especially by mid-April. However, between February and April due to multiple pulses of arrivals and departures, there is a mixture of (1) grebes that have recently arrived, (2) birds that are fattening, and (3) birds preparing to depart. It is unknown how long an individual bird stays, but both the arrival and departure of a bird is accompanied by a change in its body composition while it is still on the lake (Jehl 1997). Since the changes take several days, and because a grebe likely puts on fat during its time at Salton Sea (Yoshida 2016), it seems reasonable that an individual could be present at Salton Sea for about a month. When the grebes prepare to migrate to Great Salt Lake, they swim to the northern end of the Sea in order to decrease the distance (~50 km) that they have to fly as they continue their migration (Jehl and McKernan 2002).

Grebes preparing to depart at the north end of the lake were located farther offshore (~1 km), out of effective telescope range, so no meaningful observations of their behavior could be made by me. Since grebes preparing to leave typically stop feeding as they prepare to migrate (Jehl and McKernan 2002), they sacrifice

nothing by being farther offshore where pile worms are less common (Detwiler et al. 2002).

How Grebes Spend Their Time at Salton Sea

Dive bout time generally decreased throughout the season. This decrease could be related to the physiological state of the grebes, as later in the season (late March through late April), there is an increasing proportion of grebes preparing to migrate and these birds would have reduced their feeding. The decrease in diving also coincided with the typical timing (around March) for a pile worm spawning event (Carpelan and Linsley 1961). An increase in their food source could increase the capture efficiency of the grebes, thereby decreasing the need to spend time in dive bouts. Although, in 2014, I never observed this kind of feeding, which would have occurred at the surface, it was seen in March, 2016 (A.E. Henry pers. comm.), as noted below.

Grebes spent more time surface swimming and resting as the season progressed primarily because they dived less. Even as the length of the day increased, the extra proportion of the day was spent resting and swimming, but not diving. Regardless of physiological state, the amount of time that the grebes spent preening remained similar across each observational period because it is a maintenance behavior needed in order to maintain feather waterproofing.

Changes in Energy Budgets Across the Season

Due to the non-synchronous arrival and departure dates of the birds at Salton Sea during most of their post-wintering stopover, it is likely that individuals observed were in different physiological states. That is, during most

of my time at Salton Sea I observed a mix of grebes that were still actively feeding or preparing to migrate. That may be why the amount of energy expended ($\text{kJ}/\text{bird} \cdot \text{d}$) for the daylight hours at different times in the season were all roughly the same. However, there was an increase (28.3%) in the amount of energy expended from February to late April, which also happened to mirror the percent increase (28.4%) in the weight of the grebes. This seems to imply that difference in energy expenditure was driven by the costs associated with gaining weight, as opposed to how much time they spent in each behavior.

Even with the increase in weight, I expected the energy expenditure to be lower in late April, when the majority of the grebes are preparing to migrate. Although the amount of daily energy spent diving was relatively low late April, there was an increase in the amount of time spent surface swimming, which drove up daily energy expenditure. Changes in energy allocation throughout the season could be indicative of both physiological demands at a given time and various ecological factors such as prey abundance and distribution, or abiotic factors. All feeding was assumed to occur during diving. Grebes have been observed surface feeding at Salton Sea in March, 2016 (A.E. Henry, pers. obs.) and again in late May among grebes that did not migrate out and were probably starving (T. Anderson, pers. comm.), but I never observed this phenomenon during my study.

The calculated daily energy expenditure (DEE) can be compared to the basal metabolic rate (BMR) in terms of a ratio. According to Drent and Daan (1980), the DEE/BMR ratio of a "non-molting, non-reproductive" bird averages around 2.6. The ratio that I calculated for the Eared Grebes ranges from 2.47 (late

Table 4.1: **Salton Sea Eared Grebe Energy Budgets:** Amount of energy expended ($\text{kJ}/\text{bird} \cdot \text{d}$) at Salton Sea for each observational time period and DEE as compared to BMR ($0.592 \text{ kJ}/\text{g} \cdot \text{d}$; Ellis and Jehl 2003). Mass data are taken from Jehl (1997). The mass-specific BMR is calculated by multiplying the BMR by the mass of an average grebe during the appropriate time period.

Observational Period	Mass (g)	DEE (kJ/bird · d)	Mass-specific BMR (kJ/bird · d)	DEE/BMR
Late February	320	478.21	189.44	2.52
Early March	384	583.83	227.33	2.57
Late March	384	560.68	227.33	2.47
Early April	411	631.00	243.31	2.59
Late April	411	613.69	243.31	2.52

March) to 2.59 (early April; Table 4.1), based on a BMR of 0.592 kJ/g·d (units modified from Ellis and Jehl 2003).

Comparisons with Grebes Elsewhere

Time-Activity Budgets at Other Lakes

Time-activity budgets for Eared Grebes have also been made at Great Salt Lake (Caudell and Conover 2006) and Lake Abert (Boula 1985), a minor post-breeding staging ground in Oregon. These can be compared to the time-activity budgets that were determined for grebes at Salton Sea (Table 4.2).

The grebes spent the least amount of time in dive bouts at Salton Sea. This is likely due to the fact that the grebes feed on a prey item (pile worms) that has a much higher caloric value than prey at the other lakes. This is probably true even if a grebe were to eat several brine shrimp, for example, on a single dive (see p. 65, below). This dive bout behavior represents all daylight foraging, since the grebes I observed did not surface feed at Salton Sea. The highest amount of time spent in dive bout behavior occurred at Great Salt Lake during both the spring/summer (May to August) and fall (September to November) time periods. This fits with post-breeding grebes in the fall because these grebes are putting on fat in order to migrate. The Lake Abert dive bout behavior was representative of the entire post-breeding staging period (June through October), which also included grebes preparing to migrate. Only grebes just arriving at Salton Sea dived as much as grebes at Great Salt Lake. Of the behaviors compared, surface swimming was the least variable at 20-40%.

Table 4.2: **Time-Activity Budget Comparison:** Comparison of time-activity budgets (percent of time spent in each behavior) for Eared Grebes at Great Salt Lake during the summer and fall (numbers in table inferred from time-activity budget graphs in paper; Caudell and Conover 2006), Lake Abert (Boula 1985), and Salton Sea (this study). In order to properly compare the time activity budgets resting and preening were combined into "Other" behaviors for Lake Abert and Salton Sea.

Behavior	Great Salt Lake (Caudell and Conover 2006)		Lake Abert (Boula 1985)	Salton Sea (this study)		
	Summer	Fall	Fall	Late Feb - Early Mar	Late Mar - Early Apr	Late Apr
Dive Bout	59.0	66.0	31.0	37.2	12.0	12.2
Surface Swimming	20.8	19.7	39.0	28.6	39.9	38.0
Other	20.0	14.2	30.0	34.2	48.1	49.8

Energy Budgets of Grebes at Other Lakes

Conover and Caudell (2009) published an energy budget for Eared Grebes at Great Salt Lake for November when the grebes were still actively feeding. Conover and Caudell (2009) used energy equivalents that they had developed, and derived a budget where the total DEE ($390.6 \text{ kJ/bird} \cdot \text{d}$) was $1.2 \times \text{BMR}$ ($325.6 \text{ kJ/bird} \cdot \text{d}$), which is an extraordinarily low multiple, for an actively diving bird. Looking at a limited data set, Drent and Daan (1980) suggested that $4 \times \text{BMR}$ (based on passerines) might be a maximum multiple. Lindstrom and Kvist (1995) looked at 21 passerine migratory species and, estimating DEE by maximum energy intake, found DEE/BMR ratios ranging from 3.64 to 5.56, with no individual below 2.94. Ellis and Gabrielsen (2002) in a meta-analysis of 37 seabirds found a range from 1.8 to $4.8 \times \text{BMR}$. Recently, Marteinson et al. (2015) found in Ring-billed Gulls (*Larus delawarensis*) a DEE only $1.4 \times \text{BMR}$, but an analysis of time-activity budgets revealed that the birds spent appreciable time (70%) on their nest. The value of $1.2 \times \text{BMR}$ reported by Conover and Caudell (2009) appears to be the lowest multiple in the literature. It is hard to conceive that a swimming, diving, active bird could have a daily energy expenditure barely above its basal rate. Because of this concern, I used the energy equivalents of Ellis (1994) to create energy budgets not only from my Salton Sea time-activity data, but those of Boula (1985) for grebes at Lake Abert. I calculated the time-activity data of Caudell and Conover (2006) using the Ellis energetic costs to create a comparable Great Salt Lake energy budget for grebes. Using these budgets, I am able to compare the energy budgets at two points in the grebes' annual cycle:

(1) fall staging (Great Salt Lake and Lake Abert); and (2) post-wintering stopover (Salton Sea; Fig. 4.1).

When using the Ellis (1994) energy equivalents, the DEE/BMR ratio fell in the same range for the three lakes (Salton Sea: 2.41; Lake Abert: 2.63; and Great Salt Lake: 2.26). This is well within the range of multiples seen in other birds, as noted above. Even though Conover and Caudell (2009) calculated the same BMR as Ellis and Jehl (2003), when using their energy equivalents at Great Salt Lake the DEE/BMR ratio drops to 1.19 (Fig. 4.1). Compared to all other areas, the grebes at Salton Sea allocate the least amount of DEE to dive bout behavior. As noted, this is most likely due to the fact that each pile worm at Salton Sea has a caloric content (0.584 kJ/individual) that is roughly thirty times as high as that of brine shrimp or brine fly pupae (0.019 kJ/individual), which are the prey items of the grebes at the other lakes. Assuming that grebes eat an average of about 33,000 brine shrimp per day (calculated from Cooper et al. 1984) with a true digestibility of 87% (Conover and Caudell 2009), their daily energy intake would be equivalent to 546 kJ. In order to match the same energy intake, a grebe would need to eat 1167 pile worms (adjusted for true digestibility), which is similar to what I calculated (981-1295 pile worms; Table 3.5) based on the energetic expenditure of grebes at Salton Sea.

Grebes expended the same amount of energy in dive bouts at Salton Sea and Lake Abert, and three to four times as much at Great Salt Lake (using Ellis 1994 energy equivalents; Fig. 4.1). Based on the higher caloric value of pile worms, as opposed to brine shrimp, the grebes could have a higher caloric intake.

Figure 4.1: **Eared Grebe Energy Budgets:** Amount of energy expended (kJ/d · bird) during multiple points in the grebes' annual cycle for: grebes at Salton Sea (SS; this study); grebes fall staging at Lake Abert (LA; Boula 1985); and grebes actively feeding at Great Salt Lake in November (GSL (Ellis); Conover and Caudell 2009). For the first three bars, energetic costs determined by Ellis (1994) were used. For the fourth bar (GSL (C&C)), energetic costs determined by Conover and Caudell (2009) were used. Daily energy expenditure and DEE/BMR ratio is found in the table below the graph. Colors as described in Fig. 3.1.

Lake	SS	P	DB	R	DEE	DEE/BMR
SS	201.3	38.1	81.6	209.7	530.7	2.41
LA	231.5	67.1	112	133.3	543.9	2.63
GSL (Ellis)	50.6	29.7	321.8	335	737.1	2.26
GSL (C&C)	14.9	15.4	148.5	207.5	386.3	1.19

This seems to suggest that they are putting on fat at Salton Sea. This is supported by Yoshida (2016), which showed that the levels of triglycerides (used in putting on fat) in Eared Grebes at Salton Sea were higher than at either Mono Lake (fall) or Great Salt Lake (spring) Eared Grebes. Yoshida also found that there is no pattern in the relationship of triglycerides in the grebes at Salton Sea with mass, which further indicates that the grebes are in different physiological states during the same time period. However, at Great Salt Lake, the level of triglycerides increases with mass, which indicates that the population of grebes tends to arrive and put on fat more synchronously there (Caudell and Conover 2006).

The grebes expended the greatest amount of energy in dive bout behavior at Great Salt Lake. This may be because November is when the brine shrimp population would have begun to decline, causing them to spend more time looking for food (diving). The daily energy expenditure of grebes at Great Salt Lake and Lake Abert are both from their fall staging. However, the grebes at Great Salt Lake had a higher daily energy expenditure, when using Ellis (1994) energy equivalents, perhaps because of their much higher diving.

For all of these time periods, resting accounts for about a third of daily energy expenditure because grebes are presumed to be inactive at night. For the energy budget calculations at Great Salt Lake (Conover and Caudell 2009), all of the nighttime hours were assumed to be resting, and did not include surface swimming to a roost site as was the case at Salton Sea. This is another reason why the grebes spent so little of their daily energy expenditure surface swimming at Great Salt Lake, as compared to the other lakes. The amount of daily energy

expenditure spent preening was roughly the same at Salton Sea, Great Salt Lake, and Lake Abert, as might be expected for a behavior associated with the feather maintenance and waterproofing in a waterbird.

Energy Budgets of Other Waterbirds

Body mass is the most important predictor of metabolic rates, including overall daily energy expenditure (Nagy 1987). As Fig. 4.2 shows, energy expenditure (kJ/h) generally increases with mass. Whether expressed on a whole-bird or mass-specific basis, Eared Grebes fall close, though slightly below, the expected levels for energy expenditure. The relationship of energy expenditure to mass between diving waterbirds alone ($DEE = 0.03 \text{ Mass} + 19.00$) did not differ appreciably from that of when grazing (herbivorous) birds were also included ($DEE = 0.02 \text{ Mass} + 24.21$). The Great Cormorant points, enclosed in in the separate black box represent birds that were spending the majority of their time incubating their eggs (lower point) and birds that were feeding and raising chicks (higher point). Diving birds had a higher mass-specific energy expenditure than grazing birds, presumably because diving has a higher energetic cost than grazing.

Methodological Assessment

Comparison of Focal Animal and Scan Sampling

There are two main observational methods that are accepted in the literature for creating time-activity budgets: scan sampling and focal animal sampling. Each of the methods is useful for studying different species. Scan sampling is best used for observing species that do not periodically disappear from the view of the observer and do not cluster in large groups. The grebes at

Figure 4.2: **Daily Energy Expenditure of Waterbirds in the Literature:** Whole animal DEE (A) and mass-specific DEE (B) of waterbirds in the literature.

Diving waterbirds are enclosed by the black boxes. Two values were used for Great Cormorants incubating and raising chicks, however only the energy expenditure for the cormorants raising chicks was used in the calculation of the trendline. The average amount of energy that Eared Grebes expended at Salton Sea (this study), Mono Lake (Ellis 1994; based on two birds from Jehl 1988), and Great Salt Lake (using energy equivalents of Ellis 1994) are shown in red. Energetic costs for Great Salt Lake Eared Grebes are shown using both Conover and Caudell (2009) and Ellis (1994) energy equivalents. These two points are connected by a black line. A) Log-log plot of energy expenditure of waterbirds. B) Log-log plot of mass-specific energy expenditure. All points were included in the calculation of the trendlines. All data may be found in Table 4.2.

Table 4.3: **Daily Energy Expenditure of Waterbirds in the Literature:** List of studies that have calculated the energy expenditures of various species of waterbirds.

Species	Season	Average Mass (g)	Length	Energy Expenditure (kJ/day)	Energy Expenditure (kJ/g ^{0.75} h)	DEE/BMR	N	Foraging Method	Reference
American Black Duck (<i>Anas rubripes</i>)	Wintering	1000	24	1394	0.058	2.21	--	Dabbling	Morton et al. 1989
American Black Duck (<i>Anas rubripes</i>)	Summer (Molt)	1000	24	669	0.028	2.08	--	Dabbling	Wooley and Owen 1978
Ring-necked Ducks (<i>Aythya collaris</i>)	Wintering	700	24	678	0.040	1.94	220.5 h	Diving	Jeske and Percival 1995
Bufflehead (<i>Bucephala albeola</i>)	Wintering	388	24	1176	0.126	5.8	80 h	Diving	McKinney and McWilliams 2005
European Wigeon (<i>Anas penelope</i>)	Wintering	680	24	630	0.039	--	--	Grazing	Mayhew 1988
Atlantic Brant (<i>Branta bernicla hrota</i>)	Wintering	1390	24	1530	0.046	--	--	Grazing	Ladin et al. 2011
Greater Snow Goose (<i>Chen caerulescens atlantica</i>)	Spring Staging	3062	24	1689	0.023	2.45	--	Grazing	Bedard and Gauthier 1988
Barnacle Goose (<i>Branta leucopsis</i>)	Wintering	1790	24	976	0.023	--	--	Grazing	Owen et al. 1992
White-fronted Goose (<i>Anser albifrons albifrons</i>)	Wintering	2400	24	1750	0.030	--	440 h	Grazing	Mooij 1992
Bean Goose (<i>Anser fabalis rossicus</i>)	Wintering	3500	24	2360	0.028	--	440 h	Grazing	Mooij 1992
Great Cormorant (<i>Phalacrocorax carbo sinensis</i>)	Incubating Feeding Chicks	2230	24	789	0.015	1	--	Diving	Gremillet et al. 1995
				1913	0.036	2.3			
Least Auklets (<i>Aethia pusilla</i>)	Breeding	84	24	350	0.174	3.03	--	Diving	Obst et al. 1995
Cassin's Auklets (<i>Ptychoramphus aleuticus</i>)	Nesting	174	15	413	0.158	--	--	Diving	Hodum et al. 1998
Common Murre (<i>Uria aadige</i>)	Nesting	940	24	1789	0.079	--	--	Diving	Cairns et al. 1990
Black Guillemot (<i>Cepphus grylle</i>)	Nesting	380	24	860	0.094	3.17	--	Diving	Mehlum et al. 1993
Dovekie (<i>Alle alle</i>)	Nesting	164	24	696	0.177	3.9	--	Diving	Gabrielsen et al. 1991
Eared Grebe (<i>Podiceps nigricollis</i>)	Fall Staging (November)	550	24	391 (Conover and Caudell 2009 energetic costs)	0.030	1.19	--	Diving	Conover and Caudell 2009
Eared Grebe (<i>Podiceps nigricollis</i>)	Fall Staging (November)	550	24	737 (H.I. Ellis, unpubl. data energetic costs)	0.056	2.26	--	Diving	Conover and Caudell 2009
Eared Grebe (<i>Podiceps nigricollis</i>)	Summer Post-Breeding (July)	350	24	527.1	0.063	2.54	12.65 h	Diving	H.I. Ellis, tech. report
Eared Grebe (<i>Podiceps nigricollis</i>)	Post-Wintering Stopover	404	24	582.6	0.060	2.44	22.23 h	Diving	This Study

Salton Sea and Mono Lake rarely form distinct, small groups of individuals, rather they were spread out in large flocks, comprised of hundreds of individuals making it impossible to scan the entirety of one flock.

For this particular study, the most accurate way to determine time-activity and energy budgets for the grebes at Salton Sea and Mono Lake was using focal animal sampling. At Mono Lake, focal animal sampling revealed more diving activity (p-value < 0.001) and less resting (p-value = 0.004 (August) and p-value < 0.001 (October)) than seen using scan sampling in both August and October. This has to do with the nature of a dive bout. A dive bout is a series of dives interrupted by time spent on the surface: resting, surface swimming, or preening. Although the bird is primarily engaged in diving, the diving behavior cannot be recognized unless the bird is breaking the surface of the water. Consequently, much of dive bout behavior is scored in scan sampling as one of the surface activities, thus severely underestimating the percent of time spent in a dive bout. Because it was impossible to account for the number of grebes underwater during each instantaneous observation, the surface behaviors, surface swimming, resting, and in August preening, were overestimated. Using scan sampling observations, it is difficult, if not impossible, to determine whether an individual being observed at the surface is in the surface portion of a dive bout or not.

This same problem seemed to emerge in the work of Boula (1985), who studied the Eared Grebes at Lake Abert, another fall staging lake. In her study, which used both methods, she found grebes spent a little more than double the amount of time diving in her focal animal samples as opposed to her scan

samples. Also, surface swimming, preening, and "other" behaviors had a higher occurrence in her scan sample data than in her focal animal data, which makes sense if the grebes could not be identified when in the surface portion of a dive bout.

On the other hand, it is not impossible to use scan sampling as a way to accurately estimate the time-activity budgets of Eared Grebes. For example, Caudell and Conover (2006) were able to find one location at Great Salt Lake where grebes were found in distinct groups of about 12 individuals. When grebes are in small groups, it is possible to know the number of birds underwater by knowing the exact number of individuals in the group being observed. However, the comparison of methods at Mono Lake, shown in Figure 3.6, demonstrates that this was not the case for larger groups typically found there and at Salton Sea.

Caveats and Considerations for the Future

While I have presented a daytime time-activity and energy budget for the grebes at Salton Sea, it is still unknown if grebes are resting ("sleeping") at night as at Mono Lake (Jehl 1988) and Great Salt Lake (Caudell and Conover 2006) or if they are occasionally active. Because moonlit nights might provide enough light for grebes to see and pile worms breed at night during full moons, grebes might feed at night. In that case, my energy budget might be an underestimate. The energy budgets that have been calculated at Salton Sea might also be conservative because they do not take into account the cost of putting on fat. Since these grebes are in different physiological states due to their non-

synchronous arrival times, it is difficult to determine what portion of the population is actively putting on fat.

Grebes', and other waterbird species', migration routes and patterns are highly plastic and flexible (Zink 2002), which means that they can make changes in their migrations relatively quickly. The Salton Sea is expected to shrink considerably as the City of San Diego diverts water from its sources beginning in 2016. This would increase the salinity, and the grebes' main food source (pile worms) is likely to be affected (Kuhl and Oglesby 1979). The increase in salinity is also likely exacerbated by the current drought in the area, and the future of North American Eared Grebes might be greatly affected, because Salton Sea is the only remaining stopover point on the grebes' long vernal movement from the Gulf of California to Great Salt Lake.

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Appendix A: Observation dates for scan and focal animal samples (2014) at
Salton Sea and Mono Lake.

Table A-1: **Observation Dates (2014):** Dates that the scan sample and focal animal sample observations took place at Salton Sea and Mono Lake.

Lake	Scan Samples (2014)	Focal Animal Samples (2014)
Salton Sea	--	Feb 21 - 23
	--	Mar 10 - 12
	--	Mar 27 - 29
	--	Apr 11 - 13
	--	Apr 26 - 28
Mono Lake	Aug 22 - 23	Aug 22 - 23
	Oct 13 - 14	Oct 13 - 14

Appendix B: Salton Sea time-activity budgets for late February, early April, and
late April.

Late February

Kruskal-Wallis evaluations revealed no differences at the $p \leq 0.1$ level for surface swimming, resting, dive bout behavior, or preening, in spite of an apparent decrease in preening during midday in Fig. B-1 (see also Table 3.2). A power analysis indicated that small sample size may have contributed to the high p-values.

Early and Late April

There were no statistical differences below $p \leq 0.1$ in any of the behaviors with respect to time of day early in April or late in the month (Table 3.2; Fig. B-2). As in late February, a power analysis indicated that small sample size could have contributed to the high p-values seen during these time periods.

Figure B-1: **Salton Sea Time-Activity Budgets (Late February):** The percent of time spent in each behavior during daylight for late February at Salton Sea.

Surface Swimming (SS): blue, Preening (P): red, Dive Bout (DB): green, and Resting (R): purple.

Late February (N)	SS ($\pm$ s.e.)	P ($\pm$ s.e.)	DB ($\pm$ s.e.)	R ($\pm$ s.e.)
Morning (N=5)	17.3 $\pm$ 5.4	25.2 $\pm$ 10.4	36.8 $\pm$ 19.4	20.7 $\pm$ 10.0
Midday (N=6)	39.3 $\pm$ 13.6	1.5 $\pm$ 0.9	34.9 $\pm$ 17.0	24.3 $\pm$ 10.8
Afternoon (N=6)	15.8 $\pm$ 9.7	20.1 $\pm$ 15.5	56.4 $\pm$ 20.3	7.8 $\pm$ 5.7

Figure B-2: Salton Sea Time-Activity Budgets (Early April and Late April):

The percent of time spent in each behavior during daylight for early April, and late April at Salton Sea. Colors as described in Figure 3.1.

Early April	SS ($\pm$ s.e.)	P ($\pm$ s.e.)	DB ($\pm$ s.e.)	R ($\pm$ s.e.)
Morning (N=4)	50.9 $\pm$ 9.2	14.1 $\pm$ 7.5	7.9 $\pm$ 5.2	27.1 $\pm$ 8.3
Midday (N=6)	41.3 $\pm$ 5.6	20.2 $\pm$ 13.2	8.5 $\pm$ 8.5	30.0 $\pm$ 10.9
Afternoon (N=21)	49.3 $\pm$ 6.0	11.6 $\pm$ 3.9	9.2 $\pm$ 5.0	29.9 $\pm$ 4.3

Late April	SS ($\pm$ s.e.)	P ($\pm$ s.e.)	DB ($\pm$ s.e.)	R ($\pm$ s.e.)
Morning (N=11)	48.8 $\pm$ 10.2	16.9 $\pm$ 8.5	7.2 $\pm$ 2.9	27.1 $\pm$ 6.5
Midday (N=12)	28.0 $\pm$ 9.4	25.8 $\pm$ 10.9	20.7 $\pm$ 9.6	25.6 $\pm$ 7.4
Afternoon (N=21)	38.1 $\pm$ 7.7	11.8 $\pm$ 5.5	10.0 $\pm$ 6.5	40.1 $\pm$ 6.7

Appendix C: Mono Lake time-activity and energy budgets

Mono Lake Focal Animal Sample Data

While the time-activity budget data collected at Mono Lake does not directly fall into the main research on Salton Sea that is covered in this thesis, it may be of value as preliminary data for what the grebes do while there. These data cover two time periods that the grebes are at Mono Lake: toward the beginning of their post-breeding staging (late August) and towards the end of it (mid-October). It should be noted that the surface swimming behavior category also includes any observations of surface swimming and feeding.

Figure C-1: **Mono Lake Time-Activity Budgets (Late August and Mid-October):** The percent of time spent in each behavior over the course of the day for Late August, and mid-October at Mono Lake. Colors as in Figure 3.1.

Late August	SS (± s.e.)	P (± s.e.)	DB (± s.e.)	R (± s.e.)
Morning (N=14)	26.7 ± 5.3	10.9 ± 5.9	25.0 ± 8.9	37.5 ± 6.6
Midday (N=18)	21.8 ± 6.2	8.9 ± 3.1	36.6 ± 7.4	32.7 ± 7.0
Afternoon (N=35)	33.8 ± 5.7	17.2 ± 4.1	23.7 ± 5.6	25.3 ± 4.0

Mid-October	SS (± s.e.)	P (± s.e.)	DB (± s.e.)	R (± s.e.)
Morning (N=24)	4.5 ± 1.2	27.3 ± 6.2	44.2 ± 7.7	24.0 ± 4.1
Midday (N=32)	23.2 ± 5.5	10.5 ± 4.3	54.9 ± 7.2	11.4 ± 3.0
Afternoon (N=24)	32.8 ± 5.3	20.9 ± 6.0	26.6 ± 6.4	19.7 ± 4.7

Figure C-2: **Mono Lake 24-Hour Energy Expenditure:** Total energy expended per behavior (kJ/bird · d) during the two sampling periods at Mono Lake, as well as total amount of energy expended (kJ/bird · d) for each observational period. Colors as described in Figure 3.1.

Mono Lake	SS	P	DB	R	Total	DEE/BMR
Late August	235.3	35.1	167.0	163.6	601.0	2.90
Early October	272.2	60.3	299.6	230.1	862.2	2.91