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Alicia K. Andes, Mark H. Sherfy, Terry L. Shaffer, et al."Plasticity of Least Tern and Piping Plover nesting behaviors in response to sand temperature" (2020). *Biology Faculty Publications*. 38.
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Version of Record: https://www.sciencedirect.com/science/article/pii/S0306456519303432
Manuscript_42703bb1f1581d7168aa58003fd0ec43

ORIGINAL ARTICLE

Plasticity of Least Tern and Piping Plover nesting behaviors in response to sand temperature

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Declarations of interest: none

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Birds that nest on the ground in open areas, like Piping Plovers (*Charadrius melodus*) and interior Least Terns (*Sternula antillarum athalassos*), are exposed to high temperatures in thermally stressful environments. As a result, some ground-nesting avian species have adapted behavioral strategies to maintain thermal regulation of eggs and themselves. We assessed the impact of sand temperature on shorebird nesting behaviors by installing video cameras and thermocouples at 52 Least Tern and 55 Piping Plover nests on the Missouri River in North Dakota during the 2014—2015 breeding seasons. Daily duration and frequency of shading behaviors exhibited a nonlinear relationship with temperature; therefore, we used segmented regressions to determine at what threshold temperature (mean temperature = 25.7˚C for shading behavior daily frequency and mean temperature = 25.1˚C for shading behavior daily duration) shorebird adults exhibited a behavioral response to rising sand temperatures. Daily nest attendance of both species decreased with increasing sand temperatures in our system. Frequency and duration of daily shading behaviors were positively correlated with sand temperatures above the temperature threshold. Piping Plovers exhibited more and longer shading behaviors above and below the temperature thresholds (below: frequency=10.30 ± 1.69 se, duration=7.29 minutes ± 2.35 se; above: frequency=59.27 ± 6.87 se) compared to Least Terns (below: frequency=-1.37 ± 1.98 se, duration=-0.73 minutes ± 1.51 se; above: frequency=31.32 ± 7.29 se). The effects of sand temperature on avian ground-nesting behavior will be critical to understand in order to adapt or develop recovery plans in response to climate change.

Keywords: *Charadrius melodus*, *Sternula antillarum*, nest attendance, shading behaviors, Missouri River, shorebirds

1. Introduction

It is well documented that many shorebird species, including interior Least Terns (*Sternula antillarum athalassos*; hereafter "Terns") and Piping Plovers (*Charadrius melodus;* hereafter "Plovers") on the Missouri River, avoid establishing nests in predominantly vegetated habitats to decrease predation risk by increasing their visual detection of predators (Götmark et al. 1995, Amat & Masero 2004a, Catlin et al. 2011, Saalfeld et al. 2012, Sherfy et al. 2012). However, the trade-off for increased visual range around the nest is prolonged exposure to extreme summer temperatures. Incubating shorebirds face two problems when nesting on the ground in open, hot environments: (1) overheating of the adult while on the nest and (2) maintaining egg temperatures below lethal levels. When exposed nests of ground-nesting birds are left unattended during high temperatures (> 42˚C), even for short periods of time, the eggs are more vulnerable to hyperthermia, which results in lethal overheating of the embryos (Grant 1982, Webb 1987, Brown & Downs 2003). Even at lower temperatures (32˚C), Amat et al. (2017) reported the potential for unattended eggs to reach hyperthermic conditions for incubating Little Terns (*Sternula albifrons)*. Therefore, incubating birds in hot climates must prevent themselves and their nests from overheating by cooling their body temperatures as well as the eggs.

Hyperthermia of incubating adults and eggs is primarily avoided or reduced by adaptive behaviors that facilitate heat reduction at the nest. Shorebirds that nest in climates characterized by extreme temperatures have developed several behavioral adaptations to manage thermal stress and egg thermoregulation during incubation such as bi-parental nest attendance, shading eggs, belly-soaking, gaping and panting (Purdue 1976, Grant 1982, Amat & Masero 2004b, Saalfeld et al. 2012). Bi-parental nest attendance (the sharing of adult attendance at the nest) facilitates

70 thermoregulation of the eggs by almost continuous control of egg temperature throughout
71 incubation and thermal stress management by allowing the adults to leave when overheated
72 (Grant 1982). Nest attendance of Snowy Plovers (*C. nivosus*), Wilson's Plovers (*C. wilsonia*)
73 and Killdeer (*C. vociferous*) decreased during diurnal moderate temperatures (68%—76%) and
74 increased to > 90% during the hottest times of the day (Purdue 1976, Grant 1982, Bergstrom
75 1989). In response to rising ambient air temperatures, Lesser Black-winged Plovers (*Vanellus*
76 *lugubris*) increased bi-parental nest attendance (Ward 1990). Kentish Plovers (*C. alexandrinus)*
77 that incubated covered nests exhibited no behavior related to heat stress (Amat & Masero
78 2004b). Conversely, Kentish Plover female incubation bouts decreased (primarily female
79 uniparental incubation during the daytime) and bi-parental care of uncovered nests increased as
80 temperatures rose. Overall, past research reported a positive relationship between parental nest
81 attendance and temperature (Vincze et al. 2013)
82 The thermoregulatory role of shading behaviors (elevation of tibiotarsi until the
83 incubation patch is extended above the eggs by 2—3 cm) has been considered less frequently
84 (Downs & Ward 1997). Shading eggs was first considered a thermoregulatory mechanism to
85 cool egg temperature by convection (Dixon & Louw 1978, Bennett et al. 1981). However, more
86 recent evidence indicates that the primary purpose of shading eggs is to prevent overheating of
87 the incubating adult (Downs & Ward 1997, Brown & Downs 2003). Wilson's Plovers and
88 Killdeer spent 27.6% and 28.1% of their time shading eggs at temperatures > 23—25˚C at the
89 Aransas National Wildlife Refuge in Texas (Bergstrom 1989). Amat and Masero (2004b)
90 reported that female Kentish Plovers exhibited shading behaviors for 10.4% ± 12.8 se of their
91 time at a mean ambient temperature of ≥ 31˚C. There is a general consensus from past research
92 that the occurrence of shading behaviors increases with higher temperatures.

93 Indirect (e.g. determination of nesting behaviors using temperature data loggers) or
94 abbreviated (e.g. observations at a distance by personnel using scopes or binoculars) behavior
95 measurements were a common shortcoming of most past research that attempted to quantify
96 shorebird responses to thermal stress. In addition, the use of personnel to directly observe nests
97 to measure nesting behaviors was another limitation that decreased sample sizes for analyses. An
98 alternative approach to direct field observations of nest attendance is indirect measurements via
99 probes placed in the nest. Saalfeld et al. (2012) used iButtons placed in and around Snowy Plover
100 nests in the Texas panhandle to indirectly measure and correlate nest attendance to temperature
101 and habitat selection. The use of thermocouples to indirectly calculate nest attendance increased
102 sample size (n=104 nests) in the preceding study (Saalfeld et al. 2012), but may reduce precision
103 of nest attendance measurements according to Schneider and McWilliams (2007), who reported
104 that temperature data loggers were unsuccessful in determining nest attendance of Plovers at
105 Cape Cod National Seashore.
106 One method that would improve research focused on the relationship between
107 temperature and nesting behaviors is the combination of video cameras with temperature data
108 loggers placed at or near the nest. The integration of video cameras to quantify behaviors allows
109 direct measurement of responses to temperatures and increases sample sizes for analyses. Terns
110 and Plovers that nest along the Missouri River system are perfectly suited to study the influences
111 of temperature on nesting behaviors for several reasons including: (1) both species nest on the
112 ground in the open with full exposure to the sun, (2) both species have known adaptive behaviors
113 to cope with thermal stress and (3) sand temperatures range on a daily basis from 4.4˚C to 50˚C.
114 Our primary objective was to assess the potential impact of sand temperatures on shorebird nest
115 behavior patterns. We expected adult Terns and Plovers would exhibit more behaviors associated

116 with thermal stress, such as increased nest attendance and shading eggs, with increasing sand
117 temperatures. Since both species exhibit bi-parental care of the clutch and previous research
118 demonstrated high daily nest attendance rates (> 90% of time/day), we expected a steady
119 increase in daily nest attendance in response to rising sand temperatures (Andes 2018).
120 Conversely, we expected little to no use of shading behaviors by the adults until sand
121 temperatures reached a threshold, corresponding to a sharp increase in the frequency and
122 duration of shading behaviors.

123 **2. METHODS**

124 **2.1. Study Area and Species**

125 This study was conducted on the Garrison Reach of the Missouri River in North Dakota,
126 from the dam at Riverdale south to Bismarck, previously described by Shaffer et al. (2013),
127 during May through August from 2014 to 2015. Both Terns and Plovers are small, ground-
128 nesting shorebirds that select open, sparsely vegetated sand habitat with pebbles or gravel, such
129 as coastal and riverine shorelines, temporary sandbars and permanent islands (Anteau et al. 2012,
130 Sherfy et al. 2012, Stucker et al. 2013). Female Terns lay 2—3 eggs in a clutch, one every day,
131 that are oval, beige in color and speckled (Kirsch 1996, Thompson et al. 1997). Incubation
132 begins at the start of the egg-laying stage and lasts approximately 19—25 days (Thompson et al.
133 1997). Unless the nest is depredated or destroyed, pairs only breed once a season (Thompson et
134 al. 1997). Both adults share parental responsibilities; however, the female parent contributes the
135 most time to incubation and chick-rearing duties (Keane 1987).

136 Double-brooding by Plovers is rare (Hunt et al. 2015). First attempt clutches typically
137 contain four eggs, laid every other day, that are oval, sand colored with evenly distributed spots
138 (Cairns 1982, Elliott-Smith & Haig 2004). Multiple re-nests are possible if the previous attempts

fail; however, clutch size for re-nests decreases with attempts (Bottitta et al. 1997, Elliott-Smith & Haig 2004). Full incubation begins after the last egg is laid. However, there are reported instances when short incubation periods were observed during the egg-laying period (Cairns 1977, Whyte 1985). Both sexes incubate the nest, which lasts 25 to 28 days (Wilcox 1959, Cairns 1977, Whyte 1985, Haig & Oring 1988).

2.2. Field Methods

We used systematic grid and behavioral searches to locate and monitor Tern and Plover nests throughout the 2014 and 2015 breeding seasons (refer to Shaffer et al. (2013) for a detailed description of the monitoring methodologies). Clutch age was calculated by egg flotation at the initial nest visit (Mabee et al. 2006, Shaffer et al. 2013). Egg flotation allowed researchers to determine incubation stage as well as estimate initiation (date first egg was laid) and hatching dates for nests of both species (assuming 18- and 25-day incubation periods for Terns and Plovers (Shaffer et al. 2013)). Clutch size was recorded at the onset of incubation. Nests were monitored on a 3-day schedule until the estimated hatch date approached (< 3 days) when visits were increased to daily. Monitoring continued until nest completion when the fate was determined as either successful (hatched with at least one chick observed in the nest bowl), probable successful (evidence of hatching but no chicks present in the nest bowl), failed (nest could not have hatched based on estimated hatch date or evidence suggested infertile eggs, depredation, abandonment, destruction by weather or livestock) or unknown (Shaffer et al. 2013, Andes et al. 2019).

To observe nesting behaviors, video camera systems (miniature infrared surveillance cameras equipped with 24 LEDs and 4.3-mm lenses (Jet Security USA, Buena Park, CA) were installed at a subset of nests after incubation reached a minimum of two days and were not

removed until a nest outcome was confirmed by field personnel (refer to Andes et al. (2019) for a detailed description of the camera system design and installation). The camera was installed ≥ 1 meter away from the nests at a height of 15—25 cm. The 12-V, 35-Amp-hour batteries and 32-GB SD cards housed in a weatherproof case (SEAHORSE Protective Equipment Cases, Fuertes Cases, La Mesa, CA) were buried in the sand at least 25—30 meters away from the nest and exchanged every 3—4 days to ensure continuous recording of the nests. We used video and not thermal cameras to increase sample sizes of shorebird nesting behaviors. Furthermore, the video camera system utilized in this study was more versatile to address a wide range of behavioral and predator-specific questions (Andes et al. 2019). Terns and Plovers are both federally protected under the Endangered Species Act (U.S. Fish and Wildlife Service 1985a, U.S. Fish and Wildlife Service 1985b), and the permit authorizing this research prohibited the placement of data loggers near the nest bowl. Alternatively, we measured sand temperature with thermocouples (Onset Computer Corporation, Cape Cod, MA; hereafter "HOBO") installed > 1 meter away from the weatherproof case and battery (which were ≥ 25 meters away from the nest). We installed the thermocouples in substrate (sand, gravel, pebble or mud) similar to the surrounding nest bowl habitat because various surfaces may have different thermal capacities, which in some cases can significantly affect heating rates of eggs (Mayer et al. 2009, Gomez et al. 2019). Our intent was to reduce or minimize the differences between the nesting substrate and the thermocouples surface locations. The thermocouples were pushed into the ground, at a depth of 5—8 cm, until the temperature sensor at the top was level with the sand surface. Sand temperatures were recorded on a 30-minute interval starting at camera installation until removal after nest outcome. Both the camera system and thermocouple were removed after the brood vacated the nesting area or a nest fate was assigned in the field by researchers. We assumed that both sand and ambient

185 temperatures were highly correlated. It is well documented that ambient temperature influences
186 shorebird nest attendance and shading behaviors (Downs & Ward 1997, Browns & Down 2003,
187 Amat & Masero 2004b, Amat et al. 2012, Vincze et al. 2013, Clauser & McRae 2016, Gómez et
188 al. 2016, Amat et al. 2017). However, sand temperature was recorded because heat absorption by
189 conduction may also influence shorebird nesting behaviors as well as both incubated and
190 unattended eggs.

191 **2.3. Recording Nesting Behaviors**

192 We were interested in documenting behaviors that are impacted by temperature such as
193 nest attendance and shading behaviors. Nest attendance was defined as the adult (we were unable
194 to distinguish between male and female individuals) attending or "on" the nest, which included
195 sitting on or standing over at least one egg in the nest. We defined shading behaviors as the
196 adults visibly standing over at least one egg in the nest for a period > 3 seconds (see Multimedia
197 video clip "PipingPloverShadingBehavior.mp4" for an example of shorebird shading behavior).
198 We started recording shading behaviors when an adult first arrived to attend the nest and stood
199 over the eggs or stood up during incubation. We recorded start and stop times for all
200 observations when adults were attending the nest or shading eggs. All behavioral observations
201 were recorded within one calendar day (24-hour period) from 00:00:00 in the morning till
202 23:59:59 at night. Because nest attendance was lower when researchers were present (Andes
203 2018), we only included days with no research activities at the nest or within the nesting area for
204 analyses.

205 We were unable to watch all of the video collected from the 107 camera nests; therefore,
206 a subsample of those nests was selected to review based on the spatial and temporal distribution
207 of cameras on the Missouri River to ensure independence between nests. In other words, camera

208 nests were selected from each segment (lower, middle and upper) of the Missouri River as well
209 as across the breeding season (early, middle and late initiation dates). Within individual-sampled
210 camera nests, days were selected to ensure equal representation of incubation stage (early,
211 middle and late) as well as seasonal temperature variation (early, middle and late breeding
212 season dates). We recorded the total duration in minutes per day of nest attendance and shading
213 behaviors as well as the total frequency per day of shading behaviors for analyses.

214 **2.4. Data Analysis**

215 Sand temperature measurements were summarized as daily minimum, maximum and
216 mean by year, nest and date. We graphically explored the relationships between temperature and
217 shorebird daily nesting behaviors to determine the appropriate statistical method to analyze the
218 data. If shorebird adults only exhibited shading behaviors after a critical sand temperature was
219 reached, then we performed a segmented regression using the "segmented" package (Muggeo
220 2008) in R 3.5.2 (R Core Team 2018) to determine that threshold. Adult shading behaviors were
221 analyzed as linear relationships above and below the threshold temperature determined by
222 segmented regression. We conducted generalized linear mixed models (GLMM) using the
223 procedure PROC GLIMMIX (SAS 9.4; SAS Institute, Cary, NC) for all linear statistical
224 analyses. The response variables included daily nest attendance duration as well as daily
225 frequency and duration of shading behaviors. Daily nest attendance was defined as the total
226 minutes the adults attended at least one egg in the nest. Daily duration of shading behaviors was
227 defined as the total minutes the adults spent standing over at least one egg in the nest. Daily
228 frequency of shading behaviors was defined as the total number of occurrences. Year, categorical
229 nest and habitat identifications on the Missouri River were included as hierarchical random
230 effects to account for repeated measures (multiple days/nest and multiple nests/location/year on

231 the Missouri River). We modeled the response variables (daily nest attendance and shading
232 behaviors) in relation to daily minimum (MIN), mean (MEAN) and maximum (MAX) sand
233 temperatures. Each model contained only one temperature covariate to avoid issues with
234 collinearity. Additionally, the covariates Species (Least Tern or Piping Plover), Date (ordinal day
235 of the breeding season) and Clutch Age (age of the nest) were included as predictor variables in
236 all GLMM analyses because previous research determined that they may influence nesting
237 behaviors (Smith & Wilson 2010). We adopted an information-theoretic approach to model
238 selection and ranked models based on their Akaike's Information Criterion corrected for small
239 sample sizes (AIC_c), model weight (w_i) and model goodness-of-fit (-2ll) (Burnham & Anderson
240 2002). We conducted model selection on a set of 16 *a priori* models for daily nest attendance and
241 shading behavior response variables. Models that best described the impact of temperature on
242 nesting behaviors had the lowest AIC_c scores and the largest model weights, w_i (Burnham &
243 Anderson 2002). Estimates and 85% confidence intervals (CI) were derived from the top
244 model(s) (Arnold 2010). We used 85% confidence intervals to distinguish between
245 uninformative and informative parameters because the more commonly used 95 % CI often
246 excludes variables from top models that are supported by lower AIC scores (Arnold 2010). We
247 considered models with a $\Delta AIC_c > 2$ as noncompetitive.

248 **3. RESULTS**

249 We installed video cameras and thermocouples at 52 Tern and 55 Plover nests on the
250 Missouri River in North Dakota during the 2014—2015 breeding seasons. Of the 107 nests with
251 cameras and thermocouples, a subset of 42 were included in the GLMM analyses (Tern nests
252 =22, Plover nests=20). Data for 157 days were included in the analysis of temperature influences
253 on nest attendance and shading behaviors. There was continuous variation in daily minimum,

mean and maximum temperatures throughout both nesting seasons (2014—2015) during the duration of this study (Fig. 1). Average daily mean and maximum temperatures were slightly higher in 2015 (mean=24.6˚C, maximum=42˚C) compared to 2014 (mean=23.6˚C, maximum=39˚C), while the minimum was similar for both years (2014=13.9˚C, 2015=13.6˚C). Daily maximum temperature had a small negative influence on shorebird daily nest attendance; days with hotter temperatures corresponded to a small decline in shorebird daily nest attendance (Fig. 2). The time spent (duration in minutes) and frequency of shading behaviors for both species were higher for hotter temperatures, with the sharpest increase of these activities at daily mean $\geq$ 25˚C (Fig. 3).

3.1. Daily Nest Attendance

The variation in shorebird daily nest attendance was best explained by four top models, accounting for 52.9% of the model weight. The top three models explaining variation in daily nest attendance included: 1) MAX, 2) Intercept, and 3) Date (Table 1). We considered the fourth ranked model, MAX + Species, as uninformative because it was nested within the top model (the addition of an uninformative parameter) but did not improve model fit (Burnham and Anderson 2002). There was a negative relationship between daily nest attendance and sand temperature (Table 1). Confidence intervals for parameter estimates for both MAX and Date covariates excluded zero (Table 1). Daily nest attendance was similar between species (Tern= 1,365.1 minutes ± 10.1 se, Plover= 1,375.4 minutes ± 6.7 se).

3.2. Shading Behaviors < 25˚C

Graphical representation of shorebird daily shading behaviors revealed a nonlinear relationship between frequency and duration of these behaviors with daily mean temperature (Fig. 3). The breakpoints in temperature were estimated to range between 24-27˚C for both daily

277 duration (Tern=25.4°C ± 0.53 se, Plover=24.8°C ± 0.45 se, both species=25.1°C ± 0.34 se) and
278 frequency of shading behaviors (Tern=27.9°C ± 0.27 se, Plover=24.4°C ± 0.58 se, both
279 species=25.7°C ± 0.32 se). Therefore, we divided GLMM analyses for both species combined at
280 25.7°C for frequency and 25.1°C for duration of daily shading behaviors. For the frequency of
281 daily shading behaviors < 25.7°C, there were two top models that accounted for 83.2% of the
282 model weight. Both top models included Species and Clutch Age as covariates (Table 2). Date
283 and MEAN were also covariates included in the best and second-ranked models respectively. We
284 derived and interpreted estimates for Species, Clutch Age and Date parameters from the top
285 model. The parameter estimate for MEAN temperature was derived and interpreted from the
286 second-ranked model. There was a positive relationship between the frequency of daily shading
287 behaviors < 25.7°C and MEAN temperature (Table 3). Confidence intervals for parameter
288 estimates of Species, Date, and MEAN covariates excluded zero. Below the temperature
289 breakpoint, Plovers exhibited a higher frequency of daily shading behaviors compared to Terns
290 (Table 4).
291 There was one top model that accounted for 96.7 % of the variation in daily duration of
292 shading behaviors < 25.1°C (Table 2). We derived and interpreted the estimates for Species,
293 Clutch Age and Date from the top model. Parameter estimates derived and interpreted from the
294 top models displayed a similar effect for daily duration of shading behavior compared to
295 frequency (Table 3). Confidence intervals for the estimates included in the top model all
296 excluded zero (Table 3). Below the temperature breakpoint, Plovers exhibited a higher duration
297 of daily shading behaviors compared to Terns (Table 4).
298 **3.3. Shading Behaviors > 25°C**

For the frequency of daily shading behaviors > 25˚C, there were two top models that accounted for approximately 66.2% of the model weight, which included MEAN, MAX and Species (Table 2). We considered the third-ranked model as uninformative, increasing the combined model weight of the top two to 76.4%. We derived and interpreted parameter estimates for MEAN and Species from the top model. The MAX parameter estimate was derived and interpreted from the second-ranked model. Each increase of one degree in MEAN and MAX daily temperature > 25.7˚C resulted in the increase of daily frequency and duration of shading behaviors by 13.18 ± 1.91 se and 5.58 ± 0.78 respectively (Table 3). Confidence intervals for the estimates included in the top models all excluded zero (Table 3). Additionally, Plovers exhibited a higher daily frequency of shading behaviors > 25.7˚C compared to Terns (Table 4).

There were two top models that accounted for 59.0 % of the variation in duration of shading behaviors > 25.1˚C, which included MEAN and MAX as covariates (Table 2). We considered models 3-4 as uninformative, increasing the combined model weight of the top two to 77.7 %. The MEAN and MAX parameter estimates exhibited a similar effect on daily duration of shading behavior compared to frequency > 25.1˚C (Table 3). The confidence intervals for both MEAN and MAX parameter estimates excluded zero (Table 3). Daily duration of shading behaviors increased by 35.52 minutes ± 5.22 se and 15.00 ± 2.20 with every increase of one degree in MEAN and MAX temperatures > 25.1˚C respectively (Table 4).

4. Discussion

Terns and Plovers expressed behaviors related to thermoregulation while nesting on the Missouri River in North Dakota with sand temperatures that reached 54.7˚C during the two-year study. Appropriately, these shorebirds exhibited plasticity in their nesting behaviors in response to rising temperatures. Adults drastically increased the frequency and duration of daily shading

322 behaviors at sand temperatures above a mean daily temperature of 25°C. Our results were similar
323 to those reported from a video camera study conducted on King Rails (*Rallus elegans)* at the
324 Mackay Island National Wildlife Refuge (Clauser & McRae 2016). King Rails spent
325 significantly less time incubating and more time exhibiting shading behaviors as ambient
326 temperature increased (Clauser & McRae 2016). However, we observed only a modest response
327 of shorebird thermal behaviors in response to higher temperatures compared to most past studies
328 conducted on shorebirds (Purdue 1976, Grant 1982, Bergstrom 1989, Ward 1990, Amat &
329 Masero 2004).

330 Daily Plover and Tern nest attendance decreased with a corresponding increase in
331 temperature, which conflicts with results reported from past research (Purdue 1976, Grant 1982,
332 Bergstrom 1989, Ward 1990, Amat & Masero 2004). We expected a positive relationship
333 between daily nest attendance behaviors and sand temperature, which was not supported by our
334 results. Sand temperatures in this system only briefly (approximately 2—3 hours/day) increased
335 to ranges when thermal behaviors were exhibited. During days with prolonged warmer
336 temperatures there may be time periods (e.g. mid-morning) when eggs do not require continuous
337 nest attendance by adults to maintain optimal temperatures for embryo development. Heat
338 absorbed by unattended eggs during exposure to solar radiation during these time periods may be
339 adequate for embryogenesis (Amat et al. 2012). It is likely sand temperatures were not high
340 enough to require prolonged expenditure of thermally adapted behaviors for Terns and Plovers in
341 the Missouri River system.

342 There was a distinct pattern in the shading behaviors between Terns and Plovers in
343 response to increased temperatures. At a given sand temperature, Plovers exhibited more
344 frequent and longer shading behaviors compared to Terns. Potential reasons for this behavioral

345 difference between species may be clutch as well as egg volume and coloration. Because Plovers
346 lay larger clutches (3—4 eggs) with higher average egg volumes (17,092.9 mm^3 reviewed by
347 Elliot-Smith and Haig (2004)), they may expend more energy to regulate egg temperatures
348 compared to Terns (2—3 eggs, 16,134.5 mm^3 average egg volume reviewed in Thompson et al.
349 (1997)). This increased energy expenditure by Plovers may increase their core temperatures
350 faster, resulting in overheating more quickly, when the adults responded by exhibiting more and
351 longer shading behaviors. Eggshell coloration may also influence egg thermoregulation. Tern
352 eggs with paler eggshells may absorb less heat than those of plovers (Gómez et al. 2016),
353 resulting in plover adults overheating more quickly. Some of our observations of individual Tern
354 shading behaviors may be conservative due to observational challenges from watching video.
355 For example, a combination of camera angle, poor video quality and lighting, nest obstruction by
356 debris as well as much shorter legs made it difficult to distinguish shading behaviors for some
357 and not all nesting adult Terns. These conservative observations were the exception and their
358 potential impact was minimal on the overall estimate of frequency and duration of Tern shading
359 behaviors. Even if the overall estimate of Tern shading behaviors may be marginally
360 conservative, past research reported that clutch size did not influence mean clutch temperatures
361 (Clauser & McRae 2016), which provides support that Plovers may have overheated faster to
362 maintain incubation temperatures of more eggs, resulting in increased shading behaviors.
363 There are two primary hypotheses for plasticity of shading responses to temperature
364 fluctuations at the nest: (1) to cool egg temperatures within a nonlethal range (DuRant et al.
365 2013) and (2) to prevent overheating of adults while incubating (Downs & Ward 1997, Brown &
366 Downs 2003). Temperatures of nesting Crowned Plovers (*Vanellus coronatus*) were always
367 lower during shading behaviors compared to incubation time periods, while egg temperatures

368 were always higher during shading rather than when incubated (Brown & Downs 2003). This
369 may suggest that the heat gained by eggs due to conduction from the nest bowl substrate during
370 shading behaviors may increase the risk of egg hyperthermia compared to incubation. Since both
371 Plovers and Terns are federally protected, we were unable to measure egg or adult temperatures
372 to definitively determine the role of shading behaviors. However, the thermal breakpoints when
373 both daily duration and frequency of shading behaviors sharply increased were well below the
374 optimal temperature threshold for normal embryo development (35—38°C, Webb 1987),
375 suggesting that the birds may be regulating their body temperature and not egg temperature. If
376 the purpose of shorebird nesting behaviors in this system was to maintain egg temperatures, nest
377 attendance should increase with the rise in temperature (Browns & Down 2003). Instead, daily
378 nest attendance decreased while shading behaviors increased, which may indicate that the
379 purpose of the behaviors was to prevent overheating of the adults and not the eggs in this system.
380 It is crucial that breeding shorebirds be able to cope with fluctuating temperatures in
381 response to climate change. Increased temperature fluctuations may result in breeding pairs of
382 shorebirds that may not be able to cope with high levels of thermal stress during incubation,
383 which may decrease egg survival. The results of this study add to mounting evidence that
384 ground-nesting avian species adapt their nesting behaviors appropriately to temperature variation
385 (Grant 1982, Bergstrom 1989, Ward 1990, Amat & Masero 2004b, Saalfeld et al. 2012, Clauser
386 & McRae 2016, Vincze et al. 2017). The occurrence of thermally-related behaviors in Plovers
387 and Terns suggests that these populations may be able to adapt to future temperature fluctuations
388 due to climate change.
389 Care should be taken to develop monitoring programs that do not disrupt nesting
390 behaviors during extreme temperatures, especially for protected species such as Terns and

391 Plovers (Andes 2018). The examination of possible effects that temperatures of nesting
392 substrates inflict on avian ground-nesting behavior will be critical to understanding how to adapt
393 or develop monitoring programs in response to climate change. For Terns and Plovers, daily nest
394 attendance decreased and shading behaviors increased at mean sand temperatures ≥ 25˚C.
395 Unattended shorebird eggs at the Salton Sea in California, exposed to a similar range of
396 temperatures observed at the Missouri River, overheated and caused embryo death within two
397 minutes (Grant 1982). Therefore, research activities should be conducted at sand temperatures
398 that are within the thermal zone for normal embryo development to prevent prolonged exposure
399 of eggs from unattended nests (Grant 1982). Likewise, extended adult absences from the nest due
400 to researcher presence should be minimized. In the Missouri River system, research activities
401 were prohibited once the ambient temperature exceeded 32.2˚C. Additionally, research and
402 monitoring should be designed to minimize disturbance to normal nesting behaviors (Andes et al.
403 2019). Once a nest is located and then subsequently monitored, personnel should move far
404 enough away from the nest to allow normal nesting behaviors to resume while data are recorded.
405 Little Terns and Malaysian Plovers (*C. peronei*) were reported to reduce return times to the nest
406 after a researcher visit during times of hotter ambient temperatures (Yasué and Dearden 2006,
407 Amat et al. 2017). Since accuracy of nest fate determination decreases as clutch age increases (it
408 is easier to determine fates for nests that fail during early incubation stages), nest monitoring can
409 be minimized until the approach of the estimated hatch date (Andes et al. 2019).

410 **5. Acknowledgments**

411 We would like to acknowledge the contributions of Kasen Christiansen, Emily Foden,
412 Anna Mattson, John McClinton, Devynarae Meeder, Melissa Murillo, Jessica Perkins, Mike
413 Thiel, Dustin Toy and all of the USGS technicians for their assistance with camera setup and

maintenance. Thank you to Colin Dovichin for his help to initiate and develop this project. This work was supported by the U.S. Geological Survey 20098905-UND CESU G13AC00144; the Wheeler Foundation through the Department of Biology at the University of North Dakota; and the National Science Foundation under NSF EPSCoR Track-1 Women in Science and Engineering (WISE) Program OIA-1355466. Our field protocols were approved by the USGS Northern Prairie Wildlife Research Center Animal Care and Use Committee. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research." The data analyzed for this paper were collected under permits provided by the U.S. Fish and Wildlife Service (TE121914-0) and IACUC (#A3917-01, Protocol 1304-5). Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The dataset analyzed for this paper can be found at https://doi.org/10.5066/P9ULK0ST.

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569 **Figure 1**. Daily minimum, maximum and mean sand temperatures at sites representative of
570 interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*)
571 nests on the Garrison Reach of the Missouri River, ND in a) 2014 and b) 2015.
572
573 **Figure 2**. Interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius*
574 *melodus*) daily nest attendance (daily number of minutes spent sitting on or standing over at least
575 one egg in the nest) in relation to daily maximum sand temperature on the Missouri River, ND
576 during 2014—2015. Each dot represents the nest attendance at a single nest during one day (total
577 days=157, Least Tern nests=22, Piping Plover nests=20).

578 **Figure 3.** Segmented linear models with 95% confidence intervals for duration (a) and
579 frequency (b) of shading behaviors in relation to mean daily sand temperature exhibited by
580 interior Least Terns (*Sternula antillarum athalassos)* (left), Piping Plovers (*Charadrius melodus)*
581 (middle) and both species combined (right) on the Missouri River in North Dakota from 2014—
582 2015. The dashed vertical lines indicate the estimated breakpoints where there is a change in the
583 slope of the linear relationships between duration, frequency and mean temperature. The solid
584 vertical lines represent the standard error of the estimated breakpoints.

585 **Table 1**. A subset of model-selection results with parameter estimates, standard errors and 85% confidence intervals (CI, Arnold
586 2010) for the top 5 generalized linear mixed models (normal distribution) of interior Least Tern (*Sternula antillarum athalassos*) and
587 Piping Plover (*Charadrius melodus*) nest attendance on the Missouri River, ND during 2014—2015. Daily nest attendance (total
588 minutes spent sitting on or standing over at least one egg in the nest) was modeled in relation to the covariates: Species (Least Tern or
589 Piping Plover), Clutch Age (age of the nest), Date (ordinal day of the breeding season), MAX (maximum sand temperature), MEAN
590 (mean sand temperature) and MIN (minimum sand temperature).

Model	k[a]	-2ll[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Intercept	SE	85% CI	Estimate	SE	85% CI
MAX	2	443.6	452.6	0	0.224	1448.1	41.1	1276.7 — 1619.4	-2.0	1.0	-3.5 — -0.5
Intercept	1	447.5	454.0	1.4	0.111	1366.5	5.6	1343.0 — 1389.9	—	—	—
Date	2	445.1	454.0	1.4	0.111	1450.4	51.5	1235.8 — 1665.1	-0.5	0.3	-0.9 — -0.04
MAX + Species[f]	3	443.1	454.6	2.0	0.083	—	—	—	—	—	—
MAX + Clutch Age	3	443.5	454.9	2.3	0.071	—	—	—	—	—	—

591 [a] The number of parameters in the model
592 [b] Estimate of model goodness of fit
593 [c] Akaike's Information Criterion corrected for small sample sizes
594 [d] Distance of a model from the lowest AIC_c model
595 [e] The weight of the model
596 [f] Model has minimal support (Burnham & Anderson 2002)
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605 **Table 2**. A subset of model-selection results for generalized linear mixed model (normal distribution) analyses of Least Tern (*Sternula*
606 *antillarum athalassos*) and Piping Plover (*Charadrius melodus*) shading behaviors above and below a temperature threshold (25°C)
607 on the Missouri River in North Dakota during 2014-2015. Shading behavior (daily total number and duration in minutes that adults
608 stood over and shaded the nest) was modeled in relation to Species (Least Tern or Piping Plover), Clutch Age (age of the nest), Date
609 (ordinal day of the breeding season) and sand temperature (MIN-minimum, MEAN-mean, MAX-maximum).

	Frequency of Shading Behaviors						Duration of Shading Behaviors					
<25°C	**Model**	**k[a]**	**-2ll[b]**	**AIC_c[c]**	**ΔAIC_c[d]**	**w_i[e]**	**Model**	**k[a]**	**-2ll[b]**	**AIC_c[c]**	**ΔAIC_c[d]**	**w_i[e]**
	Species + Clutch Age + Date	4	850.0	865.1	0.0	0.544	Species + Clutch Age + Date	4	804.4	815.1	0.0	0.967
	MEAN + Species + Clutch Age	4	853.6	866.3	1.3	0.288	MAX + Species + Clutch Age	4	810.3	823.2	8.19	0.016
	MEAN + Species	3	858.1	868.7	3.6	0.088	MEAN + Species + Clutch Age	4	812.5	825.4	10.4	0.005
	MAX + Species + Clutch Age	4	857.3	870.0	5.0	0.045	MAX + Clutch Age	3	815.6	826.2	11.2	0.004
	Intercept	1	881.4	887.6	22.5	0	Intercept	1	832.4	838.7	23.7	0
>25°C	MEAN + Species	3	339.9	351.7	0.0	0.483	MEAN	2	501.6	510.6	0.0	0.389
	MAX + Species	3	341.9	353.7	2.0	0.179	MAX	2	502.9	511.9	1.3	0.201
	MEAN + Species + Clutch Age[f]	4	339.6	354.3	2.6	0.133	MEAN + Species[f]	3	501.2	512.7	2.2	0.130
	MEAN	2	346.2	355.4	3.7	0.076	MEAN + Clutch Age[f]	3	501.6	513.1	2.54	0.109
	Intercept	1	379.4	386.1	34.3	0	Intercept	1	534.0	540.6	30.1	0

610 [a] The number of parameters in the model
611 [b] Estimate of model goodness of fit
612 [c] Akaike's Information Criterion corrected for small sample sizes
613 [d] Distance of a model from the lowest AIC model
614 [e] The weight of the model
615 [f] Model has minimal support (Burhham & Anderson 2002)
616

Table 3. Estimates, standard errors (SE) and 85% confidence intervals (CI, Arnold 2010) for main fixed effects that influenced the number and duration of interior Least Tern (*Sternula antillarum athalassos*) and Piping Plover (*Charadrius melodus*) daily shading behaviors (total number and duration in minutes that adults stood over and shaded the nest) above and below a temperature threshold (25°C) on the Missouri River in North Dakota during 2014-2015. Effects included Species (Least Tern or Piping Plover), Clutch Age (age of the nest), Date (ordinal day of the breeding season) and sand temperature (MIN-minimum, MEAN-mean, MAX-maximum).

		Frequency of Shading Behaviors			Duration of Shading Behaviors		
	Effect	**Estimate**	**SE**	**85% CI**	**Estimate**	**SE**	**85% CI**
<25°C	**Intercept**	-49.51[b]	14.21	-108.68 — 9.66	-64.41[b]	14.33	-124.10 — -4.73
	MEAN	1.14[c]	0.28	0.74 — 1.54	—	—	—
	Species(Tern)[a]	-13.28[b]	2.42	-16.80 — -9.77	-11.03[b]	2.6.	-14.82 — -7.25
	Clutch Age	-0.77[b]	0.18	-1.03 — 0.55	-0.97[b]	0.19	-1.26 — -0.69
	Date	0.42[b]	0.09	0.29 — 0.55	0.52[b]	0.09	0.37 — 0.65
>25°C	**Intercept**	-308.25[d]	54.82	-536.57 — -79.93	-886.37[f]	144.89	-1489.88 — -282.86
	MEAN	13.18[d]	1.90	10.32 — 16.04	35.52[f]	5.22	27.73 — 43.30
	MAX	5.58[e]	0.78	4.40 — 6.76	15.00[g]	2.20	11.72 — 18.27
	Species(Tern)[a]	-27.95[d]	10.20	-43.33 — -12.56	—	—	—

[a] In relation to Piping Plovers
[b] Estimated from Model: Species + Clutch Age + Date
[c] Estimated from Model: MEAN + Species + Clutch Ag
[d] Estimated from Model: MEAN + Species
[e] Estimated from Model: MAX + Species
[f] Estimated from Model: MEAN
[g] Estimated from Model: MAX

632 **Table 4.** Least square means (LSM), standard errors (SE) and 85% confidence intervals (CI, Arnold 2010) for interior Least Tern (*Sternula*
633 *antillarum athalassos*) and Piping Plover (*Charadrius melodus*) daily frequency and duration of shading behaviors (total number and duration in
634 minutes that adults stood over and shaded the nest) in relation to sand temperature on the Missouri River in North Dakota from 2014-2015.

		Frequency of Shading Behaviors			Duration of Shading Behaviors		
	Effect	**LSM**	**SE**	**85% CI**	**LSM**	**SE**	**85% CI**
<25°C	**Least Tern**	-1.37[a]	1.98	-4.25 — 1.51	-0.73[a]	1.51	-2.93 — 1.47
	Piping Plover	10.30[a]	1.69	7.85 — 12.75	7.29[a]	2.35	3.87 — 10.72
>25°C	**Least Tern**	31.32[b]	7.29	20.33 — 42.31	—	—	—
	Piping Plover	59.27[b]	6.87	48.91 — 69.63	—	—	—

635 [a] Estimated from Model: Species + Clutch Age + Date
636 [b] Estimated from Model: MEAN + Species

Figure 1a

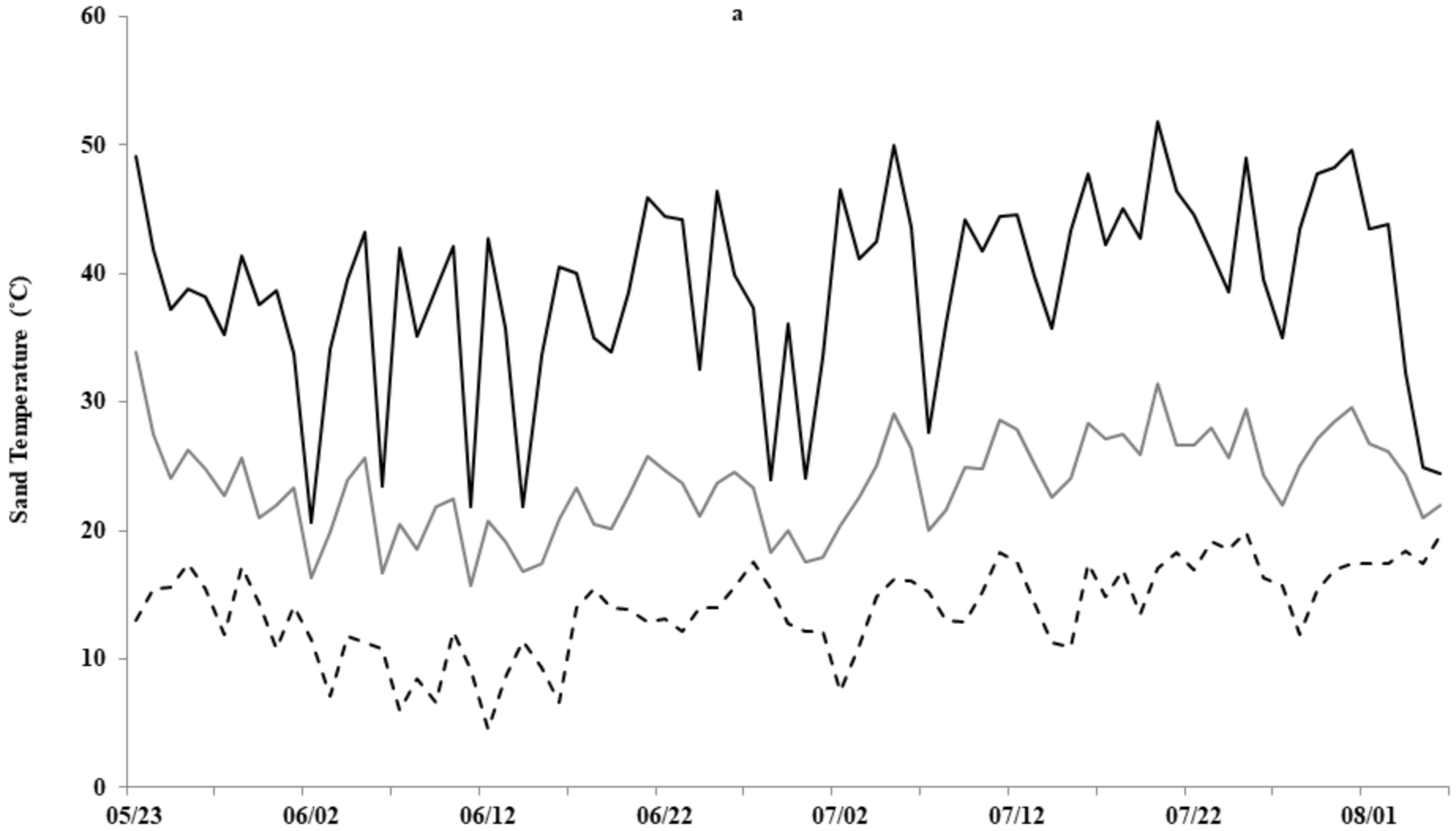

a
Sand Temperature (°C)
60
50
40
30
20
10
0
05/23
06/02
06/12
06/22
07/02
07/12
07/22
08/01

Figure 1b

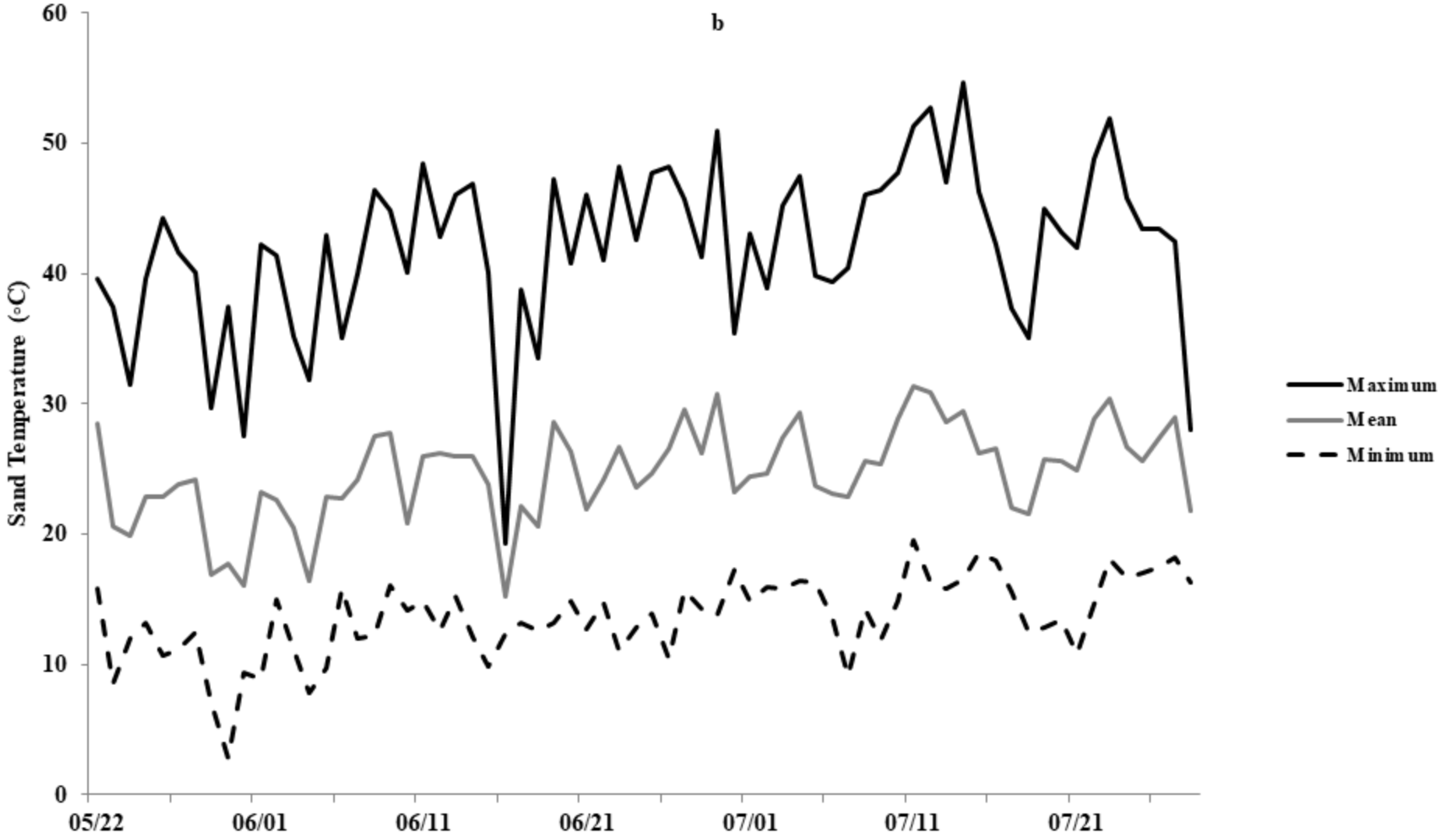
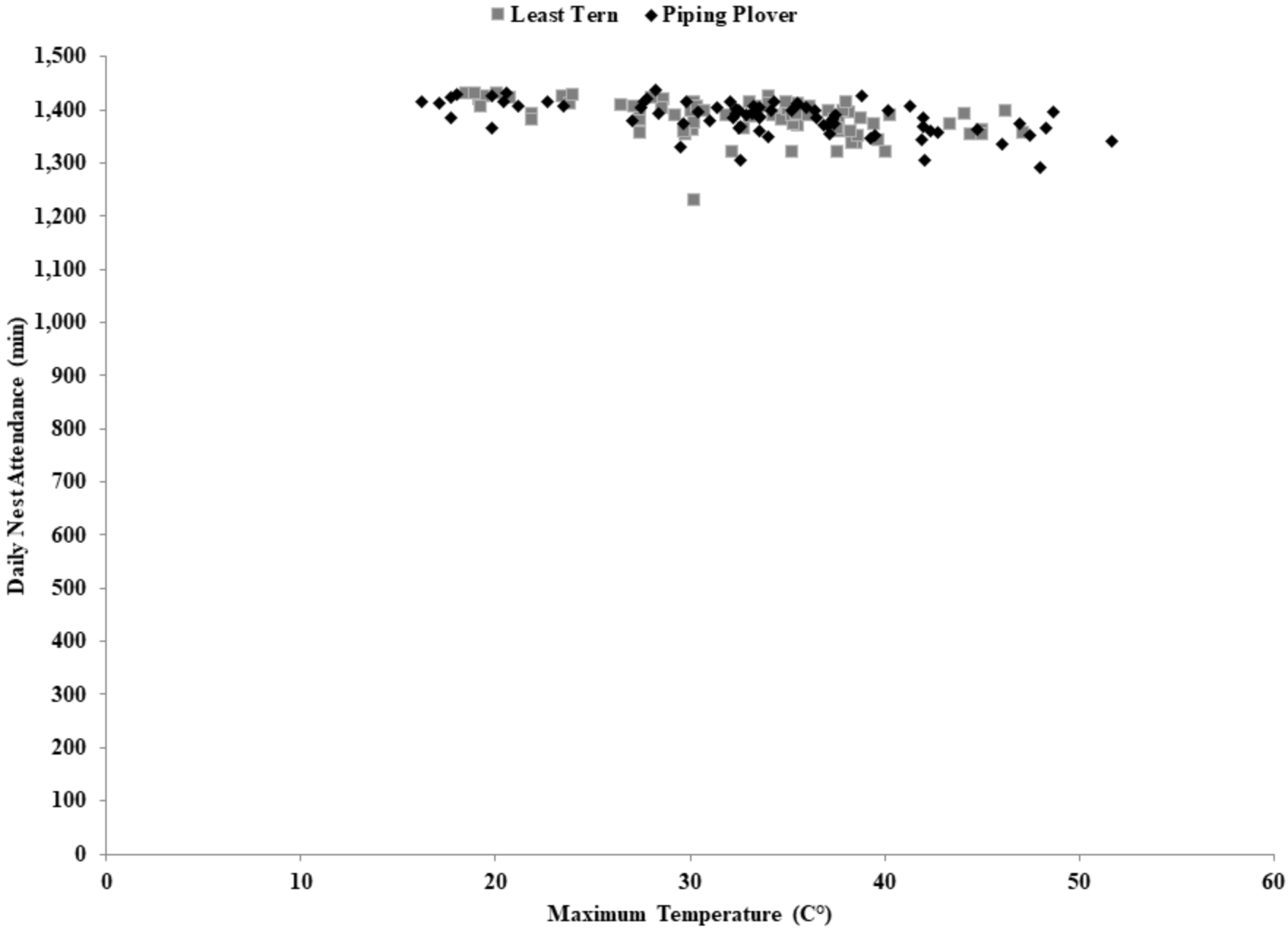
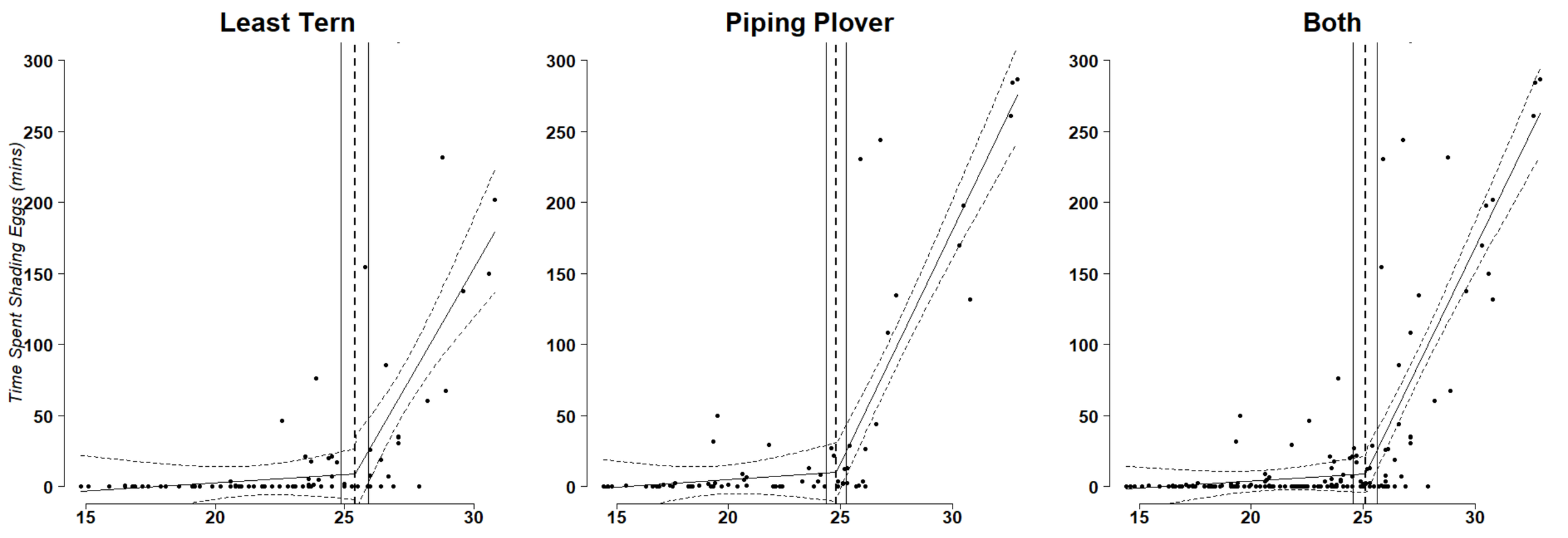
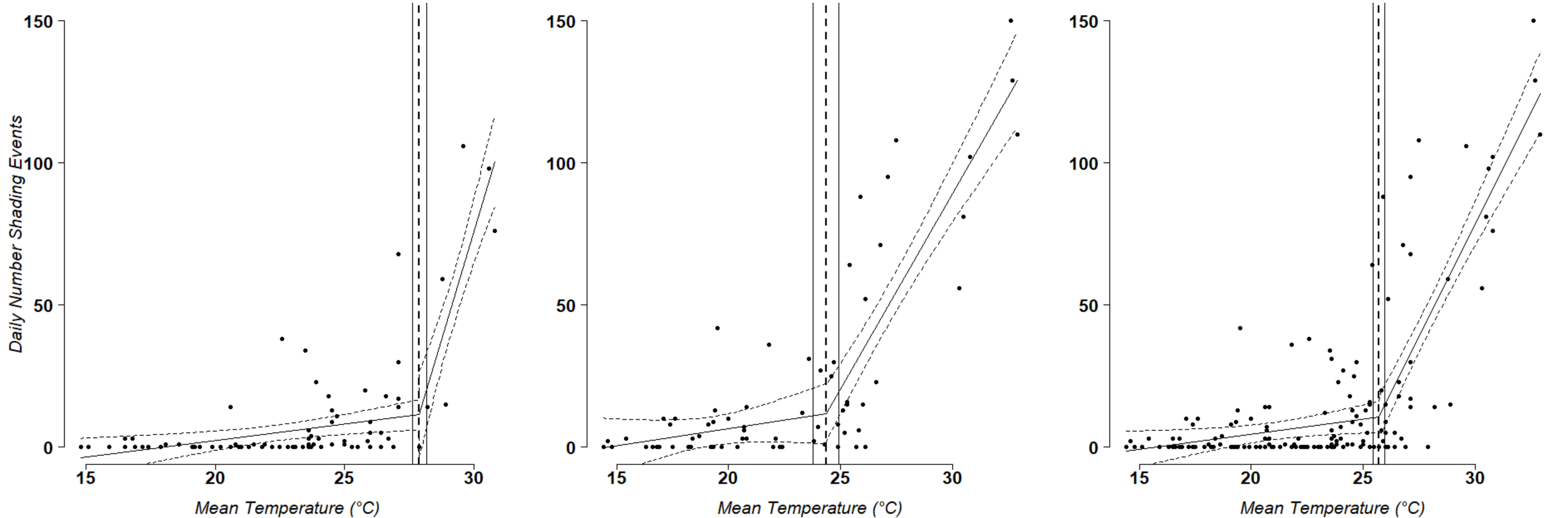

b
Sand Temperature (◦C)
60
50
40
30
20
10
0
05/22
06/01
06/11
06/21
07/01
07/11
07/21
Maximum
Mean
Minimum

Figure 2


Least Tern
Piping Plover
1,500
1,400
1,300
1,200
1,100
1,000
900
800
700
600
500
400
300
200
100
0
Daily Nest Attendance (min)
0
10
20
30
40
50
60
Maximum Temperature (C°)


Least Tern
Piping Plover
Both
Time Spent Shading Eggs (mins)
0
50
100
150
200
250
300
15
20
25
30


Daily Number Shading Events
150
100
50
0
15
20
25
30
Mean Temperature (°C)
150
100
50
0
15
20
25
30
Mean Temperature (°C)
150
100
50
0
15
20
25
30
Mean Temperature (°C)