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Environmental temperatures, artificial nests, and incubation of Cassin's auklet

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Turn of events: Environmental temperatures and artificial nest habitats influence incubation behaviors of a burrow nesting seabird

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ABSTRACT Hatching success in birds is influenced by the temperature and turning rate of the egg, but our understanding of the environmental factors that effect incubation temperatures and egg turning rates in birds is limited. Especially little is known of these effects for species that nest in burrows or crevices, such as the Cassin's auklet (*Ptychoramphus aleuticus*). On Southeast Farallon Island (SEFI), California, a subset of the Cassin's auklet (hereafter auklet) population nest in artificial nest boxes for scientific monitoring. The nest boxes are above ground and made out of a single layer of plywood. Temperatures in un-shaded nest boxes can increase significantly during extreme heat events. Shaded structures put on top of occupied nest boxes help mediate nest box temperatures but the effects of elevated temperatures on auklet incubation behaviors and egg viability remain equivocal. We used egg data loggers to measure the temperatures and turning rates of auklet eggs in natural burrows, shaded nest boxes, and un-shaded nest boxes on SEFI. Nest box (13.93 ± 1.26 °C) and egg (37.43 ± 1.92 °C) temperatures were highest and most variable in un-shaded nest boxes. Mean hourly egg turning rate was 2.11 ± 2.02 turns hour $^{-1}$ and turning rates were significantly higher at night. Egg turning rates also varied with fluctuating nest and egg temperatures, being positively correlated with nest temperatures during the day and negatively correlated with egg temperatures during the night. Given the variations we observed in egg temperature and turning rates associated with nest habitat temperature and type, our results suggest that nest box design can influence incubation behaviors of breeding birds. As seasonal temperatures and the number of extreme heat events rise, understanding the impacts of temperature on auklets nesting in artificial nest habitats can have positive implications for conservation and management of the species.

KEY WORDS Cassin's auklet, egg loggers, nest boxes, egg turning, Southeast Farallon Island

INTRODUCTION

Most bird species engage in distinct incubation behaviors, turning their eggs and regulating egg temperature (Eycleshymer 1907, Deeming 2002a). Egg turning is integral for proper embryonic development, regular rotation of the egg facilitates albumen use by the embryo and prevents the embryo from adhering to the shell membrane (New 1957, Tona et al. 2005). Regular egg turning behavior can also lead to increased hatching success, chick health, and overall reproductive success (Deeming 2002a, Tona et al. 2005, Elibol and Brake 2006). Maintaining egg temperatures is also important for proper embryonic development (Turner 2002, DuRant et al. 2013). Incubation temperatures and egg turning rates have been studied extensively in the poultry industry to maximize the hatchability of domestic fowl (Deeming 2002a). In contrast, the factors influencing egg temperatures and turning rates of wild birds are not well understood.

Optimal incubation temperatures for most birds is 30 to 40°C but the thermal tolerance of the egg can vary between species and among climates (Webb 1987). Most studies that examine the effects of egg temperature variation on incubation in wild birds have focused on the effects of egg cooling. Egg temperatures can drop below optimal levels when parents leave an egg unattended, which in some cases, can lead to suspended embryonic development and delayed hatching (Williams & Ricklefs 1984, Astheimer 1991, Reneerkens et al. 2011). Conversely, less is known about how hyperthermic incubation conditions, when egg temperatures are elevated above the optimal range for that species, affect embryonic development and hatching success of birds, though increased incubation temperatures are thought to be more detrimental to embryonic development than hypothermic temperatures (Webb 1987, Pipoly et al. 2013). When certain nesting conditions create atypically warm environments (i.e. intense sun exposure on the bird, its nest, or burrow), parent birds may be challenged to maintain optimal temperatures for themselves and their eggs. Climate models predict, and weather observations confirm, that global temperatures are increasing (Mahlstein et al. 2013) and the effects of elevated temperatures on avian incubation is of growing concern for some species (Schaper et al 2012, Pipoly et al. 2013).

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 (Wilson 1986, Libois et al. 2012). However, nest boxes can prove to be ineffective if they are implemented in ways that are not favorable to the target species or local environment (Zingg et al. 2010, Lei et al. 2014). Lei et al. (2014) found that the hatching success of African Penguins (*Spheniscus demersus*) nesting in artificial fiberglass burrows was consistently lower than hatching success in natural burrows. The authors hypothesized that the fiberglass boxes created a hotter and drier nesting environment than natural burrows, therefore increasing the risk of egg desiccation and hatching failure. In addition to possible decreases in hatching success, elevated temperatures in artificial nest habitats can cause hyperthermia in the adult birds and chicks, which can be lethal (Ropert-Coudert et al. 2004, Lei et al. 2014).

We chose to study the effects of nest temperatures on Cassin's auklet (*Ptychoramphus aleuticus*) incubation behavior and temperature on Southeast Farallon Island (SEFI), California because the population nesting in artificial nest boxes there has been exposed to increasing environmental temperatures, which has lead to heat stress for some nesting birds (Warzybok and Bradley 2010). The Cassin's auklet (hereafter auklet) is a small, diving seabird found throughout the northeastern Pacific Ocean (Manuwal 1974a). The species lays a single egg in a burrow or crevice (Manuwal 1974a). On SEFI, researchers from Point Blue Conservation Science (formally known as Point Reyes Bird Observatory) use artificial nest boxes to study the breeding biology of the Cassin's auklet. Nest boxes are above ground and made out of a single layer of plywood (Appendix Figure 1), thus being highly susceptible to environmental temperature fluctuations. In recent years, auklets nesting in artificial nest boxes exposed to direct sunlight have experienced extreme heat events when temperatures were significantly higher than average ambient temperatures during the SEFI breeding season (>25°C; Point Blue, unpublished data). Subsequent investigation determined that artificial nest boxes were significantly warmer than natural burrows, but placing shaded structures on top of nest boxes could mitigate elevated nest box temperatures (Warzybok and Bradley 2010). Annual maximum environmental temperatures on SEFI have increased nearly 3-4°C since 1970 (Warzybok and Bradley 2010). The elevated temperatures in 2008 resulted in heat stress and even death in some adult auklets (Warzybok and Bradley 2008). However as maximum temperatures on SEFI rise, the effects of increased nest chamber temperatures on auklet incubation behavior (e.g. - egg turning and egg temperature) remain unclear.

Recently developed technologies are increasing our understanding of egg turning behaviors through the use of data logging devices placed inside artificial eggs that are incubated by parent birds (Beaulieu et al. 2009, Thierry et al. 2013, Shaffer et al. 2014). Using this technology, we examined the effects of environmental temperature in natural and artificial nest habitats on the incubation behaviors of Cassin's auklets. To date very little is known about auklet incubation behavior, or the incubation behaviors of seabirds in general (Shaffer et al. 2014). The average incubation period is approximately 38 days, during which parents exchange egg attendance on a nightly basis until hatching (Manuwal 1974a). Egg neglect is rare but not uncommon among auklets (Asheimer 1991), however little else is known about their egg attendance or egg turning behaviors. During the auklet breeding season, March through August, mean monthly ambient temperatures on SEFI ranged from 11.8±1.0 to 14.5±1.0°C, respectively (years 1971-2007; Point Blue Conservation, unpublished data). The goal of our study was to determine if different nest habitat types (i.e. natural burrows, shaded and un-shaded nest boxes) influenced egg temperatures and egg turning patterns of incubating auklets. We hypothesized that egg temperatures would be higher and more variable in un-shaded boxes. We also hypothesized that egg turning rates would vary with nest temperatures, where parents turn eggs according to nest and egg temperature variation. Therefore, we expected that elevated temperatures might lead to suboptimal egg turning rates. We believe that as nest temperatures increase, auklet parents may stand up off of their eggs to allow the eggs to cool and stay within optimal incubation temperatures, resulting in a putative reduction in the frequency of egg turning.

STUDY AREA

Southeast Farallon Island (37°41'49"N 123°00'07"W) is part of the Farallon National Wildlife Refuge, located 48 kilometers west of San Francisco, California. Currently, there are about 10,000 auklet pairs that nest on SEFI (Warzybok and Bradley 2010). The auklets inhabit primarily the marine terrace and rocky slope habitat throughout the 0.3104km^2 island. Five hundred artificial nest boxes have been built on SEFI to monitor breeding auklets. Nest boxes are 20x23x40cm boxes made out of cdx plywood with a 10cm PVC pipe as an entrance (Appendix Figure 1).

METHODS

Egg and Egg Logger Design

We deployed custom-made artificial eggs containing an egg logger in selected auklet nests established between April and July of the 2012 and 2013 breeding seasons (n = 34 in 2012, n = 41 in 2013; Shaffer et al. 2014). The size, shape, and color of the artificial eggs were based on historical measurements and images of natural auklet eggs (27.5g; Manuwal 1974). Artificial eggs were made out of 1/8-inch vacuum-formed polystyrene plastic. We filled artificial eggs 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 (Conway & Martin 2000; Appendix Table 1). After adding weighting agents, an egg logger was placed in each artificial egg.

The egg loggers used in this study are fully described in Shaffer et al. (2014). In brief, each logger contained a triaxial accelerometer and magnetometer to record orientation and angle changes, and one temperature thermistor to record temperature. The egg loggers were positioned inside the center of the artificial egg where they recorded orientation and core egg temperature every second and had enough battery power to last up to a week.

Egg Logger Deployment

We deployed the egg loggers in a subset of occupied burrows and nest boxes spread across the island. We would remove the bird and the natural egg from the nest chamber, then place the egg logger in the center of the nest cup and allow the bird to return to its nest. LogTag ambient temperature loggers (MicroDAQ.com, Ltd., New Hampshire) were also deployed inside the corresponding nest of each egg logger deployment to record nest chamber temperature for the duration of the egg logger deployment. The ambient temperature loggers were placed on the ceiling of the nest box and secured with Velcro tape. These loggers recorded the temperature of the nest environment every 30 minutes.

For the egg logger and ambient temperature logger deployment, we selected nests with eggs in the early stages of incubation (1-20 days old) to control for changes in incubation behavior that may occur across the incubation period (Turner 2002). Because there is no *a priori* information to suggest that turning rates would change throughout the course of the day, we did not find it necessary to standardize the time of day at which the egg loggers were deployed. Cassin's auklets lay single egg clutches, so we removed the natural eggs from the nest during egg logger deployments, and incubated them 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 5-10 day deployments.

Natural eggs were returned to their original nests when egg loggers were collected. We followed all nests used for egg logger deployments for the remainder of the breeding season to determine the subsequent breeding success of each manipulated nest. If an egg logger was abandoned or found unincubated on daily checks, we removed it and returned the natural egg.

Data Processing

Nest Chamber Temperature – Nesting temperatures recorded by the LogTag recorders were summarized into hourly averages that were then comparable to the hourly average temperature obtained from the egg loggers.

Egg Temperature and Turning Rates – We processed egg logger data with custom routines created in MATLAB (The Mathworks, Natick, MA) following methods described in Shaffer et al. (2014). To remove any potential influence on egg temperature and turning rates caused by egg logger deployment and retrieval, we excluded the first six and last two hours of every deployment from the analysis. Eliminating the first six hours removed 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, allowing sufficient time for the auklet to settle back onto its nest post-disturbance. Excluding the last two hours from analysis removed the time between when the egg logger was removed from the nest and when it was powered off. In a study of free-living auklets, Asthemier (1991) found that incubation temperatures ranged from 30 to 42°C (32.7±3.4). Therefore we did not include temperatures below 30°C and above 42°C, removing misrepresentative temperature measurements as well as data from when the egg was abandoned or neglected.

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 approximated the cumulative inflection between angle change and turning rates and was comparable to thresholds used in previous studies (Beaulieu et al. 2009, Thierry et al. 2013, Shaffer et al. 2014).

We analyzed hourly turning rates and temperatures (mean, maximum and minimum), starting at 12:00 midnight on each deployment day, following methodology of historical egg turning studies (turns per hour, as seen in Deeming, 2002c). We also analyzed daily turning rates based on the hourly averages. We believed that expressing turning rates on a daily basis provided a more ecologically relevant metric and was comparable to other recent studies of egg turning behavior using accelerometery (Beaulieu et al. 2010, Thierry et al. 2013, Shaffer et al. 2014). Daytime and nighttime temperatures and turning rates were also analyzed. Day lengths were based on the date/time of local sunrise and sunset determined from ephemeris tables using the latitude and longitude of SEFI.

Statistical Analysis and Treatments

Nest Chamber Temperatures – Using a multi-way analysis of variance (ANOVA) we determined that nest location (location of nesting colony across the island) did not have a significant correlation with nest chamber temperature, therefore it dropped from further analyses. We evaluated the effects of nest type on nest temperature using repeated measures ANOVA with nest temperature ranges, with deployment year and day vs. night incorporated as fixed factors. A significance level α=0.05 was set for all analyses. All results are presented as means ± standard deviation. Regression analyses and ANOVA tests were performed in R (R 3.1.0, http://www.R-project.org/, accessed 10 Apr 2014)

Egg Temperatures – Using a multi-way analysis of variance (ANOVA) we determined that nest location (location of nesting colony across the island) did not have a significant correlation with egg temperature, therefore it was dropped from further analyses. We evaluated the effects of nest type on egg temperature using repeated measures ANOVA of egg temperature; with deployment year and day vs. night incorporated as fixed factors. We tested the relationship between egg temperatures and corresponding nest temperatures by running a linear regression between hourly and daily nest temperatures, and egg temperatures for each nest. We analyzed the correlations between nest and egg temperatures during day and night time periods separately using a Pearson's product-moment correlation test. Egg temperature analyses were performed in R and MATLAB.

Egg Turning Rates – After testing for normality (Normal Q-Q plot) we compared differences in turning rates during daytime and nighttime hourly rates per nest (Students T-test) in R. Then using a Pearson's product-moment correlation test in MATLAB, we analyzed the correlations between nest and egg temperatures during day and night time periods separately.

To analyze the effects of nest habitat type on egg turning rates, we used a generalized linear mixed model (GLMM) with hourly egg turning rates as the response variable and nest type, average nest temperature, average egg temperature, hour of day, and individual nest incorporated as predictor variables (based on methods from White & Bennetts 1996). The variance within the data was too great for it to fit a poisson distribution model (mean hourly turning rate=2.1, variance=4). Therefore we used a negative binomial distribution model (Bolker et al. 2009). We treated all predicting variables as fixed effects except individual nest, which was treated as a random effect. Because diurnal temperature fluctuated in a cyclical pattern (Figure 1), we were concerned that time of day could be correlated with hourly nest temperatures, producing multicollinearity. Therefore we ran a regression of nest temperature and hour; we used the residuals from the regression in our final model instead of nest temperature. Using the residuals did not change the results of our final model significantly, indicating that multicollinearity was not a concern in our model. We performed the GLMM in R using the pscl package (Jackman 2002).

RESULTS

Egg Logger Deployments

Twelve of the 56 egg loggers used in this study were neglected for a period greater than three hours during deployment. These periods of neglect significantly decreased mean hourly turning rates and were therefore removed from analysis. Egg logger abandonment occurred in twenty-eight percent of nests used (n = 22). However, 62% of birds that abandoned their nests returned for a successful breeding attempt, either resuming incubation after the natural egg was replaced or re-laying and hatching a chick later in the season. Overall, 11% (8 of 74) breeding attempts were completely abandoned after egg logger deployments.

Nest Chamber Temperatures

Nest temperatures differed between day and night, with daytime nest temperatures averaging 3.2 ± 2.6 °C higher than nighttime temperatures (± standard deviation; Table 1; t=8.42, df=49, p<0.001). Mean daytime nest temperatures were more variable than nighttime nest temperatures (Barlett's statistic, x^2=896, df=1,54, p<0.001; Figure 1). The highest mean temperatures occurred in un-shaded nest boxes (Figure 2; ANOVA, $F_{2,54}$=3.44, p=0.040). Un-shaded boxes had the highest range of daily nest temperatures and natural burrows had the lowest (Figure 2; ANOVA, $F_{2,44}$=8.38, p<0.001).

Egg Temperatures

Hourly egg temperatures were greater (0.4 ± 0.80°C) during the day than at night (Table 1; t=3.99, *df*=1,51, p<0.001). Daytime egg temperatures (38.5 ± 1.98°C) were no more variable than nighttime egg temperatures (38.1 ± 2.05°C). Un-shaded nest boxes had the highest mean daily egg temperatures and natural burrows had the lowest (Figure 2; ANOVA, $F_{2,51}$=7.28, p=0.001). Overall, daily egg temperature ranges (daily maximum to nightly minimum) did not differ among different nest habitat types. Although egg and nest temperatures were highest in un-shaded boxes and lowest in natural burrows, there was no relationship between nest and egg temperatures for daily means (Figure 3) or for daytime and nighttime means separately.

Egg Turning Rates

Mean hourly egg turning rate was 2.11 ± 2.02 turns per hour. Hourly turning rates were 25% higher during nighttime periods compared to daytime periods (Table 1; t=-5.05, df=51, p<0.001).

No difference was seen in day and nighttime egg turning rates among the different nest habitat types. Therefore, all analyses of egg turning rates were separated by time of day.

Daytime nest chamber temperatures positively correlated with hourly egg turning rates (Figure 4; Pearson, r_{49}=0.43, p=0.002). Egg turning rates in natural burrows were significantly lower than the turning rates in un-shaded boxes (Figure 5; Negative Binomial GLMM, t=2.16, p=0.04). There was a significant negative correlation between nighttime egg temperatures and turning rates (Figure 4; Pearson Correlation, r_{49}=-0.38, p=0.007).

DISCUSSION

As we hypothesized, nest and egg temperatures were warmest in un-shaded boxes and coolest in natural burrows. Furthermore, both auklet nest and egg temperatures were most variable in un-shaded nest boxes and also varied significantly with time of day. We found that the average auklet egg turning rate was 2.11 turns/hour, with higher rates during the nighttime periods. Our results were consistent with our hypotheses that egg turning rates varied with fluctuating nest and egg temperatures. However, we did not see an overall decrease in egg turning rates as nest chamber temperatures increased, as we had postulated. Instead, hourly egg turning rates were positively correlated with nest temperatures during the day and negatively correlated with egg temperatures during the night.

Nest Chamber Temperature

Artificial nest boxes were significantly warmer than natural burrows and shading reduced the temperatures in nest boxes, which is consistent with results of Warzybok and Bradley (2010). Nest boxes became warmer than natural burrows during the day, when exposed to direct sunlight, but they were also significantly cooler at night or when exposed to high winds and damp air, which are common weather conditions on SEFI during the breeding season. The daily maximum temperatures detected in un-shaded nest boxes was 35.6 ± 4.24 °C. There is no record of the temperatures of nests during the 2008 heat event, however we believe them to be much greater than the temperatures recorded in this study. Nonetheless, large fluctuations in nest temperature were observed, which could lead to auklets to expend more energy to maintain body and egg temperatures (Conway & Martin 2000). In other burrow and surface nesting seabird species, anomalous weather conditions and large-scale climatic changes have led to increased energy expenditure for thermoregulation when incubating in elevated nesting temperatures (Gaston et al. 2002, Oswald and Arnold 2012).

Egg Temperatures

Avian eggs experience a flux in heat energy. Heat input comes from the incubating parent, the nest environment, and production by the embryo itself. Conversely, heat energy from the egg can be lost to a cooler surrounding environment (Turner 2000). Egg loggers used in the present study had a single temperature thermistor located in the center of the egg so recorded temperatures were core egg temperatures without gradients, and are not exact temperatures of auklet eggs *in vivo*. Nevertheless, the egg loggers accurately detected hourly and daily temperature fluctuations and relative temperature differences caused by variations in nest temperatures and egg turning rates.

Egg temperatures were highest in un-shaded nest boxes and lowest in natural burrows. Egg temperatures from all nest types showed fluctuations, however egg temperatures were less variable than nest temperature overall (Figure 3). Moreover, hourly fluctuations in egg temperatures were not correlated with changes in corresponding nest temperatures. These results suggest that, for the nest temperatures observed in this study, auklet parents were able to buffer eggs from significant variations in nest habitat temperatures through the transfer of body heat and egg turning behaviors.

It is possible, however, that over larger nest chamber temperature fluctuations an auklets ability to maintain egg temperatures could be compromised. 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 effects of elevated ambient temperatures on nesting birds, leading to negative impacts on the birds or their eggs (Conway & Martin 2000, Pipoly et al. 2013). For the adult auklets in un-shaded nest boxes during the extreme heat event on SEFI in 2008, the inability to cope with the elevated temperatures caused severe heat stress in the nesting birds, leading to mortality in a few cases. Although the heat event in 2008 did not affect the overall hatching success of auklets (Warzybok and Bradley 2008), the auklets' ability to maintain proper incubation behavior (e.g. egg turning) could have been compromised, leading to insufficient temperature and nutrient flux through the embryo (Deeming 2002b). If the significant warming trend on SEFI over the past 4 decades continues (Warzybok & Bradley 2010, Morrison et al. 2011), mortality of adults or decreased egg viability for birds breeding in artificial nest habitats could become an increasing concern. Elevated environmental temperatures in other colonies of seabirds nesting in artificial nest habitats have caused harmful water loss in eggs and decreases in hatching success (Lei et al. 2014, Ropert-Coudert et al. 2014). In addition, extreme heat events later in the nesting season can cause heat stress for chicks in artificial nest habitats (Sherley et al. 2012, Chowdhury et al. 2014).

Egg Turning Rates

We predicted that auklet egg turning rates would vary with egg temperatures because auklet parents can regulate egg temperatures by standing up off their eggs and adjusting the rate at which they turn the egg. The relationship between egg turning rate and temperature was not as clear as hypothesized but some patterns were observed. Firstly, egg turning rates increased during nighttime periods. We believe this increase could be a byproduct of the auklet nocturnal activity. As the birds move around the nest and are more active, they are bumping the egg and increasing the turning rate. Auklets are known to be active around the colony at night and during this time it is not uncommon to find both adult auklets in the nest at once, interacting and switching off incubation duties (Manuwal 1974; Bradley, Kelsey and Warzybok personal observation).

Daytime egg turning rates increased with increasing nest temperatures (Figure 4). Un-shaded nest boxes had both higher turning rates and highest, and most variable daytime temperatures (Figures 2 & 5). Correlations between egg turning rates and nest temperatures suggest that auklets reacted to elevated nest temperatures by increasing turning rates. Although this was not taken into consideration in our initial hypothesis, upon consideration of these results we believe that this increased turning behavior can redistribute the heat of an incubated egg by increasing egg contact with the cooler ground. The negative correlation between nighttime egg turning rates and egg temperature (Figure 4) also indicates that increased egg turning rates probably leads to cooler egg temperatures. Eggs that were turned more frequently during the night, and thus exposed to cooler nighttime air and contact with the ground, were cooler than eggs turned less frequently.

MANAGEMENT IMPLICATIONS

The results of our study increase our understanding of auklet incubation behavior and how artificial nest habitats affect incubation behaviors (e.g.- egg turning rates and temperatures) of this burrow nesting seabird species. Artificial nest boxes can be an effective way to monitor and restore colonies of burrow-nesting seabird species (Wilson 1986, Libois et al. 2012). They can increase breeding success and increase adult survival, when implemented in ways that are favorable to the target species or local environment (Zingg et al. 2010, Lei et al. 2014). It is critical to our understanding of the SEFI auklet population, and their adaptation to rising temperatures, to have the population nesting in artificial nest habitats in a comparable environment to those in natural burrows.

We found that un-shaded nest boxes created more variable nesting temperatures for auklets, and that egg temperatures and turning rates corresponded with changes in nest chamber temperatures. These findings provide useful implications for artificial nest box design. Alternative nest box constructions, such as clay modules that are designed to decrease heat absorption (Carle et al. 2014), could be employed to mitigate the effects of environmental temperature fluctuations on nesting conditions of auklets. Furthermore, egg loggers could be used in future studies of burrow and crevice nesting bird species in artificial nest habitats to assure that, with changing environmental conditions, the techniques used to study, manage, and protect these species are successful.

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Associate Editor:

FIGURE CAPTIONS

Figure 1: Example data of a sample 36-hour period from one egg logger placed in a Cassin's Auklet nest box in 2012 on Southeast Farallon Island, CA. Blue = Euler angle change (angle changes in radians), Black = nest temperature, Red = egg temperature. Gray background shows nighttime periods.

Figure 2: Average hourly temperatures in different Cassin's Auklet nest habitat types on Southeast Farallon Island, CA: Natural Burrows, Shaded Nest Boxes, and Un-shaded Nest Boxes. Blue = Egg Temperatures, Gray = Nest Temperatures. Red lines indicate means, blue/gray boxes show interquartile ranges, whiskers indicate 1.5x the interquartile range of adjacent values, red plus signs are outliers.

Figure 3: Relationship between average daily nest and egg temperatures. Deployments in different nest habitat types depicted in different colors: Blue = Natural Burrows, Black = Shaded Nest Boxes, Red = Un-shaded Nest Boxes. Lines show convex hull polygons for data points from each nest habitat type.

Figure 4: 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**.** Blue = Natural Burrows, Black = Shaded Nest Boxes, Red = Un-shaded Nest Boxes. **Note**: x-axis nest temperatures for day and night (panes **C**&**D**) are on different scales (nighttime data showing a larger temperature range).

Figure 5: Average turning rates (turns per day) of eggs in different nest habitat types. Red lines indicate means, blue boxes show interquartile ranges, whiskers indicate 1.5x the interquartile range adjacent values.

TABLES

Table 1: The average turns per hour and average temperature during the day and night. Turning rates and temperatures were averaged for each day and night period over the entire deployment. Turn and temperature averages ± one standard deviation.

Time of Day	Deployment Year	N	Egg Turning Rate*	Egg Temperature (°C)*	Nest Temperature (°C)*
Day	2012	24	1.9 ± 1.7	37.8 ± 2.0	16.7 ± 3.5
	2013	32	1.9 ± 1.9	39.3 ± 1.6	17.3 ± 4.9
Night	2012	24	2.4 ± 1.9	37.5 ± 2.0	14.1 ± 1.5
	2013	32	2.7 ± 2.2	38.8 ± 1.9	13.5 ± 2.3

* = significant at p=0.05.

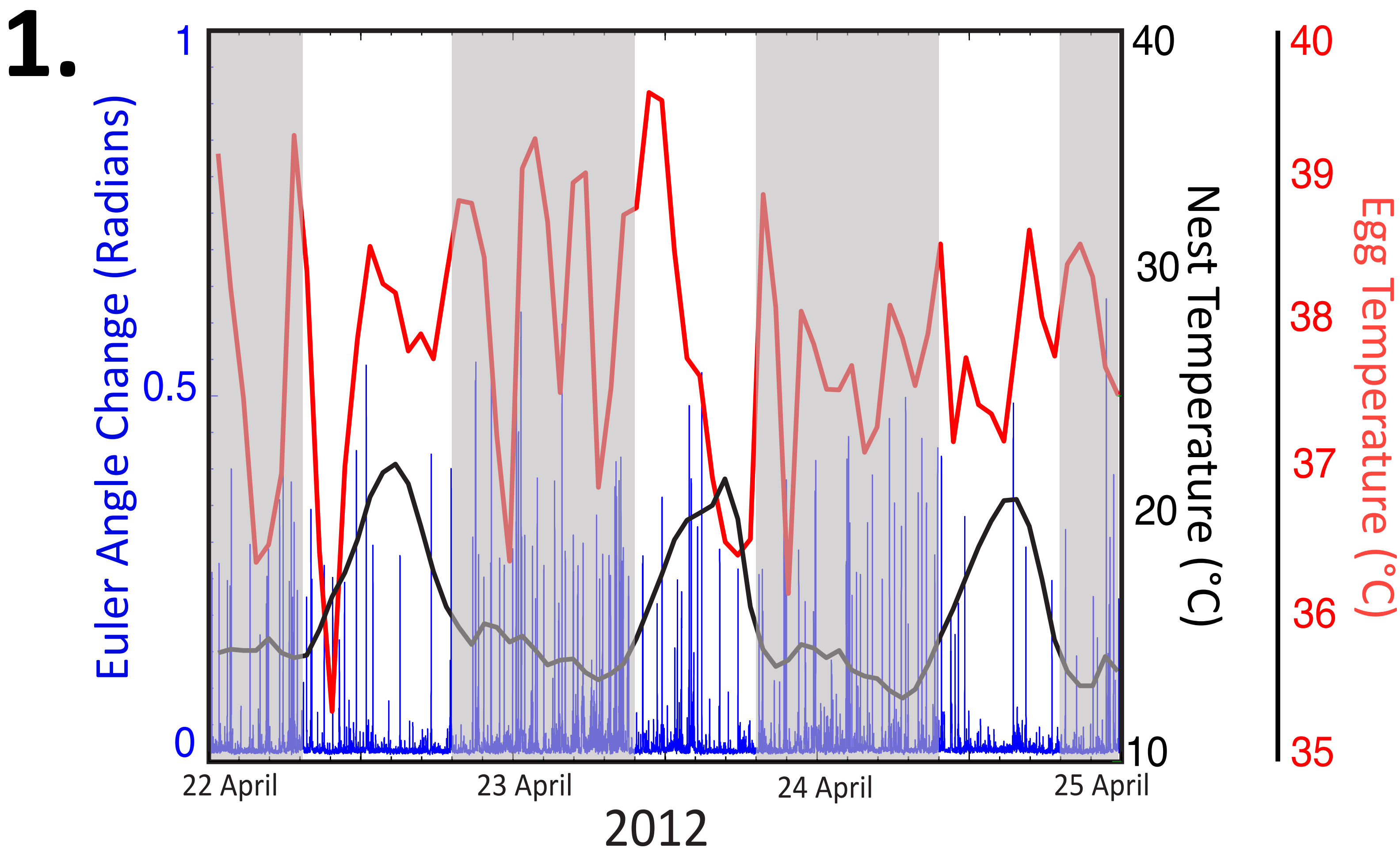
APPENDIX

Appendix Table A: 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=26)	100	16.7	39.16 (n=4)

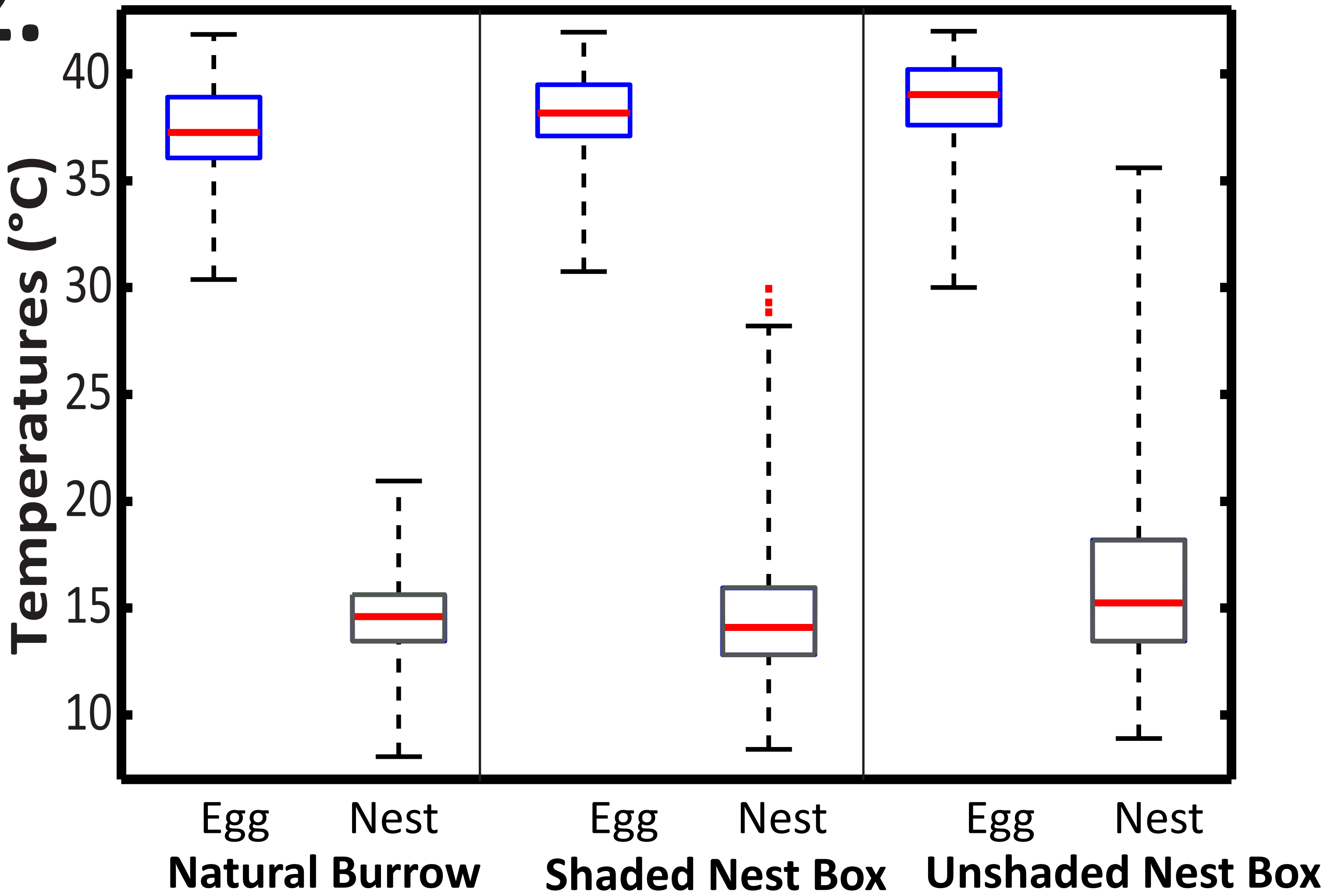
* Average temperatures of a subset of eggs were also compared to confirm that no significant difference in temperatures was found between eggs with different weighting techniques (ANOVA, f=1.27, *df*=2,9, p=0.33).

Appendix Figure 1: Different auklet nest habitat types on SEFI. (**A**) Natural Burrow, NB; (**B**) Shaded Nest Box, SB; (**C**) Un-shaded Nest Box, UB

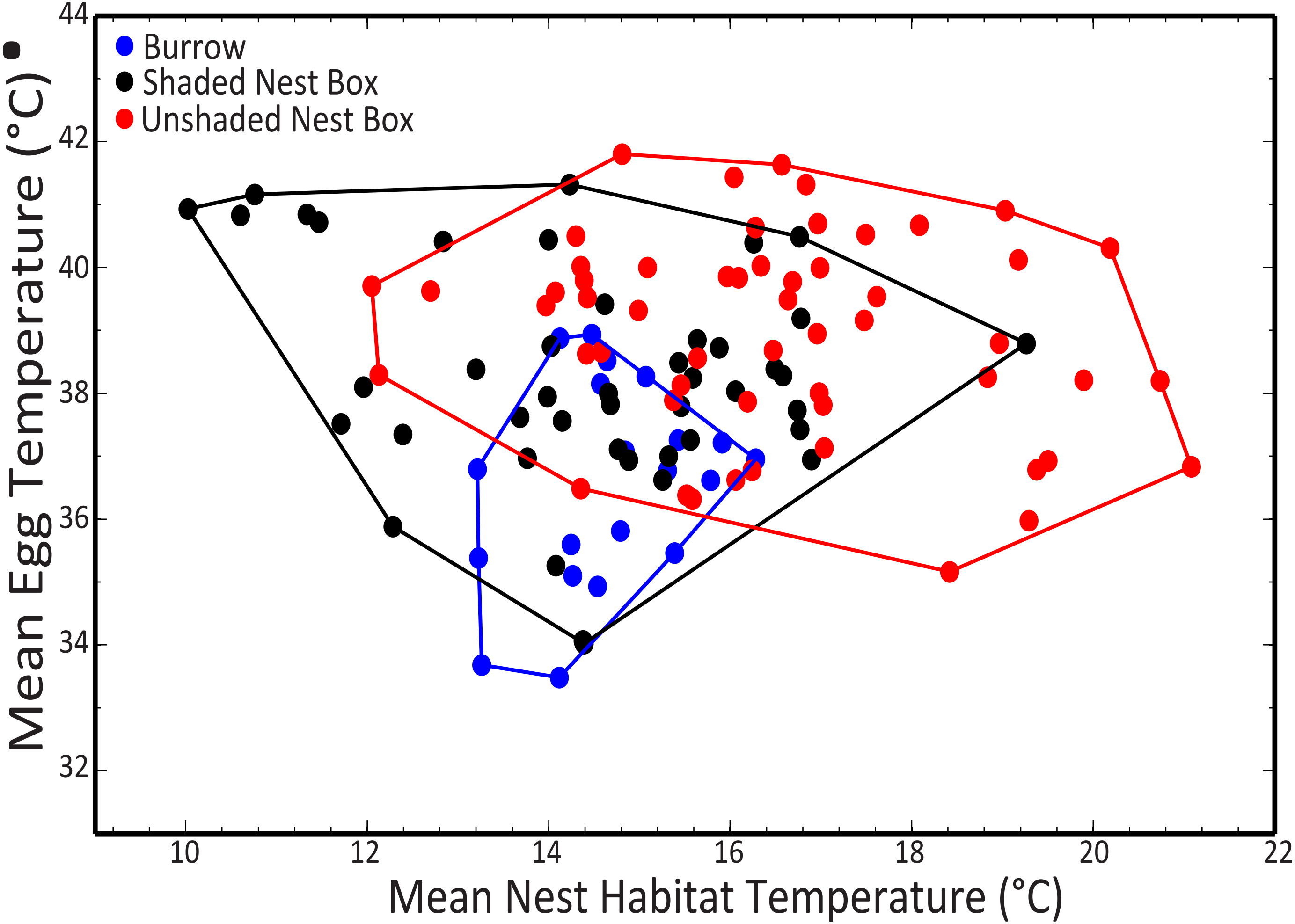


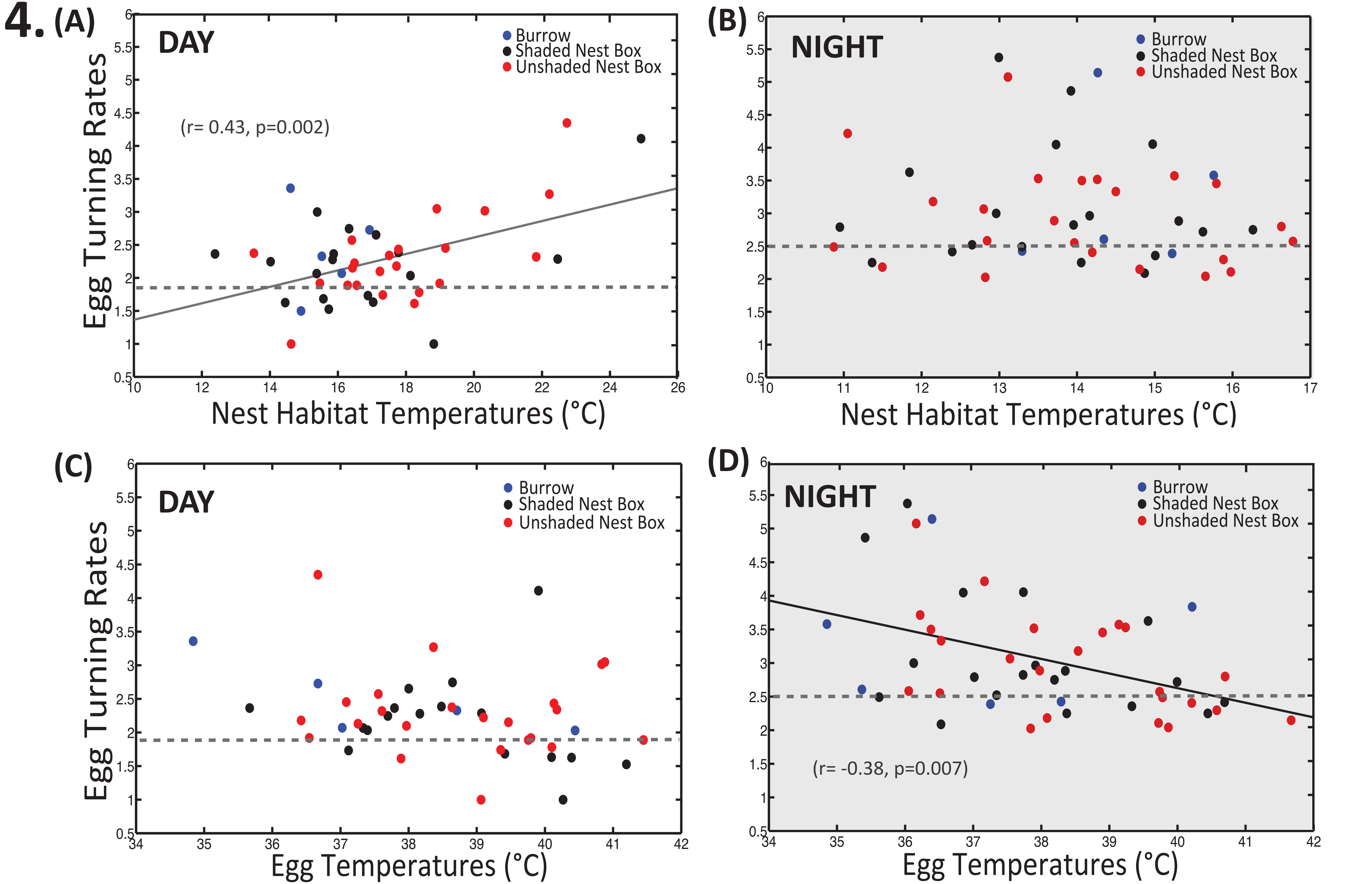
1.
Euler Angle Change (Radians)
1
0.5
0
Nest Temperature (°C)
40
30
20
10
Egg Temperature (°C)
40
39
38
37
36
35
22 April
23 April
24 April
25 April
2012

2.


Temperatures (°C)
40
35
30
25
20
15
10
Egg
Nest
Egg
Nest
Egg
Nest
Natural Burrow
Shaded Nest Box
Unshaded Nest Box

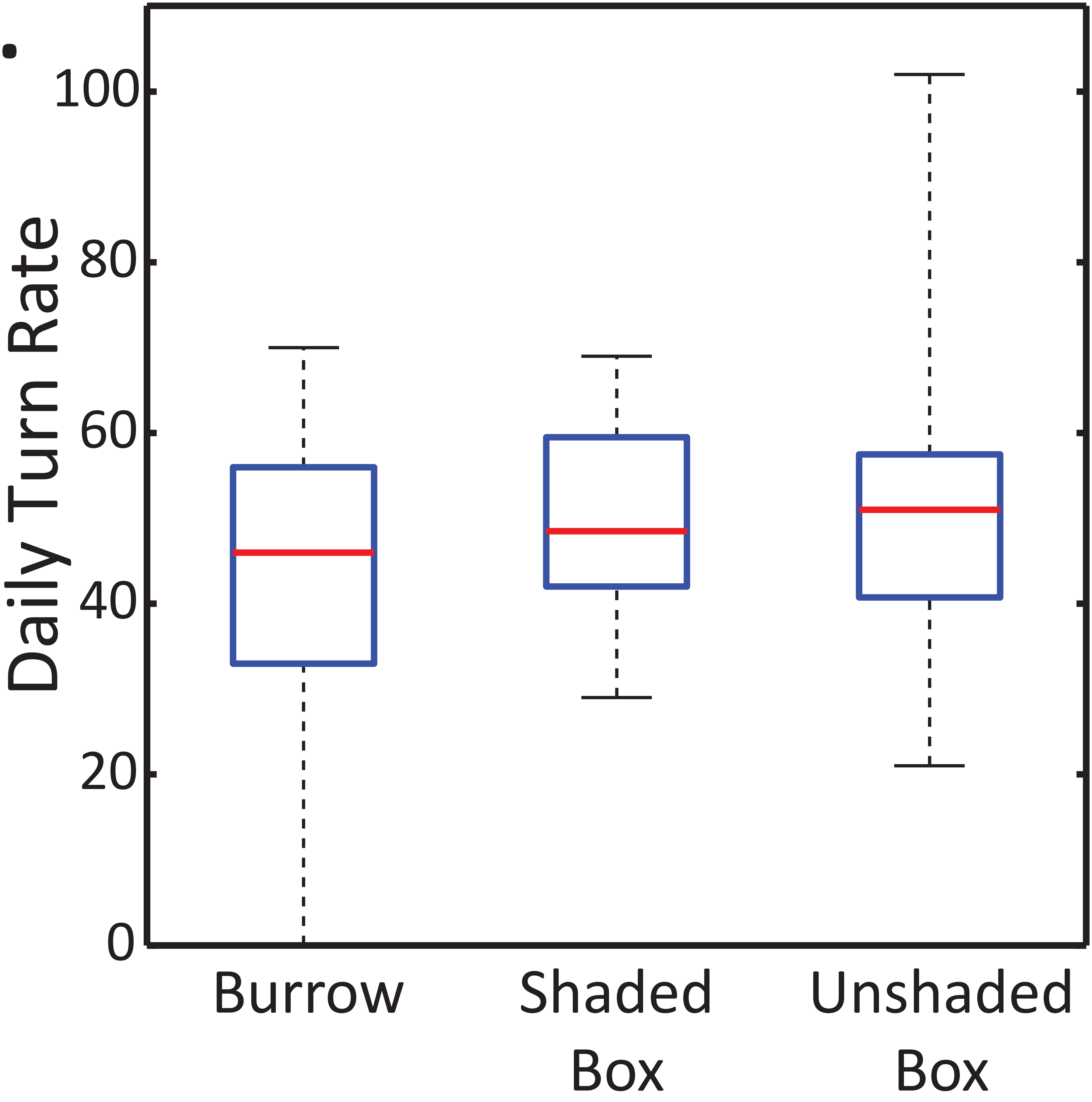
3.


Burrow
Shaded Nest Box
Unshaded Nest Box
Mean Egg Temperature (°C)
Mean Nest Habitat Temperature (°C)
44
42
40
38
36
34
32
10
12
14
16
18
20
22



4.
(A)
DAY
Burrow
Shaded Nest Box
Unshaded Nest Box
(r= 0.43, p=0.002)
Egg Turning Rates
Nest Habitat Temperatures (°C)
(B)
NIGHT
Burrow
Shaded Nest Box
Unshaded Nest Box
Nest Habitat Temperatures (°C)
(C)
DAY
Burrow
Shaded Nest Box
Unshaded Nest Box
Egg Turning Rates
Egg Temperatures (°C)
(D)
NIGHT
Burrow
Shaded Nest Box
Unshaded Nest Box
(r= -0.38, p=0.007)
Egg Temperatures (°C)

5.



Daily Turn Rate
100
80
60
40
20
0
Burrow
Shaded Box
Unshaded Box