Summer 2014

Turn of Events: How environmental temperatures and artificial nest habitats influence incubation behaviors of Cassin's auklets (Ptychoramphus aleuticus)

Emma Kelsey
San Jose State University

TURN OF EVENTS: HOW ENVIRONMENTAL TEMPERATURES AND ARTIFICIAL NEST HABITATS INFLUENCE INCUBATION BEHAVIORS OF CASSIN'S AUKLETS (*PTYCHORAMPHUS ALEUTICUS*)

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Emily Cashman Kelsey

August 2014

The Designated Thesis Committee Approves the Thesis Titled

TURN OF EVENTS: HOW ENVIRONMENTAL TEMPERATURES AND ARTIFICIAL NEST HABITATS INFLUENCE INCUBATION BEHAVIORS OF CASSIN'S AUKLETS (*PTYCHORAMPHUS ALEUTICUS*)

by

Emily Cashman Kelsey

APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

SAN JOSE STATE UNIVERSITY

August 2014

Dr. Scott Shaffer	Department of Biological Sciences
Dr. Luis Bonachea	Department of Biological Sciences
Dr. Jaime Jahncke	Point Blue Conservation Science

ABSTRACT

TURN OF EVENTS: HOW ENVIRONMENTAL TEMPERATURES AND ARTIFICIAL NEST HABITATS INFLUENCE INCUBATION BEHAVIORS OF CASSIN'S AUKLETS (*PTYCHORAMPHUS ALEUTICUS*)

by Emily Cashman Kelsey

Nest attendance behaviors are critical to hatching success for most bird species. Yet, details of avian incubation behaviors are still not well understood, especially for species that nest in burrows and crevices. Cassin's auklet (*Ptychoramphus aleuticus*) is a burrow-nesting seabird found throughout the northeastern Pacific Ocean, including Southeast Farallon Island, California (SEFI). Artificial nest boxes have been used to monitor Cassin's auklets (hereafter auklet) breeding on SEFI. Temperatures in un-shaded nest boxes can increase significantly during extreme heat events. The effects of these elevated temperatures on auklet incubation behaviors and egg viability are not clear. In this study, egg data loggers were used to measure egg temperatures and turning rates of auklet eggs in natural burrows, shaded nest boxes, and un-shaded nest boxes on SEFI during the 2012 and 2013 breeding seasons. Nest temperatures were highest and most variable in un-shaded nest boxes. Egg temperatures were highest in un-shaded boxes. Egg turning rates and egg temperature decreased during the night. During the day, egg turning rates increased with nest temperature. Overall, the results of this study show that nest habitat type can influence auklet incubation behaviors and temperatures. Increasing environmental temperatures could affect breeding Cassin's auklets, and mechanisms to further mitigate these effects should be considered.

ACKNOWLEDGEMENTS

First and foremost I would like to thank my adviser, Dr. Scott Shaffer for the opportunities, encouragement, and advice he has continually given me. I would also like to thank my committee members, Dr. Luis Bonachea and Dr. Jaime Jahncke for their support and instruction.

I owe much gratitude toward Point Blue Conservation Science for their collaboration on this project, most importantly Pete Warzybok and Russ Bradley for their assistance in the field and out. I thank the US Fish and Wildlife Service for permission to conduct this work on SEFI, and the volunteer Farallon Patrol for providing transportation to and from the island. For help with my fieldwork I want to thank Ryan Berger, Sophie Webb, Ilana Nimz, Laney White, Scarlett Hutchin, Aniko Tutha, and all the other residents of SEFI during the 2012 and 2013 seabird seasons.

I am appreciative of Corey Clatterbuck for our ongoing collaboration and grateful to the members of the ShAPE lab for their day-to-day support. I am indebted to Kat McKinnon and Philip Priolo of the Fine Art and Industrial Design departments at San Jose State University for creating the artificial eggs used in the project. For statistical advising, I would like to think Erika Taketa, Hongyue Song, and Xiangchao Qin of the Mathematics department at San Jose State University. I also would like to say thanks to Stephanie Flora of Moss Landing Marine Labs for her MATLAB wisdom.

For funding for this project, I am grateful to the CSU COAST program, CSUPERB, The Myers Oceanographic and Marine Biology Trust, and San Jose State University Biological

Sciences department fellowship and scholarship programs. Other SEFI funding was provided by the US Fish and Wildlife Service, the Baker Trust, the Campini Mead, Kimball, and Marisla foundations, and individual donors to Point Blue.

TABLE OF CONTENTS

LIST OF FIGURES

Figure

LIST OF TABLES

Table

1. Introduction

Most bird species engage in nest attendance behaviors during the incubation period. During this time they turn their eggs and maintain egg temperature through direct contact with a vascularized brood patch and/or their feet (Deeming, 2002a; Eycleshymer, 1907). Although incubating an egg incurs a cost for the bird (Reid et al., 2000; Shaffer et al., 2001; Vleck, 1981), it is essential for proper embryonic development, hatching success, proper chick health, and overall reproductive success (Astheimer 1991; DuRant et al., 2013; Reid et al., 2000; Tullett & Deeming, 1987; Weimerskirch 1995). For these reasons, optimal incubation temperatures and egg turning rates have been studied extensively in the poultry industry to maximize the hatchability of domestic fowl (Deeming, 1989; Elibol & Brake, 2006; Hepp et al., 2006; New, 1957; Tona et al., 2005). In contrast to studies on domestic species, the factors that influence the optimal egg temperatures and turning rates of wild birds are not well understood.

Most studies that have examined the effects of egg temperature variation on incubation in wild birds have focused on the influence and effects of egg cooling (Reneerkens et al., 2011; Turner, 2002; Williams & Ricklefs, 1984). When eggs are exposed to temperatures below "physiological zero" (26°C), embryonic development is suspended, thus delaying hatching (Astheimer, 1991; Deeming, 2002a). Egg cooling most commonly occurs when parents leave an egg unattended for prolonged periods (egg neglect; Astheimer, 1991; Bennett et al., 1981; Williams & Ricklefs, 1984).

Conversely, less is known about the effects of hyperthermic incubation conditions on embryonic development and hatching success of birds, though increased incubation temperatures are thought to be more detrimental to the embryonic development of chicks than hypothermic temperatures (Conway & Martin, 2000; Nichelmann, 2001; Pipoly et al., 2013; Webb, 1987). Increasing environmental temperature can affect the morphology and physiology of reptile embryos, especially prolonged heat exposure for reptiles that are not used to elevated temperatures (Bell et al., 2012; Booth, 2006). Heat effects could be similar in birds. When certain nesting conditions create atypically warm environments (i.e., intensity of sun exposure to the bird, its nest, or its burrow), parent birds could have difficulty maintaining optimal temperature for themselves and their eggs. Climate models predict, and weather observations confirm, that global temperatures are increasing (Mahlstein et al., 2013; Schaper et al., 2012). The effects of elevated temperatures on avian incubation are becoming progressively important for some bird species (Matthysen et al., 2011; Pipoly et al., 2013; Vedder 2012).

The Cassin's auklet (*Ptychoramphus aleuticus*) is a small, diving seabird found throughout the Northeastern Pacific Ocean from Northern Mexico to the Bering Sea (Manuwal, 1974a). Cassin's auklet (hereafter auklet) lays a single egg in a burrow or crevice, which is incubated continuously for approximately 39 days (37-42; Manuwal, 1974a). Both parents exchange egg attendance duties on a nightly basis. On Southeast Farallon Island (SEFI) off the coast of San Francisco, California, the breeding biology of

the Cassin's auklet has been studied by researchers from Point Blue Conservation Science (formally known as Point Reyes Bird Observatory) for over 40 years. Artificial nest boxes have been installed on the island to monitor auklet breeding biology. In recent years, auklets nesting in artificial nest boxes exposed to direct sunlight have experienced hot ambient temperatures, which have caused heat stress and even death of multiple individuals during an extreme event in 2008 (Warzybok and Bradley, 2008). Subsequent monitoring indicated that artificial nest boxes were significantly warmer than natural burrows, and that shaded structures placed on top of nest boxes could mitigate these elevated nest box temperatures (Warzybok and Bradley, 2010). The effects of these elevated temperatures on the nesting auklets are a clear concern, but the effects on the incubation behaviors of the auklets are unknown. Furthermore, annual maximum temperatures on SEFI have increased nearly 3-4°C since 1970 (Warzybok and Bradley, 2010). If this warming trend is to continue, it may impact the long-term productivity of auklet populations on SEFI and elsewhere in California.

Our understanding of incubation behaviors in wild birds has been hampered by limitations in technology capable of accurately monitoring parent incubation behavior (Beer, 1965; Drent, 1970; Gee et al., 1995; Howey et al., 1984). Recently, new technologies have overcome these limitations in monitoring incubation temperatures and egg turning by using data logging devices placed inside artificial eggs that are incubated by parent birds (Beaulieu et al., 2009; Shaffer et al., 2014; Thierry et al., 2013). Using this technology, I was able to examine the effects of environmental

temperature in natural and artificial nest habitats on the incubation behaviors of Cassin's auklets. The goal of my study was to determine if different nest habitat types (i.e., natural burrows, shaded nest boxes, and un-shaded nest boxes) influenced the egg temperatures and egg turning patterns of incubating auklets. I hypothesized that egg temperatures would be higher and more variable in warmer nest habitats and predicted that this trend would be most prominent in the un-shaded nest boxs. Secondly, I hypothesized that there would be a relationship between egg turning rates and nest temperatures, with the turning rate being negatively correlated with egg temperature. I predicted that as nest temperatures increase, auklet parents likely stand up off of their eggs to allow the eggs to cool and stay within optimal incubation temperatures. This would result in a putative reduction in the frequency of egg turning recorded by the egg loggers. Overall the results of my study could help illuminate the effects of increased nest temperatures on auklet health and reproductive success, and may help determine if further mitigation is necessary to offset future increases in global temperatures.

2. Method

2.1 Study Site and Species

Southeast Farallon Island (37°41'49"N 123°00'07"W, Figure 1) is part of the Farallon National Wildlife Refuge, located 48 km west of San Francisco, California. The reproductive success, breeding phenology, and diet of the auklet population on SEFI has been monitored since 1972. The current population is approximately 10,000 breeding pairs. Five hundred artificial nest boxes have been built to monitor breeding auklets without disturbing natural burrow and crevice habitat on the island.

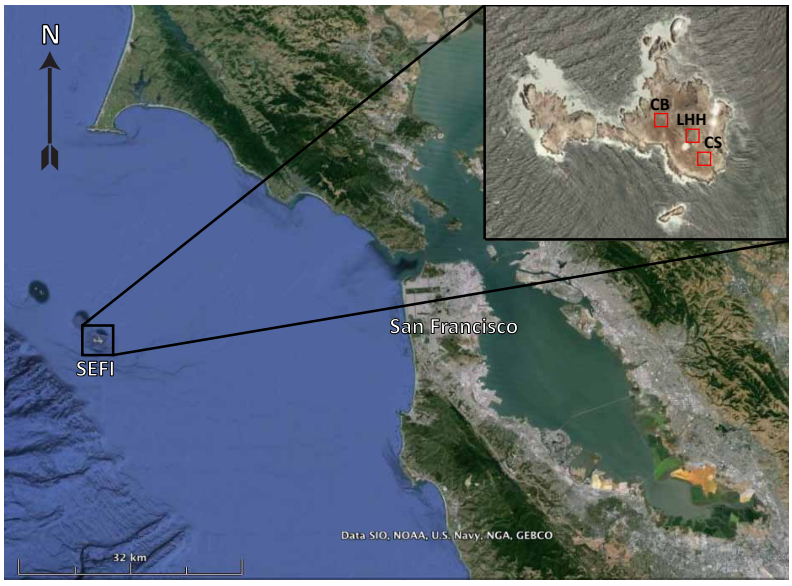

Figure 1: Southeast Farallon Island (SEFI), 48km west of San Francisco, California. **Inset:** Location of auklet habitats on SEFI used for egg logger deployments, CB= Cormorant Blind, LH= Lighthouse Hill, CS= Carpenter Shop. Source: "Southeast Farallon Island." 37°41'56.08"N 123°00'12.10"W. **Google Earth.** 2014. January 14, 20114.

Nest boxes are 20x23x40 cm boxes made out of cdx plywood with a 10 cm PVC pipe as an entrance (Figure 2).

A subset of occupied burrows and nest boxes spread across three regions of the island were used for this study (Figure 1, Appendix Table 1). Nest box checks and bird

handling followed established protocols (Pyle et al., 2001). All nest boxes were checked routinely to establish the lay date (within 14 days). All egg logger deployments occurred during early stages of incubation (within the first 20 days) because egg temperature, moisture content, and turning rates change across the incubation cycle (Roudybush & Hoffman, 1980; Turner, 2002). Therefore, I selected nests with eggs in the early stages of incubation to control for these variations. Natural burrow sites were selected from burrows in the same habitats as nest box sites (Figure 1).

All research was conducted in accordance with San José State University's Institution Animal Care and Use Committee approval (SJSU 978) and Point Blue Conservation Science protocols and Bird Banding Laboratory permit (09316). Special Use Permit 81640-2013-022 was granted by the US Fish and Wildlife Service for this study.

2.2 Egg Logger Deployment

Once nest sites were selected, an artificial egg containing an egg logger was deployed in each nest under an incubating adult auklet. Egg logger deployments lasted 5-10 days and occurred in nests with new eggs laid between April and July. A total of 34 deployments were conducted in 2012 and 41 in 2013 (Appendix Table A1, Figure A1).

LogTag ambient temperature loggers (MicroDAQ.com, Ltd., New Hampshire) recorded nest chamber temperature every 30 min. and were placed inside the corresponding nest of each egg logger deployment. Cassin's auklets lay a single egg per breeding attempt, so natural eggs were removed from the nest during egg logger

deployments, marked for specific nest identification, and incubated in a poultry incubator (Top Hatch Incubator; Brower Equipment, Houghton, IA) at approximately 35°C (95°F) and 55% humidity for the length of the deployment.

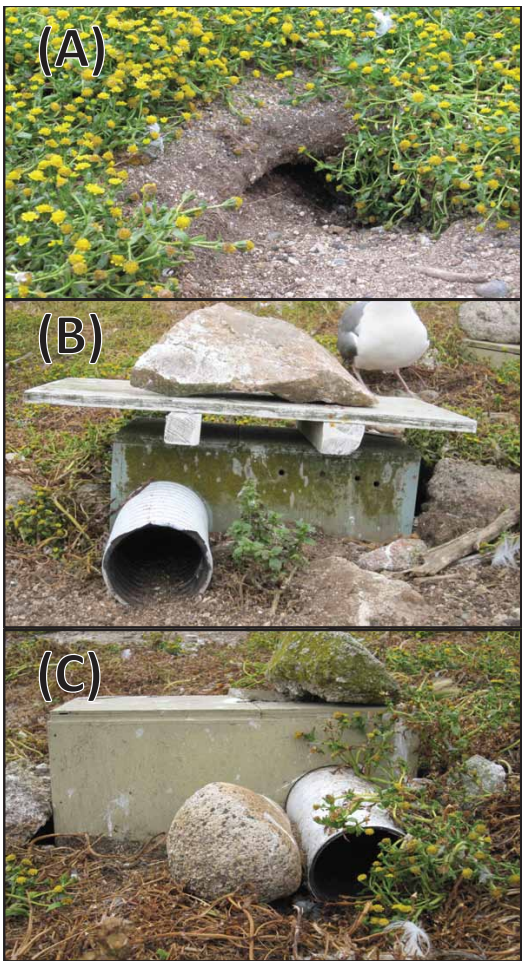

Figure 2: Different auklet nest habitat types on SEFI. (**A**) Natural Burrow, NB; (**B**) Shaded Nest Box, SB; (**C**) Un-shaded Nest Box, UB

Auklets were left undisturbed except for daily checks during the first two days of deployment, to verify the presence of an auklet in the nest. If an egg logger was abandoned or found un-incubated, it was removed and the natural egg was returned. Upon completion of a deployment period, all natural eggs were returned to their original nests. All nests used for egg logger deployments were followed for the remainder of the breeding season to determine the subsequent breeding success of each manipulated nest. The breeding success of study nests was also compared to un-manipulated nests.

Egg logger abandonment occurred, especially in the first egg logger deployments of 2012 (Appendix Table 1). Twenty-eight percent of auklets abandoned the egg logger within 1-2 days of deployment. However, 62% of these birds that abandoned their nests

returned after the natural egg was replaced, or re-laid and successfully hatched a chick later in the season. The overall number of breeding attempts abandoned after egg logger deployments was 8 of 74, or 11%.

2.3 Egg Logger Design

The egg data loggers used are fully described in Shaffer et al. (2014). In brief, egg loggers were placed inside a replica Cassin's auklet egg of the equivalent size and approximate mass (Table 1, Figure 3). Each logger contained a triaxial accelerometer and magnetometer to record orientation and angle changes (accurate to 1-2°) of the egg, as well as a temperature thermistor to record egg temperature (± 0.125°C), every second for durations of up to a week.

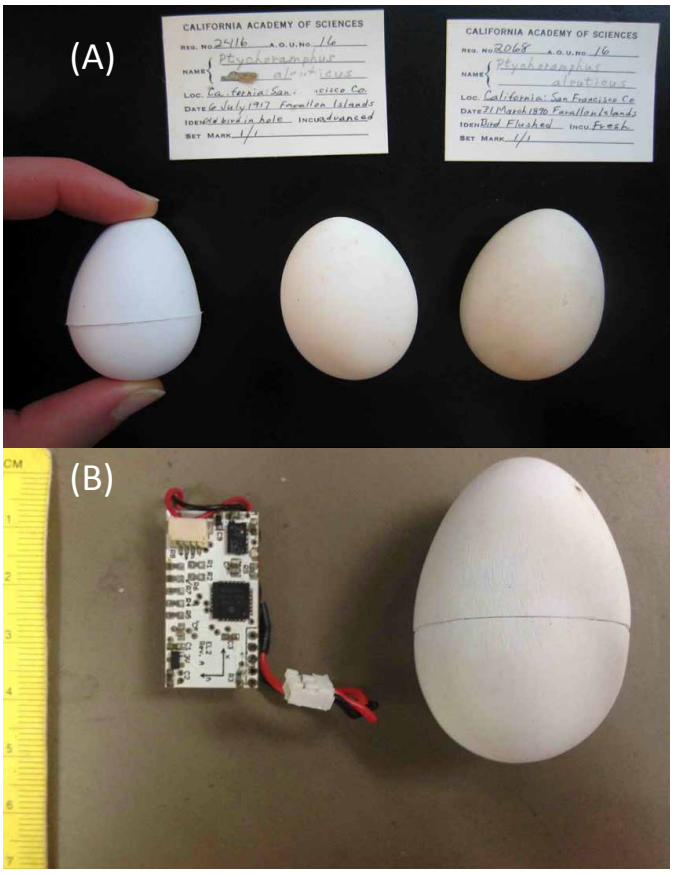

Figure 3: (**A**) An artificial and natural Cassin's auklet eggs. (**B**) Egg Logger and artificial Cassin's auklet egg.

Validation tests of egg logger function were performed using a standard poultry incubator (Top Hatch Incubator; Brower Equipment, Houghton, IA; the same incubator used to house natural auklet eggs during deployment). The rotation and temperatures recorded

by the egg loggers were compared to set turning rate and temperature of the incubator. A post processing animation of the egg logger's movement was also matched up with a video of the egg being manually moved to confirm that movements were detected in the same manner by both methods, thus confirming that the egg loggers were able to accurately measure egg temperature and movement along the x-, y-, and z-axes.

2.4 Artificial Egg Design

Artificial eggs were designed and manufactured by students in the Art and Industrial Design departments at San Jose State University. The size, shape, and color of the artificial eggs were based on historical measurements of auklet eggs (Manuwal, 1974a) and images of Cassin's auklets eggs from SEFI, housed in a permanent collection at California Academy of Sciences in San Francisco, California (Figure 3).

Artificial eggs were made of 1/8-inch vacuum-formed polystyrene plastic. Initial testing performed during the 2012 field season indicated that having the artificial eggs mass be equivalent to that of a natural auklet egg decreased abandonment rates by the auklet parents (Table 1). Therefore, artificial eggs were filled with non-ferrous barium sulfite ($BaSO_4$) and ClearGlide wire pulling lubricant (IDEAL Industries, Fort Lauderdale, FL) to increase the mass of the artificial egg without influencing the mechanics of the sensors in the logger (Table 1; Conway and Martin, 2000). Weighted eggs were used in all future deployments during the 2012 and 2013 seasons.

2.5 Data Processing

Nest Type Temperature - The nest temperature data was measured by the LogTags deployed in the nests chamber. The data from these devices were downloaded using LogTag software (MicroDAQ, Contoocook, NH). Nest temperatures were then converted to hourly averages for comparison with hourly averages of egg logger temperatures.

Table 1: Weights and temperatures of eggs used during deployments, compared to weight of natural auklet egg. Proper egg weighting decreased egg abandonment by auklets.

Weighting type	Deployment Date	Weight (g)	% natural egg weight	Abandonment Rate (%)	Ave. Temp. (°C)*
Natural egg (Manuwal 1972)	-----	27.5 (*n*=110)	----	----	----
None	4/17/2012	15.9 (*n*=18)	60	55.6	37.26 (*n*=4)
Gel	7/14/2013	22.8 (*n*=10)	83	40.0	37.76 (*n*=4)
Gel + $BaSO_4$	2013- all deployments	27.7 (*n*=24)	100	16.7	39.16 (*n*=4)

* Average temperatures of a subset of eggs were also compared to confirm that no significant difference in temperatures was found between eggs with different weighting techniques (ANOVA, F=1.27, df=2, p=0.33).

Egg Temperature and Turning - After each egg logger deployment, all data were extracted from the egg logger micro SD cards (SanDisk Coorporation, Milpitas, CA) and processed with custom routines created in MATLAB (The Mathworks, Natick, MA) following methods described in Shaffer et al. (2014). Raw accelerometer and magnetometer data were converted to 3-2-1 Euler angles (expressed as yaw, pitch, and

roll, Figure 4) to estimate instantaneous egg changes to quantify total turning rates (Shaffer et al. 2014).

To remove any potential influence on egg temperature and turning rates that could have been directly caused by experimental design during egg logger deployment and retrieval, the first six and last two hours of every deployment were not included in the analysis. The first six hours were eliminated to remove the time between when the egg loggers were turned on and when they were deployed (1-3 hours) and the initial time after the auklet was handled during deployment, in case the stress of handling influenced incubation behavior. Eliminating the last two hours from analysis removed the time between when the egg logger was recovered and when it was powered off. Based on known auklet incubation temperature ranges (Astheimer, 1991), temperatures below

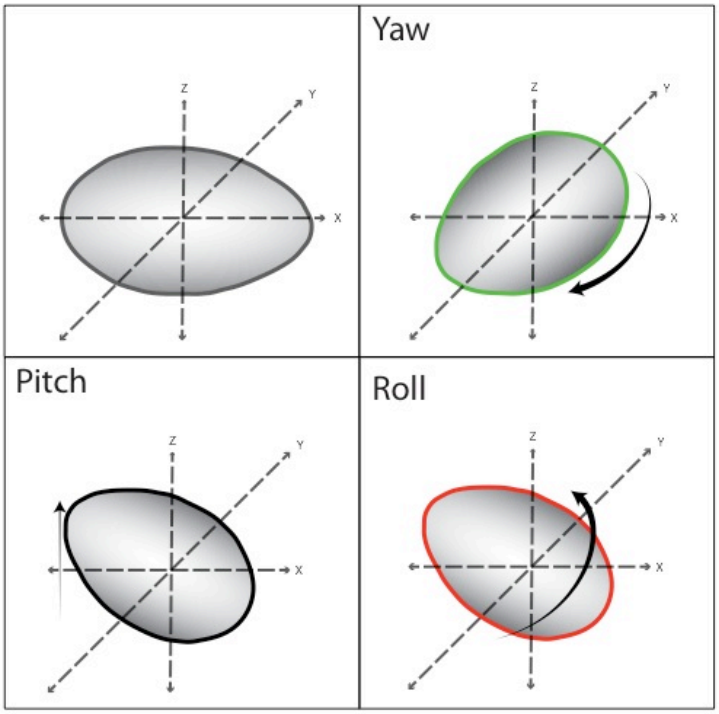

Figure 4: Graphical depiction of the conversion of egg movement along three axes (Yaw, Roll, Pitch) to 3-2-1 Euler angle changes. The egg orientation is achieved by rotating from North by the yaw angle about the Earth's fixed z-axis (down), then rotating by the pitch angle about his intermediated frame's y-axis, and rotating by the roll angle about the next frame's x-axis

30°C and above 42°C were also excluded from further analysis. This removed erroneous temperature measurements as well as data from when the egg was abandoned or neglected. Twelve of the 56 egg loggers used in this study were neglected for a period greater than three hours at some point during the deployment. These periods of neglect significantly decreased mean hourly turning rates and were therefore removed to not decrease the turning rate erroneously. Egg logger deployments containing less than 24 h of data after initial processing and clipping was also excluded. Once undesired data were clipped, the temperature data were smoothed using a running average over 5000 s (Shaffer et al., 2014).

Bird eggs have a unique chemistry and make up that, along with the influence of environmental temperatures, create distinct temperature gradients throughout the egg (Turner, 2002). Egg temperature also changes across the incubation phase, as the embryo develops (Nichelmann, 2001; Turner, 2002). Each egg logger had a single temperature thermistor located in the center of the egg so temperatures recorded in this study are considered core egg temperatures without gradients, and they are not exact temperatures of auklet eggs *in vivo*. Temperatures were tested to confirm that measurements were consistent between deployments (Table 1).

Turning rates were based on a minimum angle changes of 10° so that only deliberate movements made by the incubating auklet were analyzed. The 10° turning threshold (as used by Shaffer et al., 2014) approximated the cumulative inflection

between angle change and turning rates (Appendix Figure A2). It was also comparable to similar thresholds used in previous studies (Beaulieu et al., 2009; Thierry et al., 2013).

For the final analysis, I determined the total number of turns and average, maximum, and minimum temperatures for every hour of deployment. Daily turning rates and temperatures (mean, maximum, and minimum) were also analyzed based on hourly rates, starting at 12:00 midnight on each deployment day. Analyzing hourly turning rates followed methodology of historical egg turning studies (turns per hour, as seen in Deeming, 2002c). However, expressing turning rates on a daily basis provided a more ecologically relevant portrayal of egg turning behavior, as auklets usually switch incubation duties on a daily basis (Manuwall, 1972), and the daily turning rates were comparable to other recent studies of egg turning behavior using accelerometery (Beaulieu et al., 2010; Shaffer et al., 2014; Thierry et al., 2013).

Daytime and nighttime temperatures and turning rates were also analyzed separately. Day lengths were based on the date/time of local sunrise and sunset determined from ephemeris tables using the latitude and longitude of SEFI.

2.6 Statistical Analysis and Treatments

Nest Type Temperatures - Nest temperatures were tested for multicollinearity between nest temperature and time of day due to the cyclical diurnal cycling (Figure 5). Multicollinearity was not found to influence hourly nest temperatures. Regression analyses were performed in R (R Development Core Team 2014). The effects of nest type on nest temperature were evaluated using repeated measures analysis of variance

(ANOVA) of nest temperature at significance level α=0.05. Hourly nest temperatures were averaged for day and night time periods and were then compared between different nest types, with nest locations, deployment year, and day vs. night incorporated as fixed factors. Nest temperature ranges were analyzed by taking the difference between maximum and minimum hourly temperatures for each day, and averaging them by nest. This temperature difference was then compared between different nest types, nest locations, and deployment years using multi-way ANOVA tests. ANOVA tests were performed in R (R Development Core Team, 2014).

Egg Temperatures - The effects of nest type on egg temperature were evaluated using repeated measures analysis of variance (ANOVA) of egg temperature at significance level α=0.05. Hourly egg temperatures were averaged for day and night time periods and were then compared between different nest types, with nest locations, deployment year, and day vs. night incorporated as fixed factors. Analysis of egg temperature ranges were performed the same way as nest temperature ranges, where the difference between maximum and minimum hourly temperatures were found for each day, and then averaged by nest. The temperature averages were then compared between different nest types, nest locations, and deployment years using multi-way ANOVA tests. The relationship between egg temperatures and corresponding nest temperatures were tested running a standard linear regression between hourly nest and egg temperatures for each nest. The same regression was run for daily temperature averages. The correlations between nest and egg temperatures during day

and night time periods were analyzed separately using a Pearson's product-moment correlation test. Egg temperature analyses were performed in R (R Development Core Team, 2014) and MATLAB.

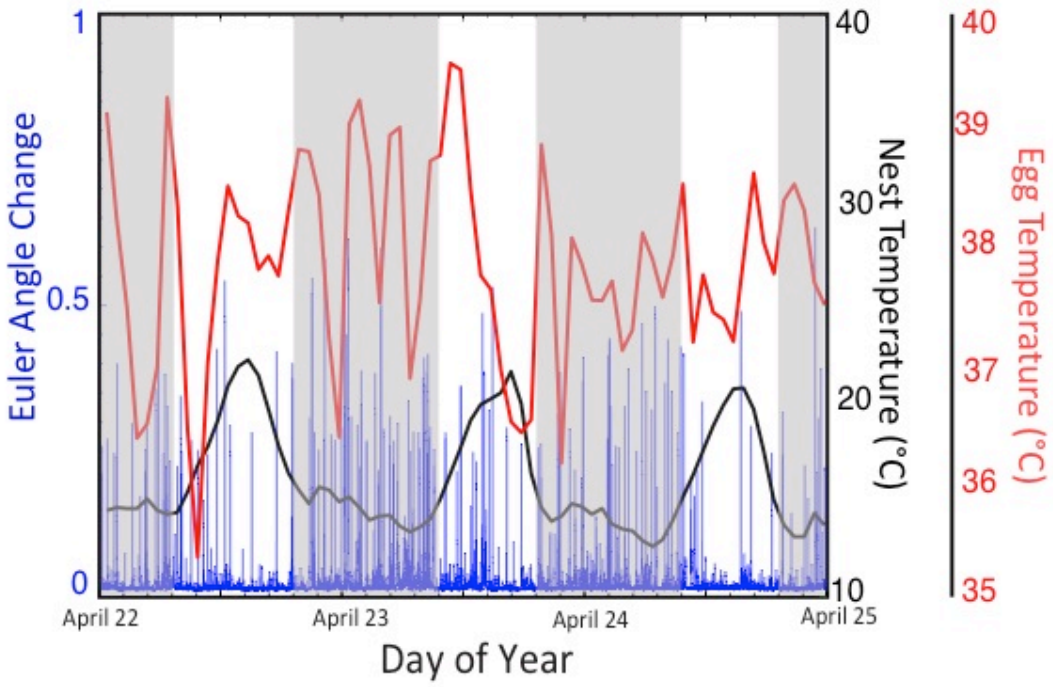

Figure 5: Example data of a sample 36-hour period from one egg logger deployment in 2012. Blue = Euler angle change (angle changes in radians), Black = nest temperature, Red = egg temperature. Gray background shows nighttime periods.

Egg Turning - Diurnal differences in turning rates were tested using a Student's t-test. Daytime and nighttime hourly turning rates were averaged per nest and data were tested for normality and even distribution. T-tests were performed in R (R Development Core Team, 2014). To analyze turning rates and egg and nest temperatures, turning rates were thus determined for day and night time periods, and then averaged by nest.

The relationship between turning rates and temperatures were analyzed using a Pearson's product-moment correlation test in MATLAB.

To analyze the effects of nest habitat type on egg turning rates, mixed effects models were used with hourly egg turning rates as the response variable and nest type, nest location, average nest temperature, average egg temperature, hour of day, individual nest, and year incorporated as predicting variables (Appendix Table 2, White & Bennetts 1996). The data fit a negative binomial distribution model, based on the procedure outlined by Bolker et al. (2009). All predicting variables were treated as fixed effects except individual nest, which was treated as a random effect. The length of egg logger deployment was variable (1-7 days), however the number of days of deployment was not found to be significant. Nest habitat location also did not have a significant effect on egg turning rates so nest habitat type and the day of deployment were not considered in egg turning models. Regression analysis was performed in R using MASS, pscl, and nlme packages (Jackman & Simon, 2002; Pinheiro et al., 2014; R Development Core Team, 2014; Venables & Ripley, 2002).

3. Results

3.1 Nest Type Temperatures

Nest temperatures differed between day and night, with daytime nest temperatures averaging 3.19 ± 2.63 °C higher than nighttime temperatures (Table 2; t=8.42, df=49, p<0.001). The variation in mean daytime nest temperatures was also greater than the

variation in nighttime nest temperatures (Barlett's statistic, x^2=896, *df*=1,54, *p*<0.001). The cyclical pattern of nest temperature fluctuations between day and night is shown in Figure 5. Mean nest habitat temperatures were different between different nest types, with the highest temperatures occurring in un-shaded nest boxes (Figure 6; Appendix Table 2; ANOVA, $F_{2,54}$=3.44, *p*=0.040) and also varied by habitat locations on the island (Figure 1; ANOVA, $F_{2,54}$=7.68, *p*<0.001). Un-shaded boxes had the widest range of daily nest temperatures and natural burrows had the lowest (Figure 6; ANOVA, $F_{2,44}$=8.38, *p*<0.001). Variations in nest temperature changes, as well as nest type and location effects, did not differ between deployment years.

Table 2: Average turns per hour and average temperature during the day and night for all deployments. Turn and temperature averages plus/minus one standard deviation.

Time of Day	Deployment Year	N	Egg		Nest Temperature (°C)*
			Turning Rate*	Temperature (°C)*	
Day	2012	1083	1.90 ± 1.72	37.80 ± 2.01	16.71 ± 3.49
	2013	883	1.93 ± 1.87	39.30 ± 1.62	17.30 ± 4.89
Night	2012	916	2.41 ± 1.95	37.51 ± 1.97	14.09 ± 1.54
	2013	842	2.69 ± 2.24	38.83 ± 1.92	13.51 ± 2.33

* Results showed significant differences between day and night time averages.

3.2 Egg Temperatures

Hourly egg temperatures varied significantly between day and night (Table 2; *t*=3.99, *df*=1,51, *p*<0.001), where egg temperatures were 0.44 ± 0.80°C higher during the day. However, the amount of variation in daytime egg temperatures (38.48 ± 1.98 °C)

was not different than the variation in nighttime egg temperatures (38.14 ± 2.05°C).

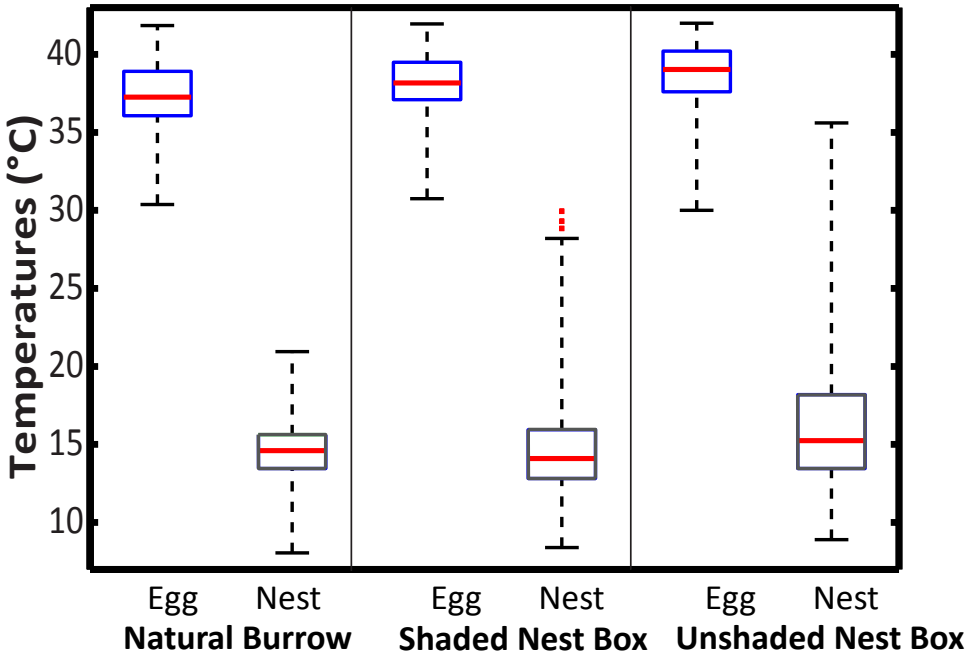

Figure 6: Average hourly temperatures in different nest habitat types: Natural Burrows, Shaded Nest Boxes, and Un-shaded Nest Boxes. Red lines indicate means, blue/gray boxes show interquartile ranges, whiskers indicate interquartile range adjacent values, red plus signs are outliers.

Mean daily egg temperatures were significantly different among nest habitat types where un-shaded nest boxes had the warmest egg temperatures and natural burrows had the coolest egg temperatures (Figure 6; Appendix Table 3; ANOVA, $F_{2,101}$=7.28, p=0.001). Deployment year was a significant factor influencing egg temperature variations between different nest types (Table 3; ANOVA, $F_{1,101}$=21.01, p<0.001). In both years, egg temperatures were highest in un-shaded nest boxes and lowest in natural burrows (Figure 6; Appendix Table 3; 2012: ANOVA, $F_{2,39}$=4.40, p=0.019; 2013: ANOVA,

$F_{2,58}$=5.35, p=0.007). Nest location on the island was also a factor that affected variation in egg temperature (ANOVA, $F_{2,101}$=13.1, p<0.001). Overall the daily egg temperature ranges (daily maximum to nightly minimum) was not different between different nest habitat types. Although both egg and nest temperatures were highest in un-shaded burrows, egg temperatures did not vary as greatly as nest temperatures. There was no relationship between nest temperatures and corresponding egg temperatures either for daily means or for daytime and nighttime means analyzed separately (Figure 7).

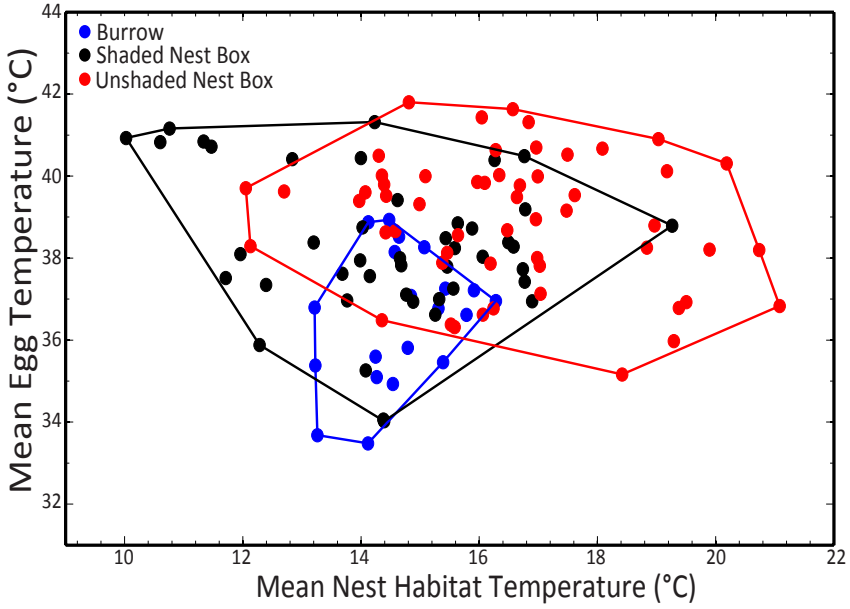

Figure 7: Relationship between average daily nest and egg temperatures. Deployments in different nest habitat types are depicted in different colors. Lines show convex hull polygons for data points from each nest habitat type.

3.3 Egg Turning

Hourly egg turning rates were 25% higher during nighttime periods compared to daytime periods (Table 2; t=-5.05, df=51, p<0.001). Therefore, all remaining analyses of egg turning rates were separated by daytime and nighttime periods.

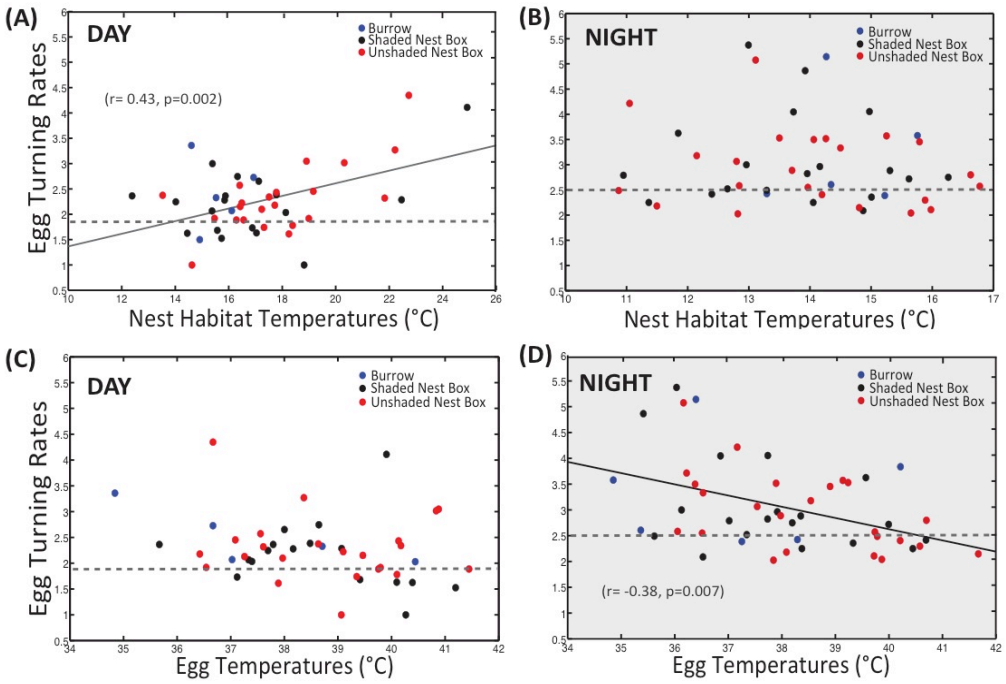

Figure 8: Daytime and night time hourly turning rates in relation to (**A**&**B**) nest temperatures, and (**C**&**D**) egg temperatures. Daytime turning rates vs. temperatures in white background, nighttime turning rates vs. temperatures in gray background**.** **Note**: x-axis nest temperatures for day and night (panes **A**&**B**) are on different scales (nighttime data showing a larger temperature range).

There was a positive correlation between daytime nest temperatures and hourly turning rates (Figure 8; Pearson, r_{49}=0.43, p=0.002) but no correlation between nighttime nest temperatures and hourly turning rates (Figure 9). Considering individual nest and hour of day, the turning rates of auklets incubating eggs in natural burrows

were significantly lower than the turning rates of auklets in un-shaded boxes (Figure 9; Negative Binomial GLMM, t=2.16, p=0.04). The turning rates of auklets in shaded boxes were intermediate to birds in natural and un-shaded boxes (Figure 9).

Comparing the variation between egg temperatures and turning rates for daytime and nighttime periods, there was no correlation between daytime egg temperatures and turning rates (Figure 8). However, there was a significant negative correlation between nighttime egg temperatures and hourly turning rates (Figure 8, Pearson Correlation, r_{49}=-0.38, p=0.007).

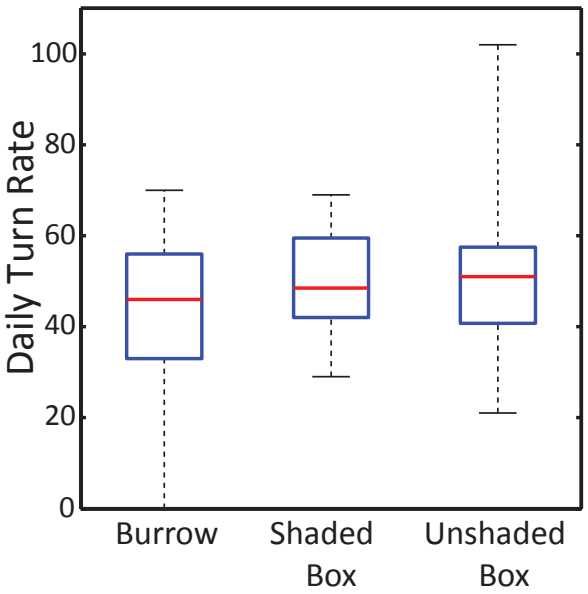

Figure 9: Average turning rates (turns per day) of eggs in different nest habitat types. Red lines indicate means, blue boxes show interquartile ranges, whiskers indicate interquartile range adjacent values.

4. Discussion

The major findings of my study were 1) both nest and auklet egg temperatures varied significantly among different nest types and with time of day; 2) average turning rates were 2 turns/hour with higher rates during the nighttime periods; and 3) egg turning rates varied with elevated nest and egg temperatures.

4.1 Nest Type Temperature

The variations in nest temperatures between different nest habitat types found in the present study agree with the results of a pilot study by Warzybok and Bradley (2010), who found that artificial nest boxes were significantly warmer than natural burrows and that shaded structures reduce the temperatures in nest boxes. The range in daily nest temperatures was also significantly higher in nest boxes than in natural burrows. Because nest boxes are above ground and made out of a single layer of plywood, they are not well insulated and thus are highly susceptible to environmental temperature fluctuations. This nest box composition means that not only do the artificial nest boxes get hot in direct sunlight, but they can also cool significantly at night and when exposed to high winds and other inclement conditions commonly experienced on SEFI during the breeding season. The large variation in nest habitat temperature can have an effect on the incubation temperatures and behaviors of the nesting birds. The daily maximum temperatures detected in un-shaded nest boxes on a regular basis may not be high enough to physiologically harm the auklets nesting inside (17.24 ± 4.27 °C); however, large fluctuations in nest habitat temperature could challenge the thermal tolerance of burrow nesting auklets, thus requiring metabolic rate adjustments to maintain body and egg temperatures (Conway & Martin, 2000). Such conditions could negatively impact both short and long-term auklet breeding success on SEFI.

4.2 Egg Temperatures

In general, avian eggs experience a flux of heat energy. Heat input comes from the incubating parent, the nest environment, and production by the embryo itself. Conversely, heat energy can be lost to the cooler ground upon which the egg rests and to the surrounding environment (Turner, 2000). Contact incubation, maintaining physical contact with the egg during incubation, allows for the incubating adult to control and maintain egg temperature. Many bird species have developed physical characteristics, such as brood patches or extra venation in their feet, to maximize the ability to transfer heat to an egg (Manuwal, 1974b; Morgan et al., 2003). Even with contact incubation, eggs can experience temperature fluctuations due to contact with the ground, egg neglect by the parent, or both. Consequently, egg turning is essential for the redistribution of heat energy across the egg (Ar & Sidis, 2002; Boulton & Cassey, 2012). Egg loggers used in the present study, having one central temperture thermister, could not detect temperature gradients across the egg or energy flow in and out. However, the egg loggers accurately detected hourly and daily temperature fluctuations and relative temperature differences caused by variations in nest temperatures and egg turning rates.

Given that auklets nest in burrows with minimal nest materials and bare ground (Manuwal, 1974a), I predicted egg temperatures would fluctuate with nest habitat type and that egg temperatures would be higher in warmer nest types. Indeed egg temperatures were highest in un-shaded nest boxes and lowest in natural burrows,

supporting my initial hypothesis. All three nest types showed some temperature fluctuations, therefore mean daily egg temperatures did not vary significantly among the different nest types. Figure 7 shows that nest temperatures were highly variable, especially in un-shaded nest boxes. However, corresponding egg temperatures were more consistent regardless of the variation in nest temperature. Furthermore, hourly fluctuations in egg temperatures were not correlated with changes in corresponding nest temperatures. These results suggest that the temperature of auklet eggs is buffered from the variations in their nest habitat temperatures. Due to the complexity of factors (both external and internal) that contribute to the avian egg temperatures (Turner, 2000), it is difficult to attribute the fluctuation (or lack thereof) of egg temperatures to a specific factor. I believe that a combination of heat loss and gain, and adult behavior, such as egg turning rates and the amount of time the adult spends standing off the egg, contribute to the auklet egg temperature variations seen in my study.

4.3 Egg Turning

I predicted that auklet egg turning rates would decrease as egg temperatures increased. The relationship between egg turning rates and temperatures was not as clear as I had predicted in my hypothesis but some distinct egg turning patterns were observed: 1) Egg turning rates increased during the night, 2) Daytime egg turning rates increased with increasing nest temperatures, and 3) Nighttime egg turning rates increased with decreasing egg temperatures.

During the day, egg temperatures were significantly higher than nighttime egg temperatures (most likely due to increases in nest temperature). Daytime turning rates increased with increasing nest temperatures (Figure 9). Furthermore, higher turning rates were found in un-shaded nest boxes, which had the highest, and most variable daytime temperatures (Figure 6, Figure 8). These correlations between egg turning rates and nest temperatures could suggest that the auklets are reacting to the elevated nest temperatures in the box by increasing turning rates, which redistributes heat and increases egg contact with the cooler ground.

During nighttime periods, there was no relationship between nest temperatures and turning rates. There was, however, a negative correlation between nighttime turning rates and *egg* temperature. When eggs were turned more during nighttime periods, they were cooler. This result suggests that as parents turn their eggs more, increasing contact with the cooler ground and air temperatures, egg heat loss increases.

A possible reason for the nighttime increase in egg turning and decrease in egg temperatures could be the nocturnal behaviors of auklets. Little is known about auklet nesting behavior because they nest in burrows and crevices. It is well documented that auklets return to their nests at dusk and commonly remain until dawn (Dawson, 1923; Manuwal, 1974a). During this time, auklet parents exchange incubation duties and the other parent returns to the sea to forage the following day. Late at night, it is not uncommon to find both adult auklets in the nest at once (Manuwal, 1974a). Therefore during this time both auklets are in the small nest chamber and the increase in egg

turning may be a byproduct of their movement around the nest, bumping or repositioning the egg as they move. Similarly, this nocturnal nest activity could explain the decrease in egg temperatures, as auklets would not be sitting as tightly on the egg, thus exposing it to the cooler nighttime air temperatures. A future study could install video cameras inside auklet nest habitats, along with the egg loggers, to record nesting behavior. This would allow us to investigate, through video, the auklet behaviors that influence the turning events recorded by the egg loggers.

It has been hypothesized in other bird species that egg turning is used to control egg temperature (Boulton & Cassey, 2012; Turner, 2002). Certainly there are factors of auklet incubation behavior that are not accounted for in the association between egg turning rates and temperatures found in this study because the correlations were relatively weak. However, I believe that the relationship between increased auklet egg temperatures and turning rates is important and should continue to be monitored if island-wide temperatures continue to increase in the future.

Although the correlations between elevated nest and egg temperatures and egg turning rates were dynamic and not fully explained, warm ambient temperatures are known to have other negative effects on Cassin's auklet populations (Adams et al., 2004; Bertram et al., 2005; Lee et al., 2007; Morrison et al., 2011). Therefore I believe there is a probability of other, sub-lethal effects of elevated nesting temperatures on auklets, besides their incubation behavior. Further study of the relationship between auklet incubation temperatures and incubation period, adult weight, chick growth, fledging

success, and fledgling survival could be done to explore the overall effects in temperature and nest habitat type on nesting auklets.

4.4 Effects on Breeding Biology

Due to abandonment issues with egg logger deployments, I was not able to evaluate the effects of different nest types used in this study on hatching success. However, it does not appear that nest temperatures, egg temperatures, and egg turning rates have a significant influence on the hatching success of the auklets. In 2008, when an extreme heat event on SEFI caused severe heat stress for birds in un-shaded nest boxes, to the point of death of 23 auklets, the overall reproductive success of the auklets during that season was equal to the long-term annual mean for the population (Warzybok & Bradley, 2010). Therefore, embryo development and hatching success did not appear to be significantly effected by the elevated nest temperatures. Although increased temperatures have been found to have negative effects on breeding success of some bird species (Pipoly et al., 2013), the viability and reproductive success are not the highest concern for the effects of increasing temperatures on breeding auklets.

The heat stresses of auklets nesting in un-shaded nest boxes in 2008 illustrate the serious impact of elevated temperatures on the physiology of the auklets nesting within. Many bird species, especially those that nest in hot climates, have evolved behavioral adaptations, such as panting and gular fluttering, to help them maintain proper body and incubation temperatures in warm ambient temperatures (Deeming, 2002b). Above a certain threshold however, behavioral adaptations can no longer

compensate for the negative effects of elevated ambient temperatures on nesting birds (Conway & Martin, 2000). This appeared to be the case for the auklets in un-shaded nest boxes in 2008. If the significant warming trend on SEFI over the past 4 decades continues (Morrison et al., 2011; Warzybok & Bradley, 2010), it could have serious negative implications for the adult auklets nesting on SEFI.

4.5 Future Directions

One of the valuable outcomes of my project relates to the future of nest box design for breeding birds. Artificial nest boxes are commonly used to facilitate monitoring, restore habitat, translocate and maintain colonies, increase breeding success, and increase adult survival of burrow-nesting seabird species (Bolton et al., 2004; Libois et al., 2012; Priddel, 1995; Wilson, 1986). Although nest boxes are widely used and accepted, they can prove to be ineffective when they are implemented in ways that are not favorable to the target species or local environment (Klein et al., 2007; Zingg et al., 2010). The elevated nest temperatures on SEFI, and resulting consequences for nesting auklets, is an example of how artificial nest boxes can create unnatural nesting temperatures for auklets in the face of climate change and rapidly increasing temperatures. The shaded structures installed on top of the nest boxes on SEFI have proven to be successful at mitigating the increased nesting temperatures felt in nest boxes but they are not a permanent solution. Studies have found that burying artificial nest boxes for burrow nesting seabird species can help alleviate the effects of environmental temperatures, as well as increase the lifespan of the nest box as seabird

habitat (Bolton et al., 2004). Researchers and collaborators at Año Nuevo Island, California created a novel alternative nest box design for the Rhinoceros auklet (*Cerorhinca moncerata*) and Cassin's auklet populations. These nest "modules" are made out of clay, are designed to be less susceptible to elevated temperatures, and are more durable than the wooden boxes used on SEFI (Hester et al., 2013). Rhinoceros and Cassin's auklet breeding pairs have successfully occupied these nest habitat modules since their implementation on Año Nuevo Island in 2010, and pilot studies are currently being conducted to test the nest habitat temperature variations between the nest modules and natural burrows (Hester et al., 2013; Carle personal communication, May 2014). Burying nest boxes is not an option on SEFI, due to the thin topsoil layer on the island but the implementation of a new nest box design, similar to the one implemented on Año Nuevo Island, should be considered for applications on SEFI.

The egg loggers used in this study have proven to be successful at recording egg turning rates and temperatures in a number of seabird species (Shaffer et al., 2014). I believe that these loggers also hold great potential for further studies of auklet incubation behavior. The egg loggers detected periods of egg neglect by the auklets. Further studying the frequency, and potential causes, of auklet egg neglect could be informative. Additionally, reproductive success rates in auklets, and other seabird species, has been found to increase with increased breeding experience of the bird (Enulie et al., 1992; Pyle et al., 2001). Lee, Warzybok, and Bradley (2012) found that first breeding attempts by auklets on SEFI resulted in smaller egg size, lower chick weights,

and decreased fledgling survival. Egg loggers could be used to explore the reasons for these differences by comparing egg temperatures, turning rates, fluctuations in temperatures and turning rates, and periods of abandonments, with auklet age and breeding experience.

In conclusion, the results of this study increase our understanding of auklet incubation behavior and illuminate what aspects of incubation behavior could be studied further. These results also show that nest type temperature plays a role in auklet incubation behaviors. It is clear that increasing environmental temperatures can affect breeding Cassin's auklets and ways to further mitigate these effects should be considered.

References

Adams, J., J. Y. Takekawa, and H. R. Carter. (2004). Stable Foraging Areas and Variable Chick Diet in Cassin's Auklets (Ptychoramphus Aleuticus) off Southern California. *Canadian Journal of Zoology, 82*(10), 1578–1595. doi:10.1139/z04-140.

Ar, A. Y. Sidis. (2002). Chapter 10: Nest Microclimate during Incubation. In Deeming, D C. (Ed.), *Avian Incubation: Behavior, Environment, and Evolution*. (143-160) 1st ed. New York, NY: Oxford University Press, Inc.

Astheimer, L. B. (1991). Embryo Metabolidm and egg neglect in Cassin's auklets. *The Condor, 93*(3), 486–495.

Beaulieu, M., A. Thierry, Y. Handrich, S. Massemin, Y. Maho, and A. Ancel. (2010). Adverse Effects of Instrumentation in Incubating Adélie Penguins (Pygoscelis Adeliae). *Polar Biology,* 33(4), 485–492. doi:10.1007/s00300-009-0725-z.

Beer, G. C. (1965). Clutch Size and Incubation Behaviour in Black-Billed Gulls (Larus Bulleri). *Auk, 82*(1), 1–18.

Bell, K., S. Blomberg, L. Schwarzkopf. (2013). Detrimental influence on performance of high temperature incubation in a tropical reptile: is cooler better in the tropics? *Oecologia*, *171*(1), 83–91. doi:10.1007/s00442-012-2409-6

Bennett, A., W. Dawson, R. Putnam. (1981). Thermal Environment and Tolerance of Embryonic Western Gulls. *Physiological Zoology*, *54*(1), 146–154.

Bertram, D. F., A. Harfenist, and B. D. Smith. (2005). Ocean Climate and El Niño Impacts on Survival of Cassin's Auklets from Upwelling and Downwelling Domains of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences, 62*, 2841–2853. doi:10.1139/F05-190.

Block, B. A., I. D. Jonsen, S. J. Jorgensen, A. J. Winship, S. A. Shaffer, S. J. Bograd, E. L. Hazen, et al. (2011). Tracking Apex Marine Predator Movements in a Dynamic Ocean. *Nature, 475*(7354), 86–90. doi:10.1038/nature10082.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. (2009). Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution. *Trends in Ecology & Evolution, 24*(3), 127–35. doi:10.1016/j.tree.2008.10.008.

Bolton, M., R. Medeiros, B. Hothersall, and A. Campos. (2004). The Use of Artificial Breeding Chambers as a Conservation Measure for Cavity-Nesting Procellariiform Seabirds: A Case Study of the Madeiran Storm Petrel (Oceanodroma Castro). *Biological Conservation, 116*(1), 73–80. doi:10.1016/S0006-3207(03)00178-2.

Booth, D. T. (2006). Influence of incubation temperature on hatchling phenotype in reptiles. *Physiological and Biochemical Zoology*, *79*(2), 274–81. doi:10.1086/499988

Boulton, R. L., P. Cassey. (2012). How avian incubation behaviour influences egg surface temperatures: relationships with egg position, development and clutch size. *Journal of Avian Biology*, *43*(4), 289–296. doi:10.1111/j.1600-048X.2012.05657.x

Conway, C. J., and T. E. Martin. (2000). Effects of Ambient Temperature on Avian Incubation Behavior. *Behavioral Ecology, 11*(2), 178–188.

Dawson, W. L. (1923). *The birds of California, Volume III*. South Moulton Company. Los Angeles, California.

Deeming, D. C. (1989). Failure to Turn Eggs during Incubation: Development of the Area Vasculosa and Embryonic Growth. *Journal of Morphology,* 201(2), 179–186. doi:10.1002/jmor.1052010207.

Deeming, D. C. (2002a). Chapter 1: Importance of evolution of incubation in avian reproduction. In Deeming, D C. (Ed.), *Avian Incubation: Behavior, Environment, and Evolution*. (1-6) 1st ed. New York, NY: Oxford University Press, Inc.

Deeming, D. C. (2002b). Chapter 6: Patterns and significance of egg turning. In Deeming, D C. (Ed.), *Avian Incubation: Behavior, Environment, and Evolution*. (63-87) 1st ed. New York, NY: Oxford University Press, Inc.

Deeming, D. C. (2002c). Chapter 11: Behavior Patterns During Incubation. In Deeming, D C. (Ed.), *Avian Incubation: Behavior, Environment, and Evolution*. (161-178) 1st ed. New York, NY: Oxford University Press, Inc.

Drent, R. H. (1970). Functional Aspects of Incubation in the Herring Gull. *Behaviour Supplement, 17*, 1–132.

DuRant, S. E., W. A. Hopkins, A. W. Carter, C. M. Stachowiak, and G. R. Hepp. (2013). Incubation Conditions Are More Important in Determining Early Thermoregulatory Ability than Posthatch Resource Conditions in a Precocial Bird. *Physiological and Biochemical Zoology, 86*(4), 410–20. doi:10.1086/671128.

Elibol, O. and J. Brake. (2006). Effect of Egg Turning Angle and Frequency during Incubation on Hatchability and Incidence of Unhatched Broiler Embryos with Head in the Small End of the Egg. *Poultry Science, 85*, 1433–1437.

Enulie, S. D., W. J. Sydeman, P. Pyle. (1992). The Importance of Mate Retention and Experience on Breeding Success in Cassin's Auklet (Ptychoramphus Aleuticus). *Behavioral Ecology*, *3*(3), 189–195.

Eycleshymer, A. C. (1907). Some Observations and Experiments on the Natural and Artificial Incubation of the Egg of the Common Fowl. *Biological Bulletin, 12*(6), 360–374.

Gee, G. F., J. S. Hatfield, and P. W. Howey. (1995). Remote Monitoring of Parental Incubation Conditions in the Greater Sandhill Crane. *Zoo Biology, 172*(1995), 159–172.

Hepp, G. R., R. A. Kennamer, and M. H. Johnson. (2006). Maternal Effects in Wood Ducks: Incubation Temperature Influences Incubation Period and Neonate Phenotype. *Functional Ecology, 20*(2), 308–314. doi:10.1111/j.1365-2435.2006.01108.x.

Hester, M., R. Carle, J. Beck, and D. Calleri. (2013). Año Nuevo State Park Seabird Conservation and Habitat Restoration: Report 2013. Oikonos Ecoystem Knowledge. Santa Cruz, CA.

Howey, P., R. G. Board, D. H. Davis, and J. Kear. (1984). The Microclimate of the Nests of Waterfowl. *Ibis, 126*(1), 16–32. doi:10.1111/j.1474-919X.1984.tb03660.x.

Jackman, S. (2012). pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University. Stanford, California. R package version 1.04.4. URL http://pscl.stanford.edu/

Klein, Á., T. Nagy, T. Csörgő, and R. Mátics. (2007). Exterior Nest-Boxes May Negatively Affect Barn Owl (Tyto Alba) Survival: An Ecological Trap. *Bird Conservation International, 17*(3), 273–281. doi:10.1017/S0959270907000792.

Lee, D. E., N. Nur, and W. J. Sydeman. (2007). Climate and Demography of the Planktivorous Cassin's Auklet Ptychoramphus Aleuticus off Northern California: Implications for Population Change. *The Journal of Animal Ecology, 76*(2), 337–47. doi:10.1111/j.1365-2656.2007.01198.x.

Lee, D. E., P. M. Warzybok, and R. W. Bradley. (2012). Recruitment of Cassin's Auklet (Ptychoramphus Aleuticus): Individual Age and Parental Age Effects. *The Auk, 129* (1), 124–132.

Libois, E., O. Gimenez, D. Oro, E. Mínguez, R. Pradel, and A. Sanz-aguilar. (2012). Nest Boxes : A Successful Management Tool for the Conservation of an Endangered Seabird. *Biological Conservation, 155*, 39–43. doi:10.1016/j.biocon.2012.05.020.

Mahlstein, I., J. S. Daniel, S. Solomon. (2013). Pace of shifts in climate regions increases with global temperature. *Nature Climate Change*, *3*(8), 739–743. doi:10.1038/nclimate1876

Manuwall, D. A. (1972). The Population Ecology of Cassin's Auklet on Southeast Farallon Island. University of California.

Manuwal, D. A. (1974a). The Natural History of Cassin's Auklet (Ptychoramphus Aleuticus). *The Condor, 76*(4), 421–431.

Manuwal, D. A. (1974b). The incubation patches of Cassin's Auklet. *The Condor*, *76*(4), 481–484.

Matthysen, Erik, Frank Adriaensen, and André A Dhondt. (2011). Multiple Responses to Increasing Spring Temperatures in the Breeding Cycle of Blue and Great Tits (Cyanistes Caeruleus, Parus Major). *Global Change Biology, 17*(1), 1–16. doi:10.1111/j.1365-2486.2010.02213.x.

Morgan, S. M., M. A. Ashley-Ross, D. J. Anderson. (2003). Foot-mediated incubation: Nazca booby (Sula granti) feet as surrogate brood patches. *Physiological and Biochemical Zoology*, *76*(3), 360–6. doi:10.1086/375430

Morrison, Kyle W., Mark J. Hipfner, Gwylim S. Blackburn, and David J. Green. (2011). Effects of Extreme Climate Events on Adult Survival of Three Pacific Auks. *The Auk, 128*(4), 707–715.

New, D. A. T. (1957). A Critical Period for the Turning of Hens' Eggs. *Journal of Embryology and Experimental Morphology, 5*(3), 293–299.

Nichelmann, M. (2001). Metabolic Responses of Chicken and Muscovy Duck Embryos to High Incubation Temperatures. *Comparative Biochemistry and Physiology, 131*, 741–750.

Pinheiro J., Bates D., DebRoy S., Sarkar D. and R Core Team (2014). _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-117, <URL: http://CRAN.Rproject.org/package=nlme>.

Pipoly, I., V. Bókony, G. Seress, K. Szabó, and A. Liker. (2013). Effects of Extreme Weather on Reproductive Success in a Temperate-Breeding Songbird. *PloS One, 8*(11), e80033. doi:10.1371/journal.pone.0080033.

Priddel, D.; N. Carlile. (1995). An Artificial Nest Box for Burrow-Nesting Seabirds. *Emu, 95*(4), 290–294.

Pyle, P., W. J. Sydeman, and M. Hester. (2001). Effects of Age, Breeding Experience, Mate Fidelity and Site Fidelity on Breeding Performance in a Declining Population of Cassin's Auklets. *Journal of Animal Ecology, 70*(6), 1088–1097. doi:10.1046/j.0021-8790.2001.00567.x.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reid, J. M., P. Monaghan, and G. D. Ruxton. (2000). Resource Allocation between Reproductive Phases : The Importance of Thermal Conditions in Determining the Cost of Incubation. *Proceedings: Biological Sciences, 267*(1438), 37–41.

Reneerkens, J., K. Grond, H. Schekkerman, I. Tulp, and T. Piersma. (2011). Do uniparental Sanderlings Calidris Alba increase egg heat input to compensate for low nest attentiveness? *PloS One, 6*(2), e16834. doi:10.1371/journal.pone.0016834.

Roudybush, T., and L. Hoffman. (1980). Conductance, pore geometry, and water loss of eggs of Cassin's auklet. *Condor, 82*, 105–106.

Schaper, S. V., A. Dawson, P. J. Sharp, P. Gienapp, S. P. Caro, M. E. Visser. (2012). Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. *The American Naturalist*, *179*(2), E55–69. doi:10.1086/663675

Shaffer, S. A., D. P. Costa, & H. Weimerskirch. (2001). Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology*, *70*(5), 864–874. doi:10.1046/j.0021-8790.2001.00548.x

Shaffer, S., C. A. Clatterbuck, E. K. Kelsey, A. Naiman, L. Young, E. VanderWerf, P. M. Warzybok, R. W. Bradley, J. Jahncke, G. C. Bower. (2014). As the egg turns: Monitoring egg attendance behavior in wild birds using novel data logging technology. *PloS One*, 9(6), e97898. doi:10.1371/journal.pone.0097898

Thierry, A., S. Massemin, Y. Handrich, and T. Raclot. (2013). Elevated Corticosterone Levels and Severe Weather Conditions Decrease Parental Investment of Incubating Adélie Penguins. *Hormones and Behavior, 63*(3), 475–83. doi:10.1016/j.yhbeh.2012.12.011.

Tona, K., O. Onagbesan, V. Bruggeman, K. Mertens, and E. Decuypere. (2005). Effects of Turning Duration during Incubation on Embryo Growth, Utilization of Albumen, and Stress Regulation. *Poultry Science,* 84(2), 315–20.

Tullett, S. G. and D. C. Deeming. (1987). Failure to Turn Eggs during Incubation: Effects on Embryo Weight, Development of the Chorioallantois and Absorption of Albumen. *British Poultry Science, 28*(2), 239–249.

Turner, J. S. (2002). Chapter 9: Maintenance of Egg Temperature. In Deeming, D C. (Ed.) *Avian Incubation: Behavior, Environment, and Evolution*. (119-142). 1st ed. New York, NY: Oxford University Press, Inc.

Vedder, O. (2012). Individual Birds Advance Offspring Hatching in Response to Increased Temperature after the Start of Laying. *Oecologia, 170*(3), 619–28. doi:10.1007/s00442-012-2335-7.

Venables, W. N. and Ripley, B. D. (2002). Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0 (MASS).

Vleck, C. M. (1981). Energetic cost of incubation in the zebra finch. *Condor*, *83*(3), 229–237.

Warzybok, P. M. and R. W. Bradley. (2008). Population size and reproductive performance of seabirds on Southeast Farallon Island, 2008. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, CA.

Warzybok, P. M. and R. W. Bradley (2010). 2010 Southeast Farallon Island Seabird Report. Apendix III. Using temperature loggers to assess microclimate differences between natural and artificial Cassin's Auklet nest sites during 2010. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1769

Webb, D. R. (1987). Thermal Tolerance of Avian Embryos: A Review. *Condor, 89*(4), 874–898.

Weimerskirch, H. 1995. Regulation of Foraging Trips and Incubation Routine in Male and Female Wandering Albatross. *Oecologia, 102*(1), 37–43.

White, G. C., and R. E. Bennetts. (1996). Analysis of Frequency Count Data Using the Negative Binomial Distribution. *Ecology, 77*(8), 2549–2557.

Williams, J. B., R. E. Ricklefs. (1984). Egg Temperature and Embryo Metabolism in Some High-Latitude Procellariiform Birds. *Physioligcal Zoology, 57*(1), 118–127.

Wilson, R. P., I. W Griffiths, P. A. Legg, M. I. Friswell, O. R. Bidder, L. G. Halsey, S. A. Lambertucci, and E. L. C. Shepard. (2013). Turn Costs Change the Value of Animal Search Paths. *Ecology Letters, 16*(9), 1145–50. doi:10.1111/ele.12149.

Wilson, U. W. (1986). Artificial Rhinoceros Auklet Burrows : A Useful Tool for Management and Research. *Journal of Field Ornithology, 57*(4), 295–299.

Yoda, K., Y. Naito, K. Sato, A. Takahashi, J. Nishikawa, Y. Ropert-Coudert, M. Kurita, and Y. Le Maho. (2001). A New Technique for Monitoring the Behaviour of Free-Ranging Adélie Penguins. *The Journal of Experimental Biology, 204*(4), 685–90.

Zingg, S., Raphaël A., and M. Schaub. (2010). Nestbox Design Influences Territory Occupancy and Reproduction in a Nestbox Design Influences Territory Occupancy and Reproduction in a Declining, Secondary Cavity-Breeding Bird. *ARDEA, 98*(1), 67–75.

Appendix

Table A1: The number of egg logger deployment in each nest type and the actual number of deployments used for analysis. Omission of deployment data was due to battery failure, logger malfunction, loss of egg logger, or nest abandonment. Deployment numbers from all dates during each breeding year were combined. Egg loggers abandoned is the number of CAAU that did not incubate egg logger.

Year	Nest Habitat	Deployments		Egg Loggers
		Done	Used	Abandoned
2012	Natural Burrow	6	3	4
	Shaded Box	14	9	7
	Un-shaded Box	14	12	4
	Total	**34**	**24**	**15**
2013	Natural Burrow	6	5	3
	Shaded Box	17	11	0
	Un-shaded Box	18	16	2
	Total	**41**	**32**	**5**

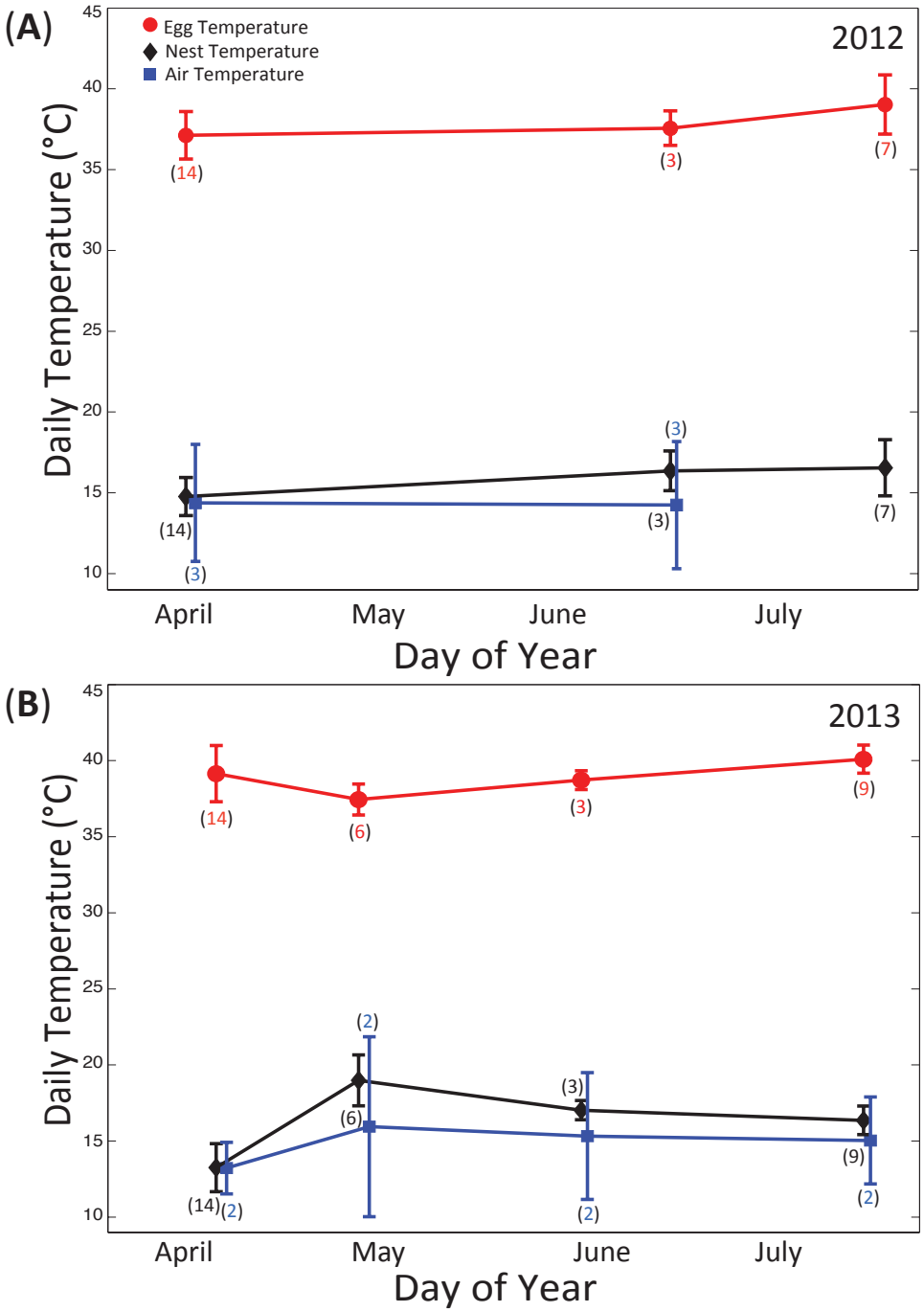

Figure A1: Time series plot of daily average ambient air, nest, and egg temperatures from all egg logger deployments across (**A**) 2012 and (**B**) 2013 auklet nesting seasons. Circles = egg temperatures, diamonds = nest temperatures, and squares = ambient air temperatures. Sample sizes given in ().

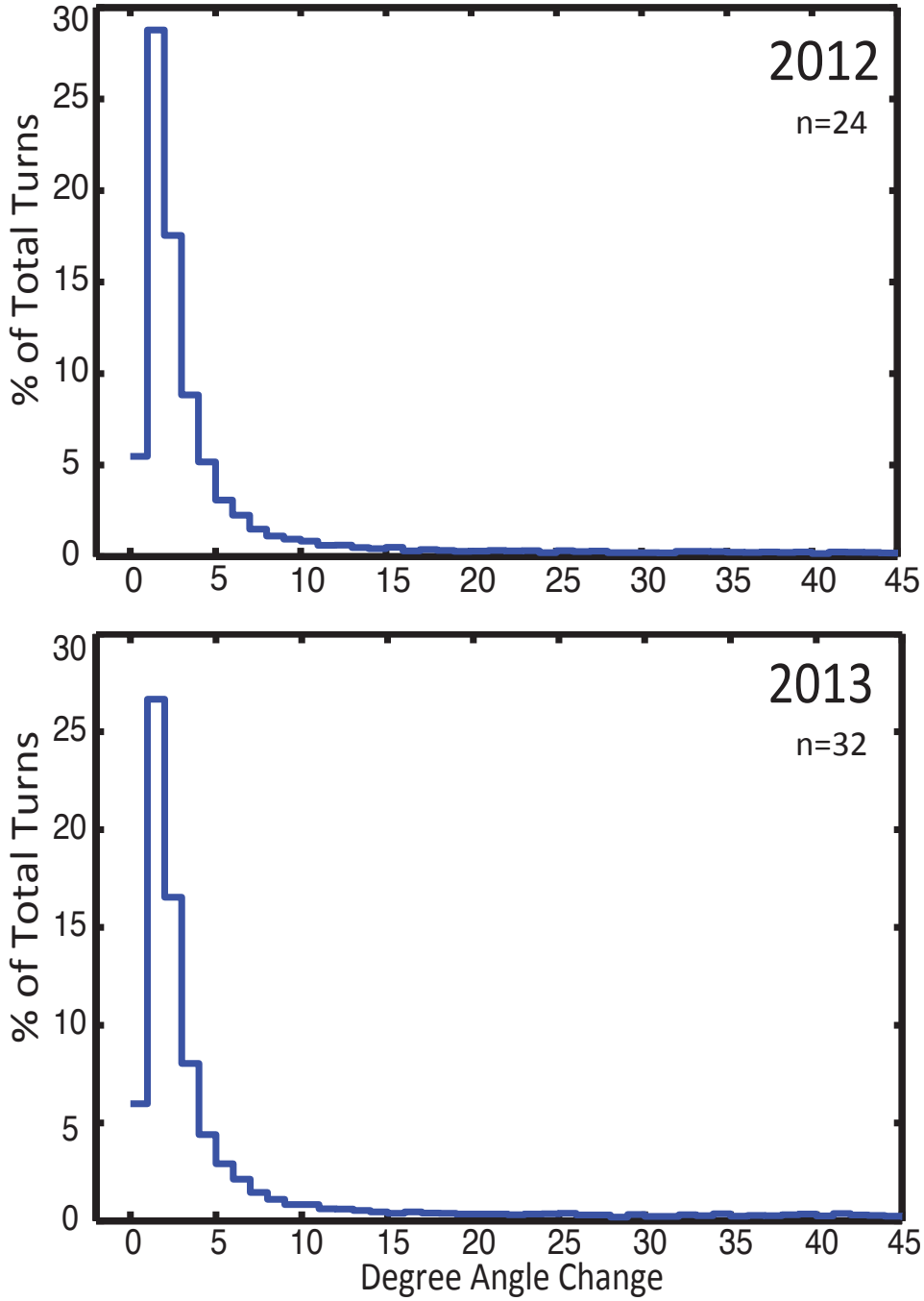

Figure A2: Frequency histograms of the total degree angle change that occurred during each turning event in (**A**) 2012 and (**B**) 2013 deployments. These frequent but small angle changes <10° were considered 'noise' generated by micro-movements of the egg loggers, so a minimum turning threshold of 10° was set for all measured turning events.

Table A2: The average hourly egg and nest temperatures during 2012 and 2013 deployments. Averages ± standard deviation. Habitat Types (Figure 2): NB= Natural Burrow, SB= Shaded Box, UB= Un-shaded Box.

Habitat Type	Temperature (°C)			
	2012		2013	
	Egg	Nest	Egg	Nest
NB	35.95 ±1.00	15.35 ±0.53	37.43 ± 1.92	13.93 ± 1.26
SB	37.18 ± 0.88	15.23 ± 1.39	39.04 ± 1.23	15.5 ± 2.26
UB	37.94 ± 1.67	16.42 ± 1.22	39.04 ± 1.15	16.22 ± 2.12