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

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7 Kelsey et al. • Auklet Incubation Behavior

8

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

11

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24 **ABSTRACT** Hatching success in birds is influenced by the temperature and turning rate of the
25 egg, but our understanding of the environmental factors that effect incubation temperatures and
26 egg turning rates in birds is limited. Especially little is known of these effects for species that
27 nest in burrows or crevices, such as the Cassin's auklet (*Ptychoramphus aleuticus*). On
28 Southeast Farallon Island (SEFI), California, a subset of the Cassin's auklet (hereafter auklet)
29 population nest in artificial nest boxes for scientific monitoring. The nest boxes are above
30 ground and made out of a single layer of plywood. Temperatures in un-shaded nest boxes can
31 increase significantly during extreme heat events. Shaded structures put on top of occupied nest
32 boxes help mediate nest box temperatures but the effects of elevated temperatures on auklet
33 incubation behaviors and egg viability remain equivocal. We used egg data loggers to measure
34 the temperatures and turning rates of auklet eggs in natural burrows, shaded nest boxes, and un-
35 shaded nest boxes on SEFI. Nest box (13.93 ± 1.26 °C) and egg (37.43 ± 1.92 °C) temperatures
36 were highest and most variable in un-shaded nest boxes. Mean hourly egg turning rate was 2.11
37 ± 2.02 turns hour⁻¹ and turning rates were significantly higher at night. Egg turning rates also
38 varied with fluctuating nest and egg temperatures, being positively correlated with nest
39 temperatures during the day and negatively correlated with egg temperatures during the night.
40 Given the variations we observed in egg temperature and turning rates associated with nest
41 habitat temperature and type, our results suggest that nest box design can influence incubation
42 behaviors of breeding birds. As seasonal temperatures and the number of extreme heat events
43 rise, understanding the impacts of temperature on auklets nesting in artificial nest habitats can
44 have positive implications for conservation and management of the species.

45

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

47 INTRODUCTION

48 Most bird species engage in **distinct incubation** behaviors, turning their eggs and
49 regulating egg temperature (Eycleshymer 1907, Deeming 2002a). **Egg turning is integral for**
50 **proper embryonic development**, regular rotation of the egg facilitates albumen use by the embryo
51 and prevents the embryo from adhering to the shell membrane (New 1957, Tona et al. 2005).
52 **Regular egg turning behavior can also lead to increased hatching success, chick health, and**
53 **overall reproductive success** (Deeming 2002a, Tona et al. 2005, Elibol and Brake 2006).
54 **Maintaining egg temperatures is also important for proper embryonic development** (Turner 2002,
55 **DuRant et al. 2013**). Incubation temperatures and egg turning rates have been studied
56 extensively in the poultry industry to maximize the hatchability of domestic fowl (**Deeming**
57 **2002a**). **In contrast**, the factors influencing egg temperatures and turning rates of wild birds are
58 not well understood.

59 **Optimal incubation temperatures for most birds is 30 to 40°C but the thermal tolerance of**
60 **the egg can vary between species and among climates** (Webb 1987). Most studies that examine
61 the effects of egg temperature variation on incubation in wild birds have focused on the **effects** of
62 egg cooling. **Egg temperatures can drop below optimal levels when parents leave an egg**
63 **unattended, which in some cases, can lead to** suspended embryonic development and delayed
64 hatching (Williams & Ricklefs 1984, Astheimer 1991, Reneerkens et al. 2011). Conversely, less
65 is known about how hyperthermic incubation conditions, **when egg temperatures are elevated**
66 **above the optimal range for that species, affect** embryonic development and hatching success of
67 birds, though increased incubation temperatures are thought to be more detrimental to embryonic
68 development than hypothermic temperatures (Webb 1987, Pipoly et al. 2013). When certain
69 nesting conditions create atypically warm environments (i.e. **intense sun exposure on the bird, its**

70 nest, or burrow), parent birds may be challenged to maintain optimal temperatures for
71 themselves and their eggs. Climate models predict, and weather observations confirm, that
72 global temperatures are increasing (Mahlstein et al. 2013) and the effects of elevated
73 temperatures on avian incubation is of growing concern for some species (Schaper et al 2012,
74 Pipoly et al. 2013).

75 Artificial nest boxes are commonly used to facilitate monitoring, restore habitat,
76 translocate and maintain colonies, increase breeding success, and increase adult survival of
77 burrow-nesting seabird species (Wilson 1986, Libois et al. 2012). However, nest boxes can
78 prove to be ineffective if they are implemented in ways that are not favorable to the target
79 species or local environment (Zingg et al. 2010, Lei et al. 2014). Lei et al. (2014) found that the
80 hatching success of African Penguins (*Spheniscus demersus*) nesting in artificial fiberglass
81 burrows was consistently lower than hatching success in natural burrows. The authors
82 hypothesized that the fiberglass boxes created a hotter and drier nesting environment than natural
83 burrows, therefore increasing the risk of egg desiccation and hatching failure. In addition to
84 possible decreases in hatching success, elevated temperatures in artificial nest habitats can cause
85 hyperthermia in the adult birds and chicks, which can be lethal (Ropert-Coudert et al. 2004, Lei
86 et al. 2014).

87 We chose to study the effects of nest temperatures on Cassin's auklet (*Ptychoramphus*
88 *aleuticus*) incubation behavior and temperature on Southeast Farallon Island (SEFI), California
89 because the population nesting in artificial nest boxes there has been exposed to increasing
90 environmental temperatures, which has lead to heat stress for some nesting birds (Warzybok and
91 Bradley 2010). The Cassin's auklet (hereafter auklet) is a small, diving seabird found
92 throughout the northeastern Pacific Ocean (Manuwal 1974a). The species lays a single egg in a

93 burrow or crevice (Manuwal 1974a). On SEFI, researchers from Point Blue Conservation
94 Science (formally known as Point Reyes Bird Observatory) use artificial nest boxes to study the
95 breeding biology of the Cassin's auklet. Nest boxes are above ground and made out of a single
96 layer of plywood (Appendix Figure 1), thus being highly susceptible to environmental
97 temperature fluctuations. In recent years, auklets nesting in artificial nest boxes exposed to
98 direct sunlight have experienced extreme heat events when temperatures were significantly
99 higher than average ambient temperatures during the SEFI breeding season (>25°C; Point Blue,
100 unpublished data). Subsequent investigation determined that artificial nest boxes were
101 significantly warmer than natural burrows, but placing shaded structures on top of nest boxes
102 could mitigate elevated nest box temperatures (Warzybok and Bradley 2010). Annual maximum
103 environmental temperatures on SEFI have increased nearly 3-4°C since 1970 (Warzybok and
104 Bradley 2010). The elevated temperatures in 2008 resulted in heat stress and even death in some
105 adult auklets (Warzybok and Bradley 2008). However as maximum temperatures on SEFI rise,
106 the effects of increased nest chamber temperatures on auklet incubation behavior (e.g. - egg
107 turning and egg temperature) remain unclear.

108 Recently developed technologies are increasing our understanding of egg turning
109 behaviors through the use of data logging devices placed inside artificial eggs that are incubated
110 by parent birds (Beaulieu et al. 2009, Thierry et al. 2013, Shaffer et al. 2014). Using this
111 technology, we examined the effects of environmental temperature in natural and artificial nest
112 habitats on the incubation behaviors of Cassin's auklets. To date very little is known about
113 auklet incubation behavior, or the incubation behaviors of seabirds in general (Shaffer et al.
114 2014). The average incubation period is approximately 38 days, during which parents exchange
115 egg attendance on a nightly basis until hatching (Manuwal 1974a). Egg neglect is rare but not

116 uncommon among auklets (Asheimer 1991), however little else is known about their egg
117 attendance or egg turning behaviors. During the auklet breeding season, March through August,
118 mean monthly ambient temperatures on SEFI ranged from 11.8 ± 1.0 to $14.5 \pm 1.0^\circ\text{C}$, respectively
119 (years 1971-2007; Point Blue Conservation, unpublished data). The goal of our study was to
120 determine if different nest habitat types (i.e. natural burrows, shaded and un-shaded nest boxes)
121 influenced egg temperatures and egg turning patterns of incubating auklets. We hypothesized
122 that egg temperatures would be higher and more variable in un-shaded boxes. We also
123 hypothesized that egg turning rates would vary with nest temperatures, where parents turn eggs
124 according to nest and egg temperature variation. Therefore, we expected that elevated
125 temperatures might lead to suboptimal egg turning rates. We believe that as nest temperatures
126 increase, auklet parents may stand up off of their eggs to allow the eggs to cool and stay within
127 optimal incubation temperatures, resulting in a putative reduction in the frequency of egg
128 turning.

129

130 **STUDY AREA**

131 Southeast Farallon Island ($37^\circ 41' 49''\text{N}$ $123^\circ 00' 07''\text{W}$) is part of the Farallon National Wildlife
132 Refuge, located 48 kilometers west of San Francisco, California. Currently, there are about
133 10,000 auklet pairs that nest on SEFI (Warzybok and Bradley 2010). The auklets inhabit
134 primarily the marine terrace and rocky slope habitat throughout the 0.3104km^2 island. Five
135 hundred artificial nest boxes have been built on SEFI to monitor breeding auklets. Nest boxes
136 are $20 \times 23 \times 40\text{cm}$ boxes made out of cdx plywood with a 10cm PVC pipe as an entrance
137 (Appendix Figure 1).

138

139 METHODS

140 Egg and Egg Logger Design

141 We deployed custom-made artificial eggs containing an egg logger in selected auklet nests
142 established between April and July of the 2012 and 2013 breeding seasons ($n = 34$ in 2012, $n =$
143 41 in 2013; Shaffer et al. 2014). The size, shape, and color of the artificial eggs were based on
144 historical measurements and images of natural auklet eggs (27.5g; Manuwal 1974). Artificial
145 eggs were made out of 1/8-inch vacuum-formed polystyrene plastic. We filled artificial eggs
146 with non-ferrous barium sulfite (BaSO_4) and ClearGlide wire pulling lubricant (IDEAL
147 Industries, Fort Lauderdale, FL) to increase the mass of the artificial egg without influencing the
148 mechanics of the sensors in the logger (Conway & Martin 2000; Appendix Table 1). After
149 adding weighting agents, an egg logger was placed in each artificial egg.

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

155 Egg Logger Deployment

156 We deployed the egg loggers in a subset of occupied burrows and nest boxes spread across the
157 island. We would remove the bird and the natural egg from the nest chamber, then place the egg
158 logger in the center of the nest cup and allow the bird to return to its nest. LogTag ambient
159 temperature loggers (MicroDAQ.com, Ltd., New Hampshire) were also deployed inside the
160 corresponding nest of each egg logger deployment to record nest chamber temperature for the
161 duration of the egg logger deployment. The ambient temperature loggers were placed on the

162 ceiling of the nest box and secured with Velcro tape. These loggers recorded the temperature of
163 the nest environment every 30 minutes.

164 For the egg logger and ambient temperature logger deployment, we selected nests with
165 eggs in the early stages of incubation (1-20 days old) to control for changes in incubation
166 behavior that may occur across the incubation period (Turner 2002). Because there is no *a priori*
167 information to suggest that turning rates would change throughout the course of the day, we did
168 not find it necessary to standardize the time of day at which the egg loggers were deployed.

169 Cassin's auklets lay single egg clutches, so we removed the natural eggs from the nest during
170 egg logger deployments, and incubated them in a poultry incubator (Top Hatch Incubator;
171 Brower Equipment, Houghton, IA) at approximately 35°C (95°F) and 55% humidity for the
172 length of the 5-10 day deployments.

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

177 **Data Processing**

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

181 *Egg Temperature and Turning Rates* – We processed egg logger data with custom
182 routines created in MATLAB (The Mathworks, Natick, MA) following methods described in
183 Shaffer et al. (2014). To remove any potential influence on egg temperature and turning rates
184 caused by egg logger deployment and retrieval, we excluded the first six and last two hours of

185 every deployment from the analysis. Eliminating the first six hours removed the time between
186 when the egg loggers were turned on and when they were deployed (1-3 hours) and the initial
187 time after the auklet was handled during deployment, allowing sufficient time for the auklet to
188 settle back onto its nest post-disturbance. Excluding the last two hours from analysis removed
189 the time between when the egg logger was removed from the nest and when it was powered off.
190 In a study of free-living auklets, Asthemier (1991) found that incubation temperatures ranged
191 from 30 to 42°C (32.7±3.4). Therefore we did not include temperatures below 30°C and above
192 42°C, removing misrepresentative temperature measurements as well as data from when the egg
193 was abandoned or neglected.

194 Turning rates were based on a minimum angle changes of 10° so that only deliberate
195 movements made by the incubating auklet were analyzed. The 10° turning threshold
196 approximated the cumulative inflection between angle change and turning rates and was
197 comparable to thresholds used in previous studies (Beaulieu et al. 2009, Thierry et al. 2013,
198 Shaffer et al. 2014).

199 We analyzed hourly turning rates and temperatures (mean, maximum and minimum),
200 starting at 12:00 midnight on each deployment day, following methodology of historical egg
201 turning studies (turns per hour, as seen in Deeming, 2002c). We also analyzed daily turning
202 rates based on the hourly averages. We believed that expressing turning rates on a daily basis
203 provided a more ecologically relevant metric and was comparable to other recent studies of egg
204 turning behavior using accelerometry (Beaulieu et al. 2010, Thierry et al. 2013, Shaffer et al.
205 2014). Daytime and nighttime temperatures and turning rates were also analyzed. Day lengths
206 were based on the date/time of local sunrise and sunset determined from ephemeris tables using
207 the latitude and longitude of SEFI.

208 **Statistical Analysis and Treatments**

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

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

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

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

245

246 RESULTS

247 Egg Logger Deployments

248 Twelve of the 56 egg loggers used in this study were neglected for a period greater than three
249 hours during deployment. These periods of neglect significantly decreased mean hourly turning
250 rates and were therefore removed from analysis. Egg logger abandonment occurred in twenty-
251 eight percent of nests used (n = 22). However, 62% of birds that abandoned their nests returned
252 for a successful breeding attempt, either resuming incubation after the natural egg was replaced

253 or re-laying and hatching a chick later in the season. Overall, 11% (8 of 74) breeding attempts
254 were completely abandoned after egg logger deployments.

255 Nest Chamber Temperatures

256 Nest temperatures differed between day and night, with daytime nest temperatures averaging 3.2
257 ± 2.6 °C higher than nighttime temperatures (\pm standard deviation; Table 1; $t=8.42$, $df=49$,
258 $p<0.001$). Mean daytime nest temperatures were more variable than nighttime nest temperatures
259 (Barlett's statistic, $\chi^2=896$, $df=1,54$, $p<0.001$; Figure 1). The highest mean temperatures
260 occurred in un-shaded nest boxes (Figure 2; ANOVA, $F_{2,54}=3.44$, $p=0.040$). Un-shaded boxes
261 had the highest range of daily nest temperatures and natural burrows had the lowest (Figure 2;
262 ANOVA, $F_{2,44}=8.38$, $p<0.001$).

263 Egg Temperatures

264 Hourly egg temperatures were greater ($0.4 \pm 0.80^\circ\text{C}$) during the day than at night (Table 1;
265 $t=3.99$, $df=1,51$, $p<0.001$). Daytime egg temperatures ($38.5 \pm 1.98^\circ\text{C}$) were no more variable
266 than nighttime egg temperatures ($38.1 \pm 2.05^\circ\text{C}$). Un-shaded nest boxes had the highest mean
267 daily egg temperatures and natural burrows had the lowest (Figure 2; ANOVA, $F_{2,51}=7.28$,
268 $p=0.001$). Overall, daily egg temperature ranges (daily maximum to nightly minimum) did not
269 differ among different nest habitat types. Although egg and nest temperatures were highest in
270 un-shaded boxes and lowest in natural burrows, there was no relationship between nest and egg
271 temperatures for daily means (Figure 3) or for daytime and nighttime means separately.

272 Egg Turning Rates

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

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

277 Daytime nest chamber temperatures positively correlated with hourly egg turning rates
278 (Figure 4; Pearson, $r_{49}=0.43$, $p=0.002$). Egg turning rates in natural burrows were significantly
279 lower than the turning rates in un-shaded boxes (Figure 5; Negative Binomial GLMM, $t=2.16$,
280 $p=0.04$). There was a significant negative correlation between nighttime egg temperatures and
281 turning rates (Figure 4; Pearson Correlation, $r_{49}=-0.38$, $p=0.007$).

282

283 **DISCUSSION**

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

293 **Nest Chamber Temperature**

294 Artificial nest boxes were significantly warmer than natural burrows and shading reduced the
295 temperatures in nest boxes, which is consistent with results of Warzybok and Bradley (2010).
296 Nest boxes became warmer than natural burrows during the day, when exposed to direct
297 sunlight, but they were also significantly cooler at night or when exposed to high winds and

298 damp air, which are common weather conditions on SEFI during the breeding season. The daily
299 maximum temperatures detected in un-shaded nest boxes was 35.6 ± 4.24 °C. There is no record
300 of the temperatures of nests during the 2008 heat event, however we believe them to be much
301 greater than the temperatures recorded in this study. Nonetheless, large fluctuations in nest
302 temperature were observed, which could lead to auklets to expend more energy to maintain body
303 and egg temperatures (Conway & Martin 2000). In other burrow and surface nesting seabird
304 species, anomalous weather conditions and large-scale climatic changes have led to increased
305 energy expenditure for thermoregulation when incubating in elevated nesting temperatures
306 (Gaston et al. 2002, Oswald and Arnold 2012).

307 **Egg Temperatures**

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

316 Egg temperatures were highest in un-shaded nest boxes and lowest in natural burrows.
317 Egg temperatures from all nest types showed fluctuations, however egg temperatures were less
318 variable than nest temperature overall (Figure 3). Moreover, hourly fluctuations in egg
319 temperatures were not correlated with changes in corresponding nest temperatures. These results
320 suggest that, for the nest temperatures observed in this study, auklet parents were able to buffer

321 eggs from significant variations in nest habitat temperatures through the transfer of body heat
322 and egg turning behaviors.

323 It is possible, however, that over larger nest chamber temperature fluctuations an auklets
324 ability to maintain egg temperatures could be compromised. Many bird species, especially those
325 that nest in hot climates, have evolved behavioral adaptations, such as panting and gular
326 fluttering, to help them maintain proper body and incubation temperatures in warm ambient
327 temperatures (Deeming 2002b). Above a certain threshold however, behavioral adaptations can
328 no longer compensate for the effects of elevated ambient temperatures on nesting birds, leading
329 to negative impacts on the birds or their eggs (Conway & Martin 2000, Pipoly et al. 2013). For
330 the adult auklets in un-shaded nest boxes during the extreme heat event on SEFI in 2008, the
331 inability to cope with the elevated temperatures caused severe heat stress in the nesting birds,
332 leading to mortality in a few cases. Although the heat event in 2008 did not affect the overall
333 hatching success of auklets (Warzybok and Bradley 2008), the auklets' ability to maintain proper
334 incubation behavior (e.g. egg turning) could have been compromised, leading to insufficient
335 temperature and nutrient flux through the embryo (Deeming 2002b). If the significant warming
336 trend on SEFI over the past 4 decades continues (Warzybok & Bradley 2010, Morrison et al.
337 2011), mortality of adults or decreased egg viability for birds breeding in artificial nest habitats
338 could become an increasing concern. Elevated environmental temperatures in other colonies of
339 seabirds nesting in artificial nest habitats have caused harmful water loss in eggs and decreases
340 in hatching success (Lei et al. 2014, Ropert-Coudert et al. 2014). In addition, extreme heat
341 events later in the nesting season can cause heat stress for chicks in artificial nest habitats
342 (Sherley et al. 2012, Chowdhury et al. 2014).

343 **Egg Turning Rates**

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

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

365 **MANAGEMENT IMPLICATIONS**

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

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

384

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400

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522 *Associate Editor:*

523

524 **FIGURE CAPTIONS**

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

529

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

535

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

540

541 **Figure 4:** Daytime and night time hourly turning rates in relation to **(A&B)** nest temperatures,
542 and **(C&D)** egg temperatures. Daytime turning rates vs. temperatures in white background,
543 nighttime turning rates vs. temperatures in gray background. Blue = Natural Burrows, Black =
544 Shaded Nest Boxes, Red = Un-shaded Nest Boxes. **Note:** x-axis nest temperatures for day and
545 night (panes **C&D**) are on different scales (nighttime data showing a larger temperature range).

546

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

550 **TABLES**

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

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

554 * = significant at p=0.05.

555

556 **APPENDIX**

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

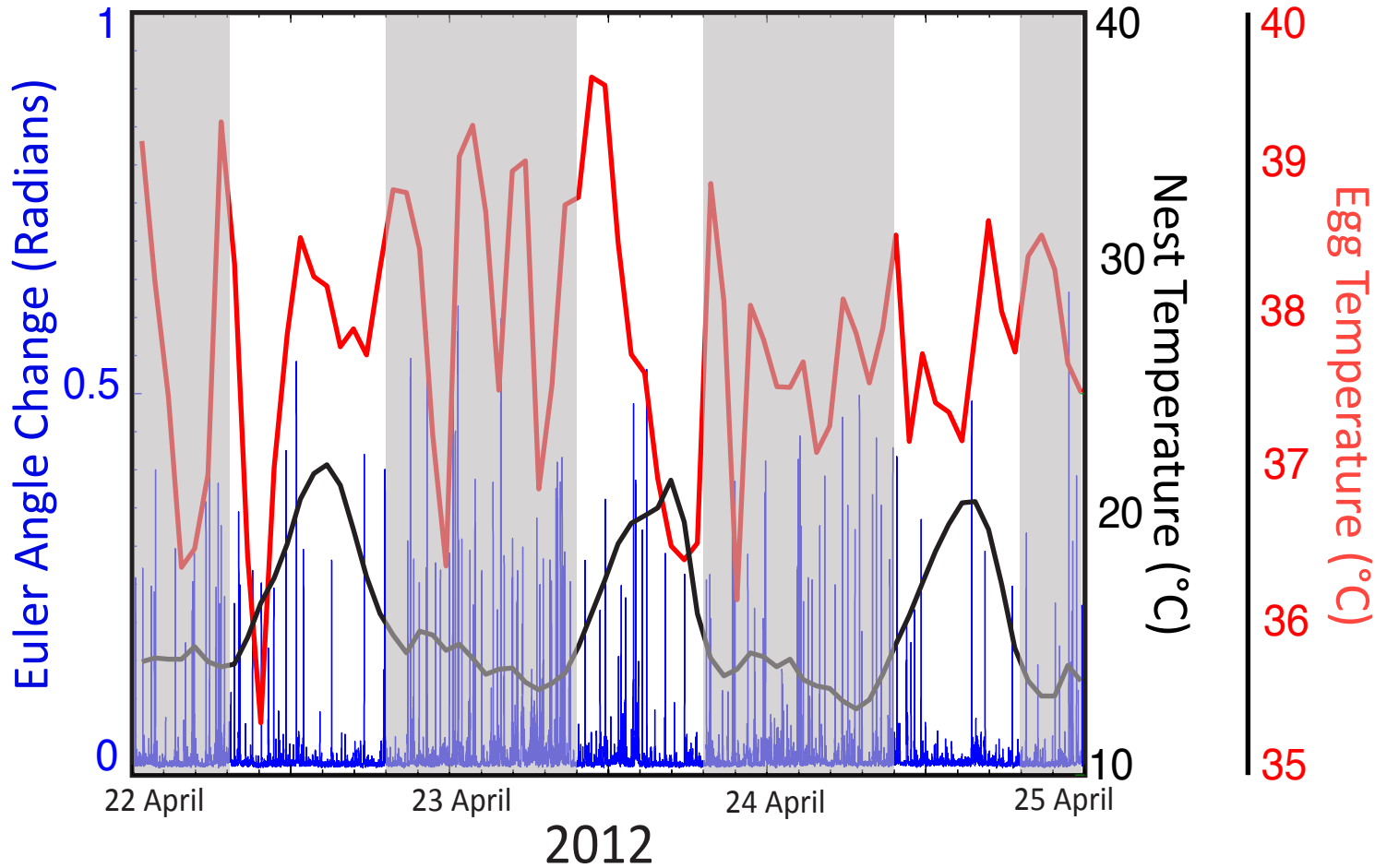
Weighting type	Deployment Date	Weight (g)	% natural egg weight	Abandonment Rate (%)	Ave. Temp. (°C)*
Natural egg (Manuwal 1972)	-----	27.5 (n=110)	----	----	----
None	4/17/2012	15.9 (n=18)	60	55.6	37.26 (n=4)
Gel	7/14/2013	22.8 (n=10)	83	40.0	37.76 (n=4)
Gel + BaSO ₄	2013- all deployments	27.7 (n=26)	100	16.7	39.16 (n=4)

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

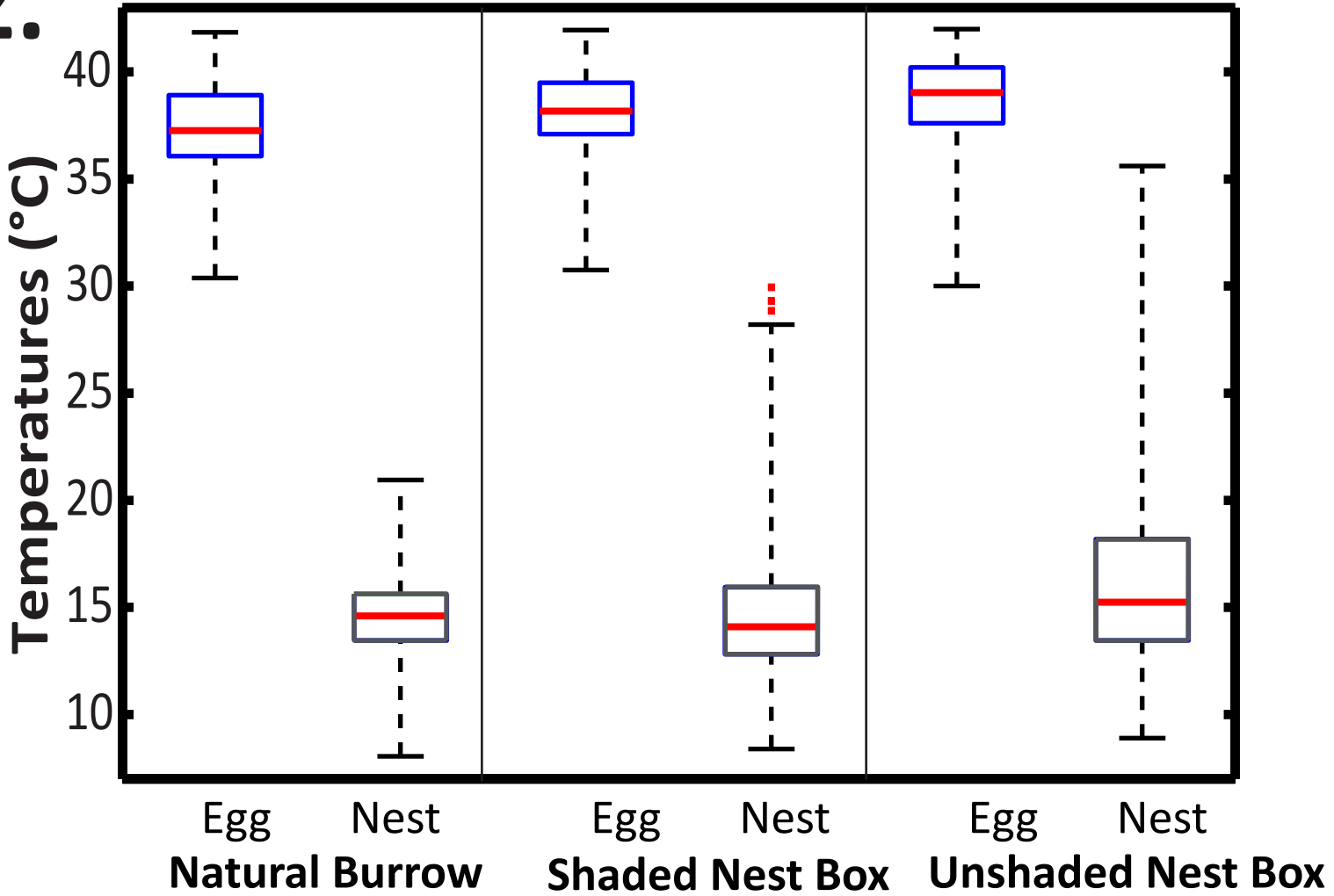
562

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

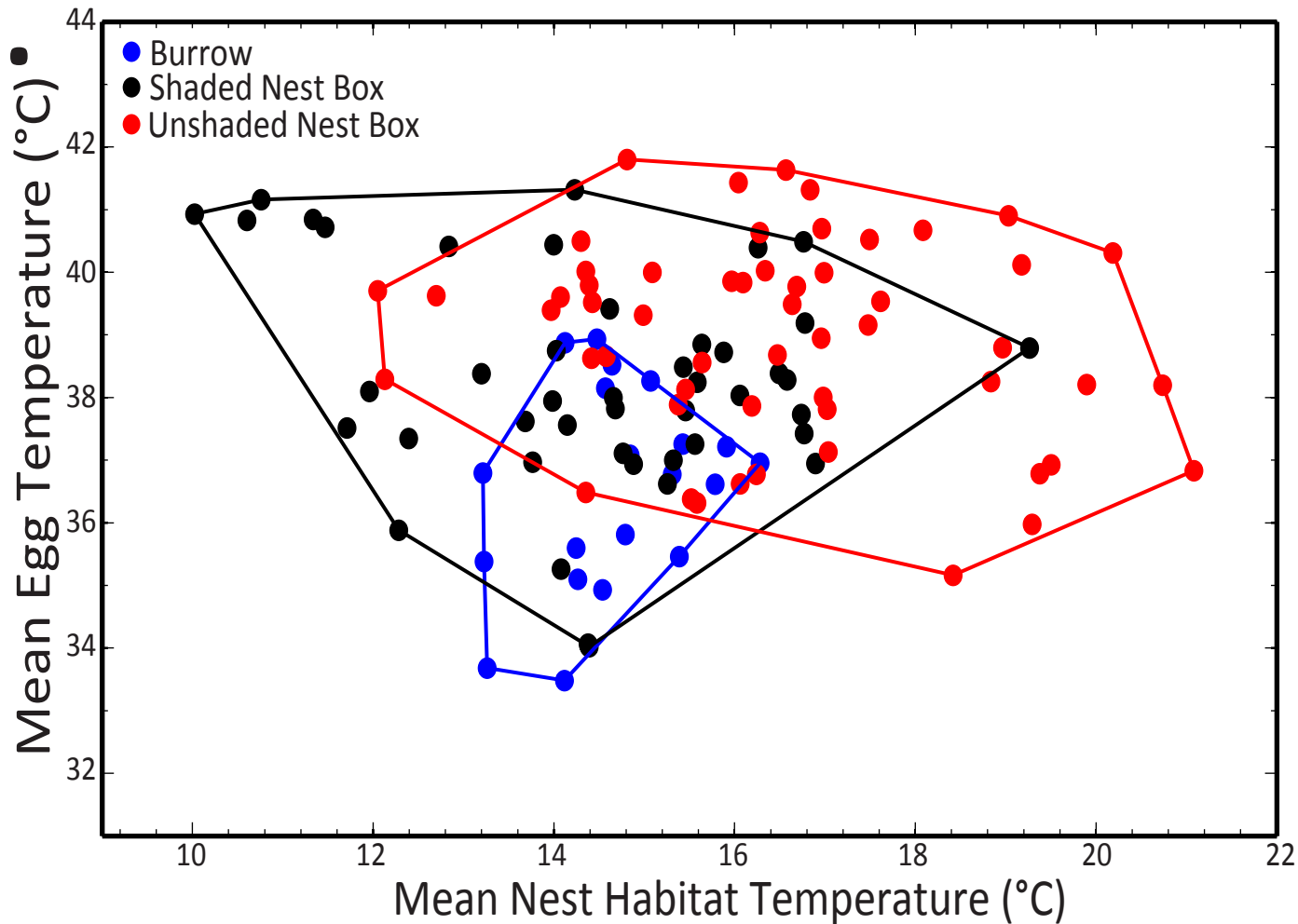
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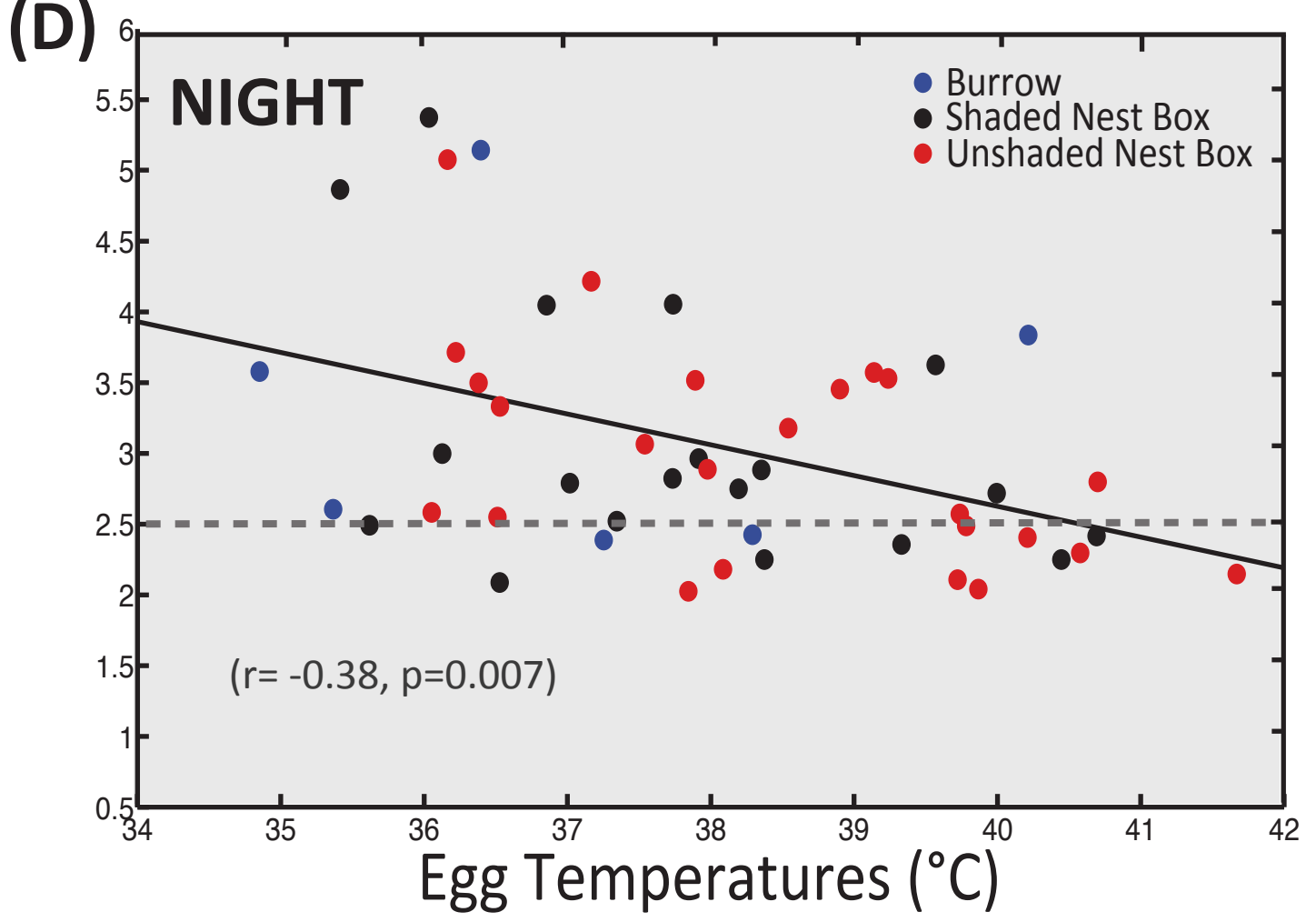
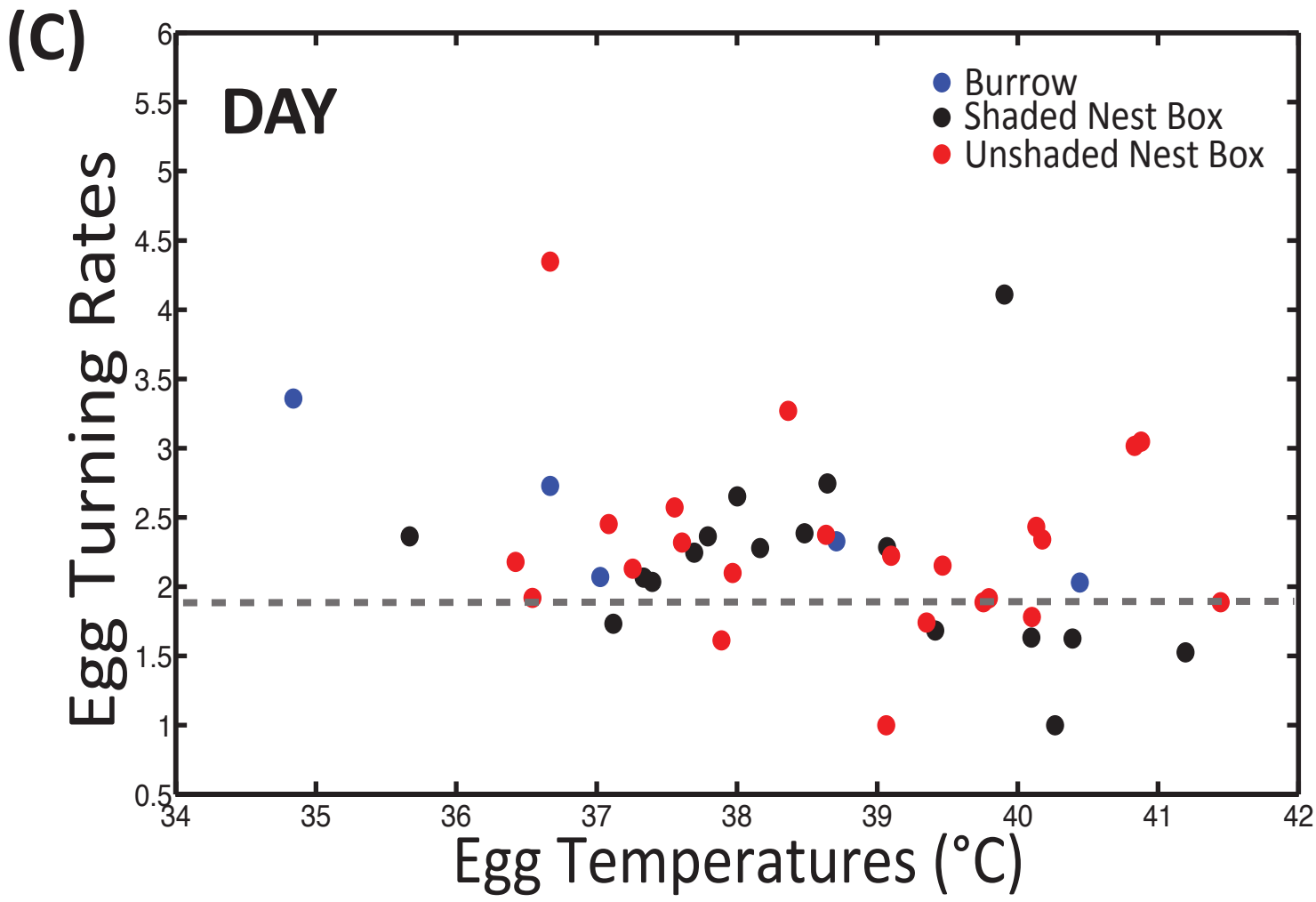
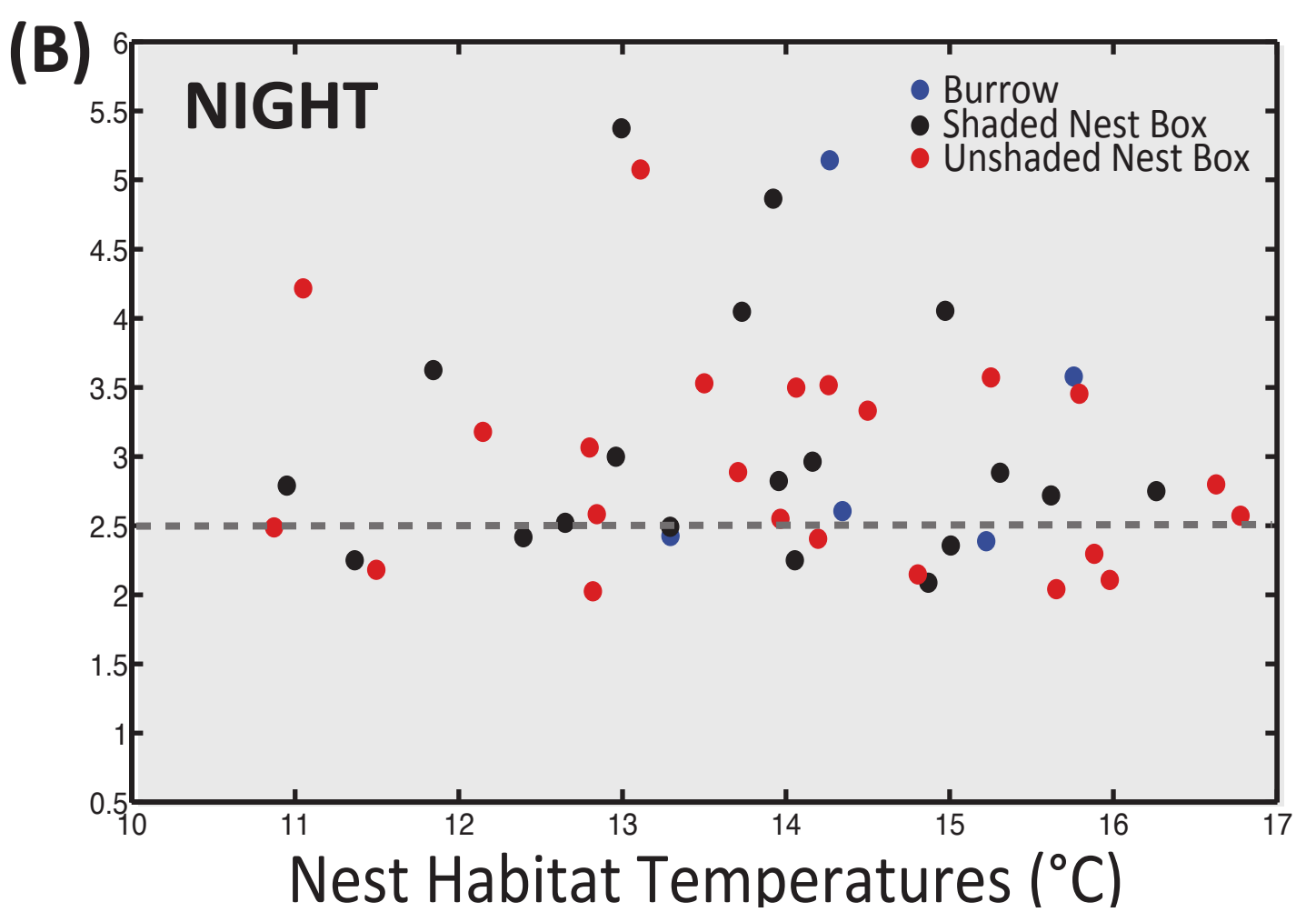
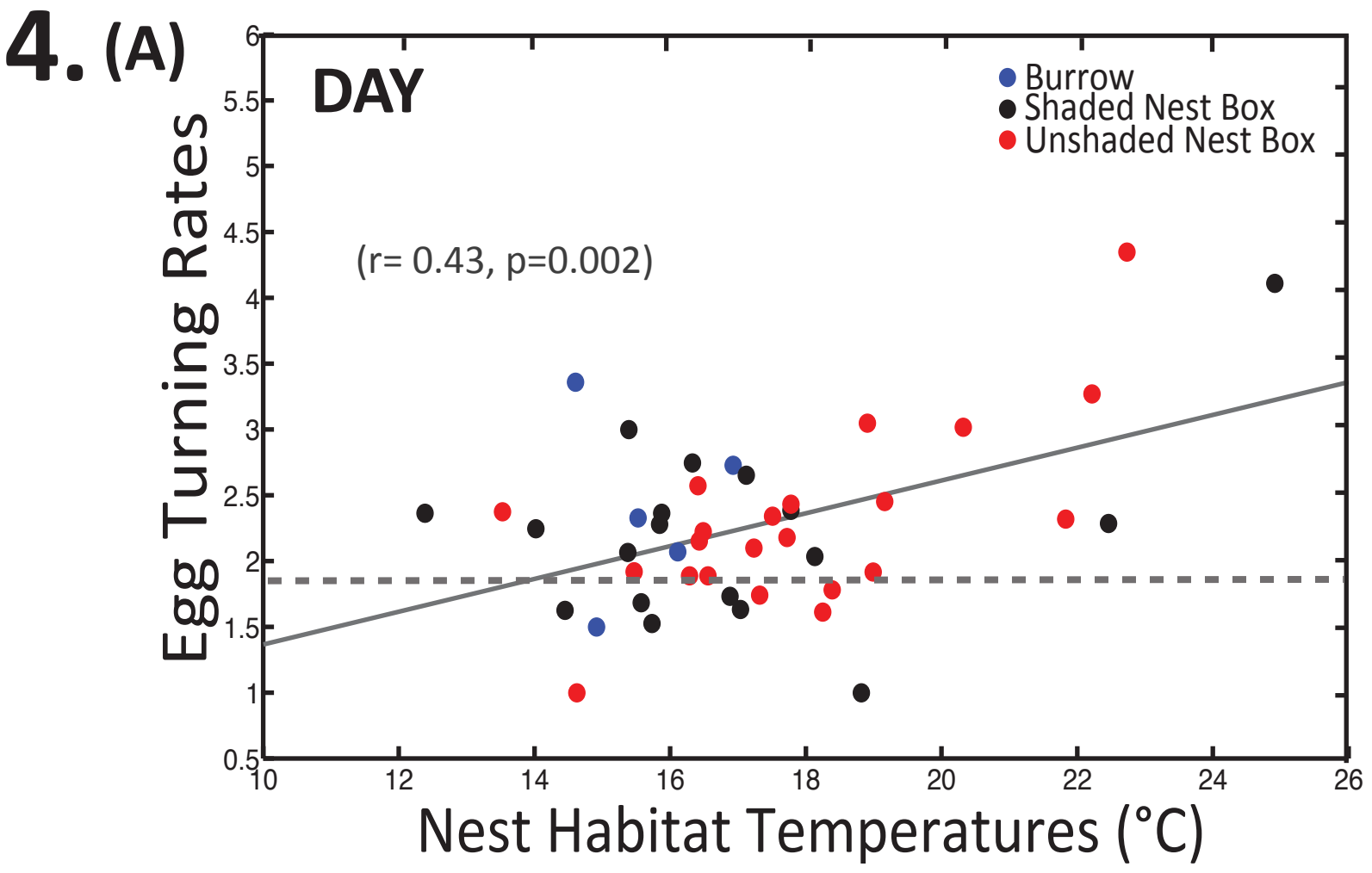


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3.





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